RESEARCH ARTICLE

Love thy neighbour?—Spatial variation in density dependence of nest survival in relation to predator community

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Abstract

Aim: In many species, density-dependent effects on reproduction are an important driver of population dynamics. However, it is rarely considered that the direction of density dependence is expected to vary over space and time depending on antipredator behaviour and predator community. Aggregation may allow for effective group mobbing against avian nest predators while aggregation may also attract mammalian predators, causing negative density dependence. We aim to quantify spatial variation in the effect of conspecific breeding density on nest survival in a mobbing bird species (Eurasian oystercatcher; *Haematopus ostralegus*) and identify whether this variation in density dependence can be explained by the predator community.

Location: Country-wide (The Netherlands).

Methods: We integrated reproductive data with breeding territory maps of Eurasian oystercatchers and occupancy maps of avian and mammalian predator species across the Netherlands for a 10-year period.

Results: Spatial variation in the composition of the predator community explained the effects of neighbour density, showing decreasing nest survival when both conspecific density and mammalian dominance increased. Also, heterospecific density (from breeding godwits and lapwing) has an additional effect on the oystercatcher nest survival. Strikingly, this pattern did not extend to mammal-free island populations.

Main conclusions: Our study provides evidence that both the strength and sign of density dependence can vary spatially within species, implying that it is dangerous to generalize results from a single local population to large-scale management implications and modelling exercises. The study also suggests that conservation actions that aim to attract breeding birds should be prioritized in areas with fewer mammalian predators, but this idea requires further testing on island populations.

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1 | INTRODUCTION

Density dependence is a key factor for understanding and managing the dynamics of species (Ringelman et al., 2012). Density dependence can take positive or negative directions. At high population densities close to the carrying capacity, population density and growth are generally negatively related due to increased competition for resources (Dunn et al., 2015), predator attraction (Gunnarsson & Elmberg, 2008) or parasite transmission (Deredec & Courchamp, 2006), which prevents populations from growing further (Mayer et al., 2019). On the other hand, at low population size, density dependence can be positive due to problems in, for example, finding mates or deterring predators (Kramer et al., 2011). If declining populations reach low densities, positive density dependence could lead to an acceleration of decline, ultimately causing an extinction vortex (Luque et al., 2016), which is also known as an Allee effect (Allee, 1927). This may occur even if the original factor that caused the initial population decline is no longer present.

Most empirical studies of density dependence focus on a single local population from which the results may be generalized over a larger spatial scale (Ackerman et al., 2004; Nummi & Saari, 2003; Prop & Quinn, 2003; Stephens & Sutherland, 1999). However, the mechanisms that shape density dependence strongly depend on the ecological circumstances (e.g. presence and behaviour of particular predators; Hogstad, 1995) and are thus expected to vary spatiotemporally (Knipl & Rost, 2016; Tobin et al., 2007; Walter et al., 2017), which may make broad generalization unreliable.

Predator-driven density dependence (Cresswell & Quinn, 2011; Olson et al., 2015) has been increasingly identified as important to the dynamics of wild animal populations (Kramer et al., 2009). This holds particularly for bird species, where predation is one of the main causes of reproductive failure (Møller et al., 2018; Palmer et al., 2019). Whether aggregation during the reproductive season (i.e. breeding at high density) incurs a benefit or a cost in birds, and thus results in a positive or negative density effect on nest survival, may depend on how predators and prey interact (Forsman et al., 1998; Ringelman, 2014) and on the presence and behaviour (e.g. cognitive and perceptual ability) of nest predators (Auger-Methe et al., 2016; Blanco & Bertellotti, 2002; Rangen et al., 2001).

Anti-predator behaviour by the parents, like predator mobbing (Krams et al., 2009), can reduce nest predation rates if birds nest close to each other and help in protecting neighbouring nests (Larsen & Grundetjern, 1997; Quinn & Ueta, 2008). However, if the anti-predator behaviour of the prey species is ineffective, for example if densities become too low for group defence to be effective (Sönnichsen et al., 2013), spacing out to avoid predators may be a more efficient predator avoidance strategy (Picman, 1988). If predators can learn to exploit areas with higher nest densities (Larivière & Messier, 1998; Ringelman, 2014; Yahner & Mahan, 1996) or by exhibiting "area-restricted searching" behaviour once they find a nest (Bernard, 2004), this will increase the predation risk of nests at high densities. Area-restricted searching is well known for a variety of mammalian predators, which mainly use olfactory cues and are nocturnal (Hogstad, 1995; Nummela et al., 2013; Rangen et al., 2000). Avian nest survival may thus be negatively density-dependent in the presence of predator species that exploit areas with high nest densities and where deterrence is ineffective, while positively density-dependent if other predators occur that can be cooperatively deterred by prey.

Inter-population variation in density dependence is likely to be highly relevant, but only a limited number of these studies relate it to predation (Banda & Blanco, 2009; Lebeuf & Giroux, 2014; Oro et al., 2006). Existing studies have focussed on the role of a single predator species concerning predator-driven density dependency. Notably, studies focussing on a wider range of species that make up the predator community are lacking, even though its importance has been emphasized in the literature (Rangen et al., 2001).

The Eurasian oystercatcher (*Haematopus ostralegus*) is a particularly relevant species to investigate spatial variation in density-dependent nest survival. There is concern that the ongoing population decline over much of the Netherlands (Roodbergen & Teunissen, 2019) of this near-threatened bird species (BirdLife International, 2021) could accelerate due to positive density-dependent nest survival. The reason for this is that experimental and observational evidence from one population dominated by avian predators showed that nests with no neighbours within 50 m rarely survived, while nest predation was virtually absent in the presence of nearby neighbours in this mobbing species (Bailey et al., 2017). The key challenge is now to understand if such exceptionally strong positive dependence also occurs across populations experiencing a diversity of predator communities over a large spatial scale.

To better understand the importance of density-dependent effects on a landscape scale, we investigated (i) the spatial variation in density-dependent nest survival of oystercatchers in the Netherlands and (ii) whether this variation was correlated with the composition of local predator community. We hypothesize that there is substantial spatial variation in the sign and strength of the density effect on nest survival across populations. We predict that there is a positive effect of conspecific neighbour density on nest survival in areas dominated by avian predators due to the mechanism of predator deterrence and effective mobbing behaviour (Figure 1a; as in Bailey et al., 2017). On the other hand, we expect that density has a negative effect on nest survival in areas dominated by mammalian predators, where the mechanism of predator avoidance may play an important role (Figure 1b). Possibly, when both predator groups are present, density dependence may not be apparent as positive and negative effects cancel one
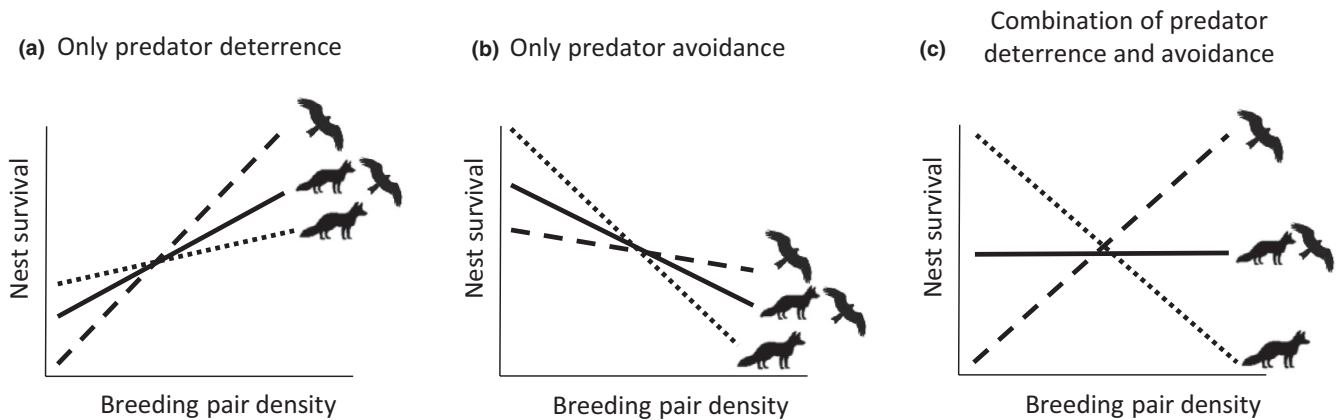
(a) Only predator deterrence   **(b)** Only predator avoidance   **(c)** Combination of predator deterrence and avoidance

FIGURE 1 Illustration of possible relationships between nest survival and breeding pair density with different predator communities (avian-dominated: dashed line, mammalian-dominated: dotted line or mixed: solid line; see also profile drawings) for a situation in which (a) only predator deterrence, (b) only predator avoidance and (c) a combination of both mechanisms shape density dependence of nest survival. Note that for the purpose of our study, the density-dependent relationships depicted are under the general assumptions that deterrence is more effective against avian predators than mammalian predators and that predators, especially mammals, have learned or use search behaviours to exploit areas with high nest densities (i.e. predation is not incidental). Density-dependent relationships are however more complex and deviations from the above will result in different relationships, as covered in Section 4

another out (Figure 1c; for more complex predictions see Discussion). Finally, other species nesting nearby may also provide anti-predator benefits (Semeniuk & Dill, 2006), or may also attract nest predators. We therefore considered the contribution of other bird species that breed in similar habitats as oystercatchers, that are also known for their mobbing behaviour against predators, and that suffer from similar nest predators (Møller et al., 2018).

To our knowledge, this is the first study investigating density-dependent nest survival across multiple populations, also incorporating a wide range of predator species (predator composition) rather than focussing on one specific predator species. Therefore, our study aims to provide a better understanding of the factors that drive spatiotemporal variation in density dependence, which can be important for species conservation and management.

2 | METHODS

2.1 | Study system

The Eurasian oystercatcher is a long-lived bird that, historically, bred on saltmarshes and dunes along the coastline of Europe, where it feeds on intertidal mudflats. Since the 1950s, it colonized inland breeding areas up to a few hundred kilometres from the coast, and it now predominantly breeds on agricultural land in many parts of Europe (Goss-Custard, 1996). Oystercatcher breeding pairs are highly territorial and show extreme site fidelity to their breeding area (Goss-Custard, 1996). Oystercatchers are well known for their intensive group mobbing behaviour (Gochfeld, 1984), with typically multiple breeding pairs jointly chasing avian predators throughout the incubation and chick-rearing phase.

During the breeding season (April until July), oystercatchers lay eggs in a shallow nest scrape on the ground (clutch size 1–4, typically

3), which they incubate for 27 days. Vegetation around nests and cryptic egg colours and markings provide the major source of nest concealment, as they use little nesting material. Following nest loss, one or more replacement clutches may be laid.

We focussed our study on 10 years (2009–2018) during which nationwide data were available on (i) oystercatcher nest survival, (ii) breeding density of oystercatchers and three co-occurring heterospecifics and (iii) predator community (10 years for mammalian predators and 3 years for avian predators). At breeding sites on salt-marshes on the Dutch Wadden Sea islands, mainly avian predators like gull species (*Laridae*) and western marsh harriers (*Circus aeruginosus*) are present (Verboven et al., 2001; Figure S1). In Inland breeding areas, in addition to avian predators like gulls and crows (*Corvidae*), oystercatchers also have to deal with mammalian predators like the red fox (*Vulpes vulpes*), stoat (*Mustela ermine*), beech marten (*Martes foina*) and European polecat (*Mustela putorius*) (Teunissen et al., 2008; Figure S1), which do not occur on island sites, except for stoat being present on the island of Texel (Figure S1).

2.2 | Reproductive, conspecific and heterospecific breeding density data

Data on oystercatcher nest survival were available across the Netherlands, including GPS coordinates of exact nest locations. Nests were revisited several times and the fate of the nest was noted. The nest survival is defined as the probability that a nest will survive until the next day (daily nest survival), which thus accounts for differences in exposure time. This accounts for the fact that nests are found part-way through the nesting stage and are therefore biased towards successful nests (Mayfield method; Aebischer, 1999).

We used breeding density of oystercatchers (conspecific) and of three sympatric species (heterospecific) as a proxy for mobbing

density. Data from the Dutch Breeding Bird Monitoring program (BMP) were used to obtain a measure of meadow bird (Eurasian oystercatcher, common redshank (*Tringa totanus*), northern lapwing (*Vanellus vanellus*) and black-tailed godwit (*Limosa limosa*)) breeding density around all oystercatcher nest locations. BMP is based on intensive territory mapping in fixed study plots carried out by well-trained volunteers that follow a standardized protocol (Van Turnhout, 2010). In short: territory mapping is based on a large, and annually constant, number of field visits (5–10 between March and July depending on species) in which all birds with territorial behaviour (e.g. song, pair bond, display, alarm, nests) are recorded on maps. Species-specific interpretation criteria are used to determine the number and exact locations of "territories" per species at the end of the season (since 2011 using an automated procedure; Van Dijk et al., 2013). The number of "territories" is considered a reliable proxy of true abundance and we expect approximate linear relationships between the surveyed samples and the total density of each species (Van Turnhout et al., 2010).

The scale at which density is measured can impact the outcome of analyses (Bailey et al., 2017). On the islands of Ameland (Island 1) and Schiermonnikoog (Island 2), the nesting density within a radius of 50 m and 100 m around a focal nest explained the most variation in predation rates (Bailey et al., 2017; Martig, 2017). We assume that the effective mobbing distance is similar in other populations, but since breeding densities are lower in inland areas, we used a 100-m radius to determine breeding density, as this resulted in most variation of breeding density in our data. Therefore, we overlaid a circle with a radius of 100 m (3.14 ha) around each nest location on the BMP territory maps and calculated the number of breeding territories within this area (including the focal breeding pair). We only included focal nests in the analysis for which at least 85% of the 100-m radius circle was included within a BMP census area (Figure S2). The breeding densities for the local populations (ranging from 0.64–1.6 pairs/ha) and the country-wide dataset (ranging from 0.32–1.28 pairs per ha) showed similar range (Table S1).

Overlaying the nest survival data with the territory maps resulted in 661 observations consisting of two types of datasets: (a) a "country-wide dataset," based on country-wide nest data collected by trained volunteers (yellow dots in Figure 2) and (b) "local population datasets," based on highly detailed nest data from local populations collected by professional researchers (blue, green and purple dots in Figure 2). Spatially separate studies on the same island (on "Island 1" and "Island 3"; Figure 2) were treated as separate populations, since habitat and nest survival of the local populations differ within the islands. Note that the method of density estimation did not differ between the two dataset types (both based on the BMP) and nest survival was sampled in the same way in both datasets.

2.3 | Predator community

We constructed indices of predator community by constructing nationwide species distribution models for each potential predator

species (based on presence–absence data). We recorded predation events with cameras placed at oystercatcher nests to (a) identify which predator species should be taken into account and (b) to quantify its relative importance as a nest predator. Subsequently, we calculated a predator community index for each nest location.

We used species distribution modelling to estimate the probability of presence for each potential predator species. Mammal presence–absence data for a 10-year period (2009–2018) from the Dutch National Database on Flora and Fauna (www.ndff.nl) were used. Nationwide avian presence–absence data and distribution maps were available from the Sovon Bird Atlas project (Sovon Vogelonderzoek Nederland, 2018) for a 3-year period only (2013–2015), but localized annual survey counts reveal little inter-annual variation for the whole study period (2009–2018; Figure S3). Note that the multiple years of data were pooled to one single static distribution model per species. Observed predator presence data were combined with open-access landscape data to estimate the probability of presence (ranging from 0 to 1) for each predator species for each 1x1km grid cell nationwide (Figure S1) with the R package SDMaps (Kampichler et al., 2020). For more details on the methodology, see Text S1. These predator maps can be used to give an indication of the probability of presence for each predator species.

To choose which predators' species distribution models should be taken into account for the predator community index and to quantify their relative importance as a nest predator, we identified predation events based on camera trap monitoring (Figure S4). Camera traps were placed near 177 nests (1.5–2 m from the nest at 50–70 cm height) in different habitats (on random allocation within each study area) throughout the Netherlands (36 cameras were placed on island saltmarshes, 94 cameras on island farmland and 47 cameras on mainland farmland) (Figure S4), during which 95 predation events were detected. Mammalian predators made up 20.2% of predators detected on camera traps. These included red fox (9.5%), European hedgehog (*Erinaceus europaeus*) (3.2%), brown rat (*Rattus norvegicus*) (3.2%), beech marten (2.1%), stoat (1.1%) and other unidentifiable mammal species (1.1%). Area-restricted searching is well known for red foxes (Larivière & Messier, 1998), beech martens (Kitikidou et al., 2014; Rödel & Stubbe, 2006), stoats (King & Powell, 2006), European polecats (Lode, 2000) and striped skunks (*Mephitis mephi*) (Nams, 1997). Avian predators made up 68.6% of all detected predators and included carrion crow (*Corvus corone*) (23.2%), western marsh harrier (21.1%), common gull (*Larus canus*) (6.3%), unknown gull species (5.3%), herring gull (*Larus argentatus*) (4.2%), unknown predatory bird species (4.2%), oystercatcher (2.1%), lesser black-backed gull (*Larus fuscus*) (1.1%) and common buzzard (*Buteo buteo*) (1.1%). The remaining 11.2% were unidentifiable predators (Figure S4). Note that camera traps were placed at a subset of locations (mostly islands) to identify the predator species, rather than randomly placed throughout all populations to estimate the predator density.

Monitoring schemes of mammalian and avian predators differed (Text S1, Table S2) and because we aimed to make the probability of presence comparable between both predator types (avian and
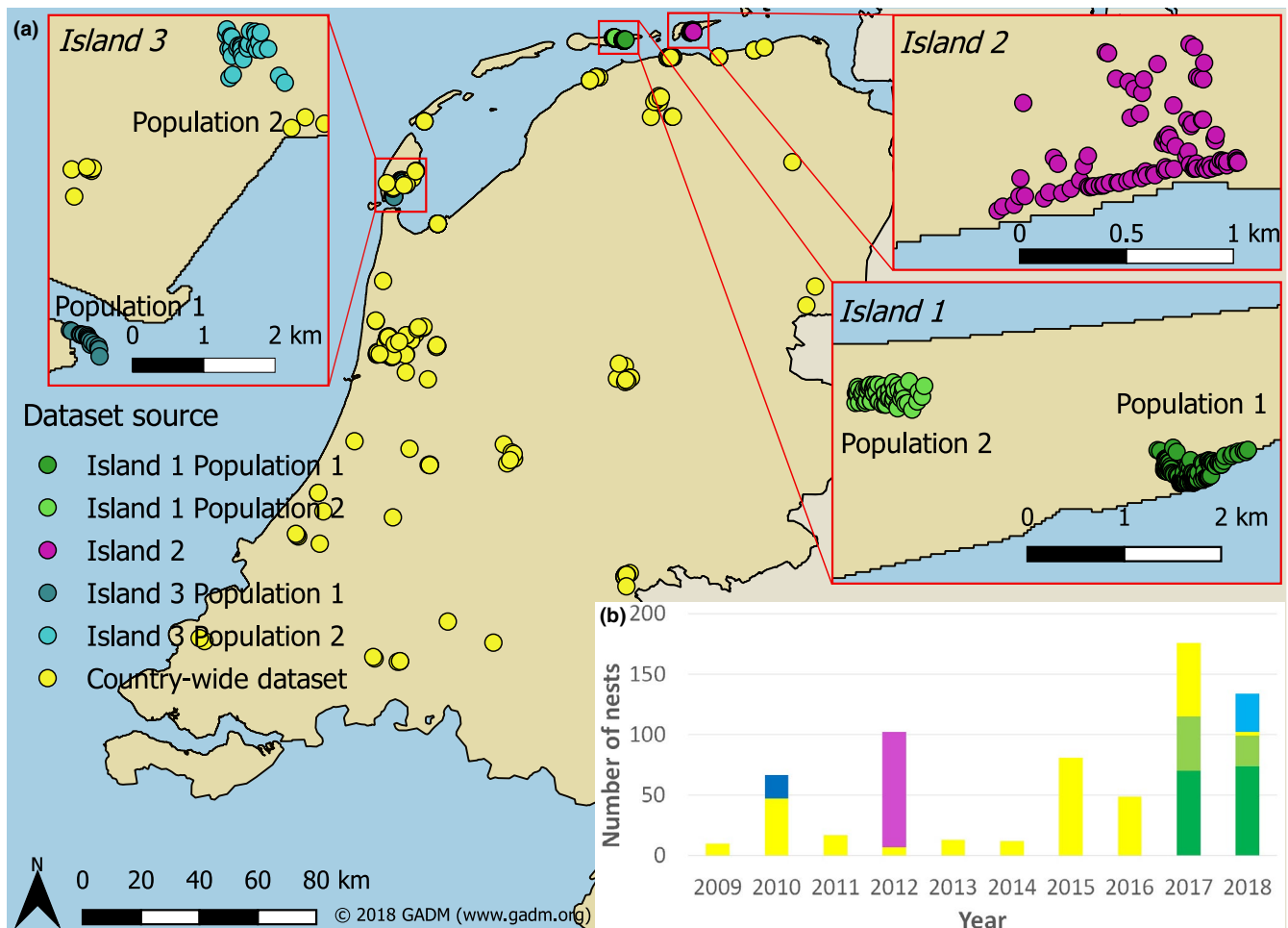
FIGURE 2 (a) Map of the Netherlands with the distribution of nest locations and their data source. Country-wide dataset (yellow dots) including spatially well-distributed nest locations collected by trained volunteers; two local populations are located on the island 1 (green dots) and 3 (blue dots); one local population is situated on the island 2 (purple dots). (b) showing the number of nests included in the analysis per year and dataset source

mammal), we normalized the data (per predator type) using the formula $(x - x_{min})/(x_{max} - x_{min})$. Gull species are colony birds and have large foraging areas compared to the other predator species, and we accounted for their larger space use by taking the mean probability of presence of a 3 km-radius buffer around the nest location (Rock et al., 2016), whereas we used a 1-km radius for all other predator species. We excluded two predator species that together accounted for 6.4% of all camera-recorded nest predation events: brown rat was excluded as there were too little field data to produce reliable species distribution maps for this species, while hedgehog was excluded because this mammal is not expected to exhibit area-restricted searching behaviour at the spatial scale at which oystercatchers breed (Schmidt & Whelan, 1999).

We calculated a "mammalian dominance index" by dividing the sum of the probability of presence of all mammalian predators by the sum of the probability of presence of all mammalian plus avian predator species. This resulted in a value of 1 for only mammalian predators present and of 0 for only avian predators present. Finally, some predators may be more important than other predators (in terms of oystercatcher nest predation) and thus their presence could be

weighted based on predation threats. Weighting was based on frequency of predation events from the camera trap monitoring (Figure S4; Table S3). This resulted in two potential "mammalian dominance index" proxies, a "weighted" and an "unweighted" one (Table S4).

2.4 | Data analysis

2.4.1 | Local population analysis

To test for statistical differences in density-dependent nest survival between the local populations (island study sites), we used a generalized linear mixed model (GLMM) with binomial distribution and logit-link function for nest survival (N). We included the main effects and interaction between the linear covariate density (D) and the factor local population (P) as explanatory variables. To account for confounding effects of predictors other than density that could influence nest survival, we included distance to the coast (C) (reflecting distance to benthic or terrestrial food source) as a continuous fixed effect. We also included random intercepts u and v to account

for the variation in nest survival among years (i) and habitat types (j). Habitat type was based on data from CBS Statistics Netherlands, which was combined into one variable consisting of seven classes, with the most common classes being grassland, arable land and nature areas (Table S5). The regression model is shown in equation 1 with ε indicating the residuals, β_0 the intercept and β_{1-4} the regression coefficients of the model.

$$\text{Logit}(N_{ij}) \sim \beta_0 + \beta_1 D_{ij} + \beta_2 P_j + \beta_3 D_{ij} P_j + \beta_4 C_j + u_i + v_j + \varepsilon_{ij} \quad (1)$$

2.4.2 | Predator community analysis

To identify if either the "weighted" or "unweighted" mammalian dominance index better explains the variation in density-dependent nest survival of oystercatchers, we used an information theoretic model selection approach using Akaike information criterion (AIC) (Burnham & Anderson, 1998). The index with the lowest AIC (the "unweighted" mammalian index; Table S4) was selected and is from here on referred as "mammalian dominance index" (Figure 3). To determine whether spatial variation in density-dependent nest survival can be explained by the predator community, we adjusted equation 1 by replacing the local population (P) term by the linear covariate mammalian dominance index (M) (Equation 2).

$$\text{Logit}(N_{ij}) \sim \beta_0 + \beta_1 D_{ij} + \beta_2 M_j + \beta_3 D_{ij} M_j + \beta_4 C_j + u_i + v_j + \varepsilon_{ij} \quad (2)$$

We first fitted the model (Equation 2) on the country-wide citizen science dataset that was collected across the Netherlands and over many years. Since the dataset does not include many nests from islands with low mammalian dominance, we subsequently investigated whether the five island populations (on Islands 1–3; Figure 2) fit the model results of the country-wide dataset. Bailey et al. (2017) conducted a similar research for the local population of Island 2, but in a different year than shown in Figure 2. Therefore, we transformed the density metric used in Bailey et al. (2017) (Text S2, Table S6) and added it in the visualization of the main results (Figure 4). We analysed the country-wide and island datasets separately using this two-step approach as they have large differences in the spatiotemporal sampling and barely overlapping predator communities (see Section 4). We assume nests to be spatially independent from each other in the statistical analysis because we did not find support for spatial autocorrelation in the data (Figure S5).

To quantify if other meadow bird species play a role in the density-dependent nest survival (both contributing to group mobbing and predator avoidance), we used the same model that was selected as the best-fitting model for the "country-wide dataset analysis" and replaced the oystercatcher density by densities of different meadow bird compositions (oystercatcher + lapwing, oystercatcher + godwit, oystercatcher + redshank, oystercatcher + godwit + lapwing, or all four species combined). Statistical analyses were done in R (version 4.1.2) with package lme4.
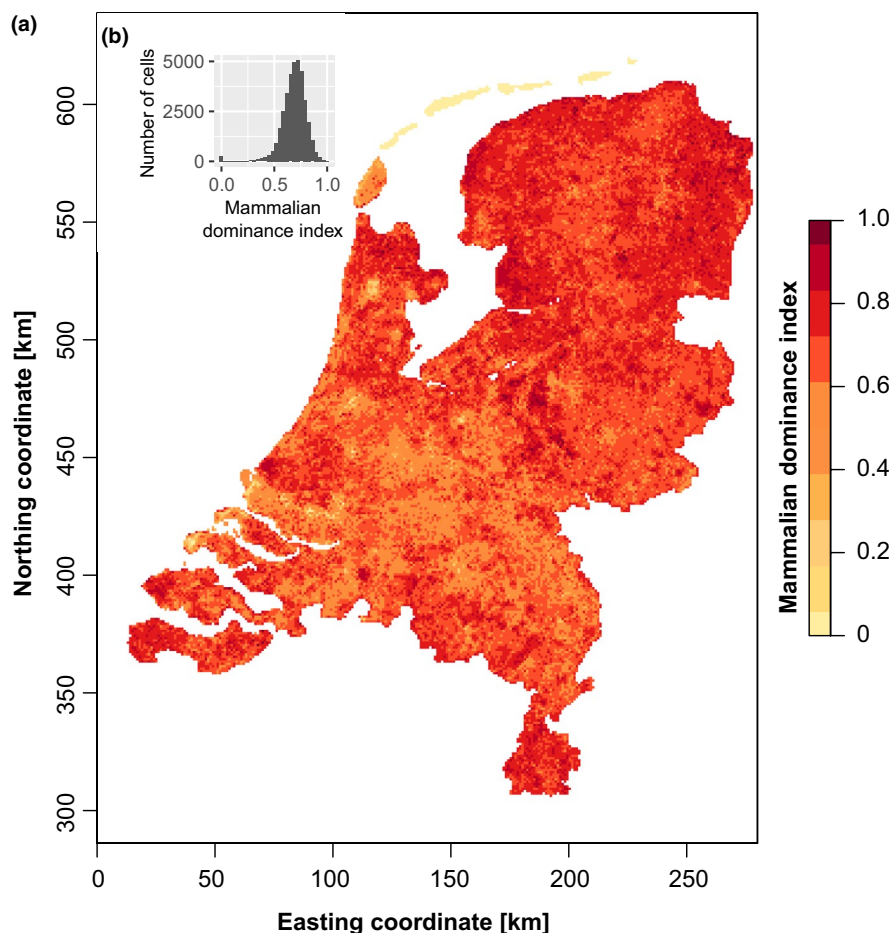

FIGURE 3 (a) Overview of the spatial distribution of the mammalian dominance index used in the analysis and (b) the distribution of the number of cells across the mammalian dominance index. 0 indicates that no avian predators are present, whereas at 1 only mammalian predators are present. Note that the small peak at 0 mammalian dominance index (in b) (meaning only avian predators are present) comes from the five mammalian predator-free Wadden Sea islands. Coordinates are in the Dutch RD coordinate system, where one unit is 1 km
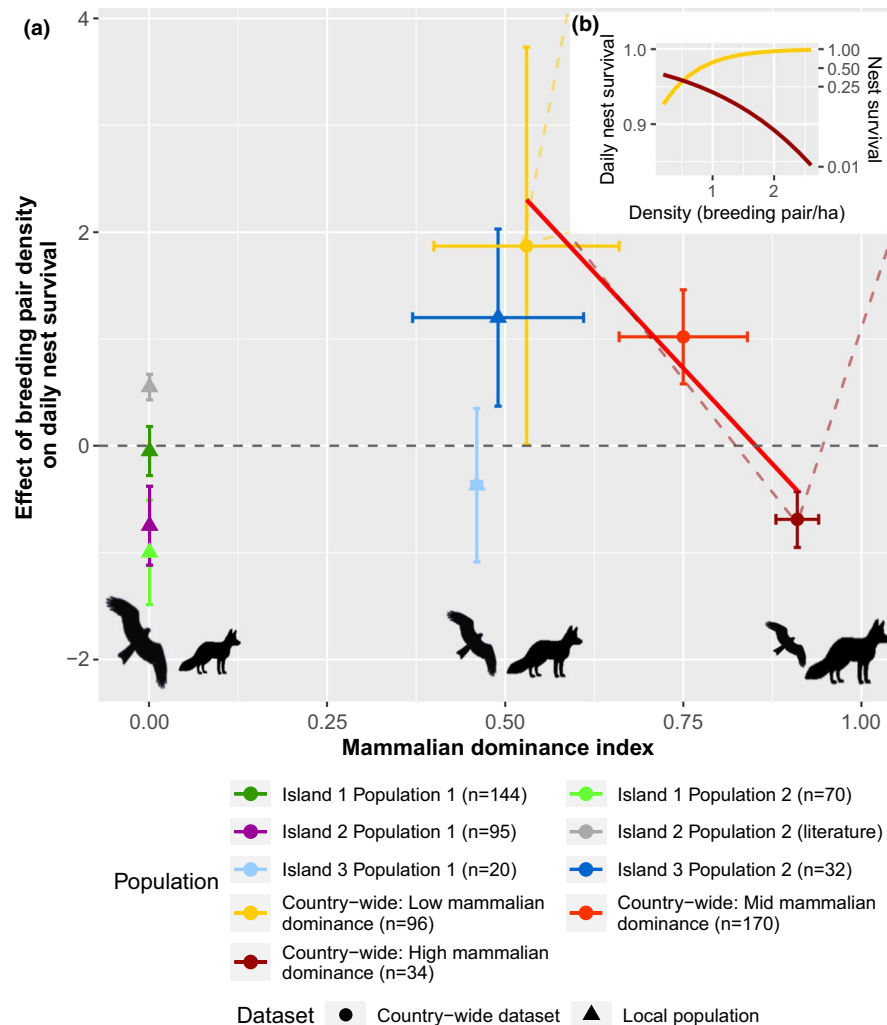
FIGURE 4 (a) Model estimates of the effect of conspecific breeding density on oystercatcher nest survival (±SE as error bar) as a function of mammalian dominance index. Note that the mammalian dominance index (a) is the ratio of the probability of presence of mammalian and avian predators (Figure S8). Dashed horizontal line represents the point at which no density-dependent nest survival occurs. The solid line indicates the model fit of the interaction between the mammalian dominance index and breeding density based on the country-wide dataset only. Horizontal error bars indicate the range (standard error) of the mammalian dominance index in each population. The grey triangle (close to/above the dark green triangle) is extracted from Bailey et al. (2017) and transformed to the density metric used in this study (Text S2, Table S6). Island 2 population 2 represents exactly the same area as population 1 (on island 2), but in a different year. (b) illustrates that the parameter estimates plotted in panel (a) are the slope from the relationships between daily nest survival and breeding density from the binomial model, showing here the example the different relationships at low (yellow) and high (red) mammalian dominance. To show the effect on the nest survival for the whole breeding period (27 days of incubation), we show the nest survival on the logarithmic secondary y-axis. For the visualization, the slopes of each population (point in a) and its 95% confidence interval see Figure S6. Note that statistical analysis for the country-wide dataset (yellow, orange and red dot) was done using the continuous mammalian dominance index; the index was split into three categories only for visualization purpose here

3 | RESULTS

In the country-wide dataset, oystercatcher breeding density showed different effects on nest survival depending on mammalian dominance (Figure 4; $\beta = -7.17$, SD = 3.07, $p = .02$, $n = 300$; Table S7). This indicates that, in accordance with our hypothesis (Figure 1b), there is a negative effect of density on the nest survival at relatively high mammalian dominance, while the density effect is positive at relatively low mammalian dominance (Figure 4).

Density-dependent nest survival also varied considerably among the more avian predator-dominated local island populations, with both

the strength and the direction of the relationship varying (Figure 4; Figure S6). Two island populations corresponded well with the predictions of the significant interaction between the mammalian dominance index and the breeding density in the country-wide dataset (Island 3 population 2; Island 2 population 2; Figure 4). They match our initial prediction that density-dependent effects will be positive when there is lower mammalian dominance. Note that the habitat of Island 3 population 2 is comparable to the habitat of the country-wide dataset (being mainly agricultural areas). Three of the mammalian predator-free island populations (Island 1 and 2) did not match the expectation and did not fit the model prediction of the country-wide dataset (Figure 4).

Specifically, based on the avian-dominated predator community on these three island populations, we would have predicted strong positive density dependence, based on the deterrence hypothesis (Figure 1a), but we actually found negative density dependence for the Island 1 population 1&2 and Island 2 population 1 (Figure S6; Table S7).

Including the heterospecific density of other meadow birds (black-tailed godwit, Northern lapwing, and common redshank) on the oystercatcher nest survival supports the results that are found when focusing only on breeding oystercatchers ($\beta = -1.6$, SD $= 0.51$, $p = .002$, $n = 300$; Table S8). Breeding density of heterospecifics shows an interaction effect with mammalian probability of presence, where nest survival of oystercatchers is lower if density of breeding meadow birds and mammalian probability of presence are both high (Figure S7). Especially by adding the density of godwits alone, or together with breeding lapwings, next to the oystercatcher density, improved the model fit significantly with a ΔAIC of 9 (Table S8). Also, breeding lapwings (as single heterospecific species) in the surrounding of an oystercatcher nest increased the model fit by ΔAIC of 6. Breeding common redshanks, next to breeding oystercatcher density, showed least improvement of the model with ΔAIC of 3 (Table S8).

4 | DISCUSSION

We investigated how density-dependent nest survival of a mobbing bird species varies spatially and tested whether the predator community can explain the observed country-wide spatial variation in sign and strength of density dependence. Our results show—in line with our prediction—that there is no consistent positive effect of density on nest survival across populations. The relative dominance of mammalian predators explains the spatial variation in both the direction and strength of density-dependent nest survival in the country-wide dataset. Nest survival in mammalian-dominated predator communities was negatively density-dependent, in line with the predator avoidance hypothesis (Figure 1b), while more avian-rich predator communities exhibited positive density dependence in line with the predator deterrence hypothesis (Figure 1a). However, data from local island populations without mammalian predators (relevant for this study species and aim), being mainly in saltmarsh habitat, did not fit this relationship, suggesting that the predator avoidance and deterrence hypothesis cannot explain patterns of density dependence in (most) island populations.

The general implications of our study are best illustrated by what it can teach us about population decline in our study species. The Dutch oystercatcher population (which comprises 30% of the species' European breeding population) has undergone a strong continuous decline over the past three decades (Roodbergen & Teunissen, 2019), and declining reproductive output has been implicated as a contributing demographic cause (Allen et al., 2021). The concern of a nationwide Allee effect in the Dutch oystercatcher population was not supported by our study, since we could not find any consistent positive density-dependent nest survival in our country-wide

analysis. This suggests that Allee effects do not seem to be omnipresent. Thus, the ongoing nationwide decline must be caused by other reasons than Allee effects and either the original drivers of decline may still be active, or new ones have appeared (Allen et al., 2021). Other potential causes may be agriculture intensification (nest destruction due to increased frequencies of agricultural activities e.g. mowing, low food availability because of use of artificial fertilizers and pesticides; Hulscher & Verhulst, 2003; Duriez et al., 2005), human disturbance and climate change (Van de Pol et al., 2014).

Our study showed that the predator community modulates the effect of density-dependent nest survival in the country-wide dataset, to such an extent that it varies between negative and positive density dependence. Thus, our study suggests that, in addition to group mobbing behaviour shaping the density dependence in this species (Bailey et al., 2017), the mechanism of predator avoidance and presence of mammalian predators likely also plays an important role (Figure 1c). Visualizing the probability of presence for mammalian as well as avian predators separately (Figure S8) shows that the predator avoidance mechanism seems to play a larger role than the predator deterrence mechanism in explaining the pattern found when investigating the effect of the mammalian dominance index (Figure 4). The predator deterrence mechanism (Figure 1a) can explain our results at below-average mammalian dominance. This adds to the study from Oro et al. (2006) who investigated the predator–prey system of two gull species (predator species *Larus michahellis* and prey species *Larus audouinii*) and showed that small groups of the prey species were unable to defend their nests against a large number of the predators. In their study, fecundity was reduced at low prey density compared to high prey density. From our results, we interpret that a predator avoidance mechanism acts in sites with high mammalian dominance (Figure 1b), which adds to similar results by Banda and Blanco (2009). These authors found negative density-dependent nest survival due to mammalian predator attraction (foxes and rats) in red-billed choughs (*Pyrrhocorax pyrrhocorax*), resulting in lower breeding survival at high nest density. As far as we know, our study is the first investigating the effect of a broad range of predator species (predator composition) by combining the two possible mechanisms of predator deterrence and avoidance in one study. Though such a comprehensive approach is more challenging, it may be the only relevant approach for the many species that face a broad predator community and complex predator–prey interactions.

In fact, our results tentatively suggest that it is inefficient for breeding oystercatchers to occur at high densities in agricultural breeding areas where mammalian dominance is relatively high. We also found an additional benefit from heterospecifics in terms of anti-predator behaviour. Heterospecific anti-predator benefits have been found in various species groups like reptiles (Vitousek et al., 2007), fish (Semeniuk & Dill, 2006), mammals (Lea et al., 2008) and birds (Magrath et al., 2015). Heterospecific benefits have even been suggested for other meadow birds (Møller et al., 2018), such that for each species (northern lapwing, common redshank, black-tailed godwit, dunlin and ruff), survival was higher when the density of

heterospecifics was higher. When investigating the meadow bird density rather than only oystercatcher breeding density, we found the same relationships, namely a positive effect of breeding density on the nest survival at avian-dominated areas and a negative effect of breeding density on nest survival at areas dominated by mammals. This indicates that in areas where it is advantageous to breed at high density (e.g. higher avian probability of presence, where mobbing is effective), it is beneficial to also have other meadow birds breeding in the surrounding. However, in areas of high mammalian predator presence, it is also disadvantageous for the oystercatcher nest survival, if other meadow birds breed close by. Our results may therefore indicate that conservation actions that aim to attract breeding meadow birds should be prioritized in regions with a relatively low ratio of mammalian compared to avian predators.

However, we note that a "low mammalian dominance" (and thus relatively high avian dominance) in our country-wide dataset has a median of 0.53, which indicates a relatively mixed probability of presence of avian and mammalian predators. Therefore, to confidently translate our results into conservation implications for island breeding oystercatchers (on saltmarshes), we would ideally analyse density and nest survival data from more years and sites, particularly in areas with low mammalian dominance. In addition, more support from other studies that focus on the effect of predator composition on density-dependent nest survival is needed to confirm whether such a conservation prioritization strategy is suitable.

Strikingly, our results were inconsistent across the Netherlands. Lebeuf and Giroux (2014) also found mixed results in terms of density-dependent nest survival in Canada geese (*Branta canadensis maxima*) that they hypothesized was caused by having different mammalian predator species present at different study sites. We expected all the island populations with extremely low mammalian dominance to exhibit positive density-dependent nest survival based on the experimental evidence by Bailey et al. (2017). A possible reason why these local island populations do not fit the relationship of the nationwide dataset may be extreme predation levels in the limited years of study. Ringelman et al. (2012) hypothesized that at extreme predation levels (high or low), it can be difficult to detect density dependence.

The negative density-dependent nest survival found in some island populations (with mainly avian predators) could also be explained by a stronger effect of avian predator attraction compared to the effective mobbing strategy of the prey species. Arguably the schematic predictions in Figure 1 are a simplification of the hypotheses and do not show all possible nuances of the mechanisms involved. For instance, it may be possible that some avian predators are also effective in finding high nest densities and when they would not be deterred, the strength of the negative relationship may be comparable to that of mammalian predators. Nevertheless, we assume, based on literature mentioned in the introduction, that avian predators (relevant for this study) are less efficient in finding high nest densities and at the same time are easier deterred by oystercatchers than mammalian predators (relevant for this study), as stated in the hypotheses.

Several key methodological decisions (e.g. including the choice of heterospecifics, predators and effective mobbing distance)

were partly based on previous field studies done on a small spatial scale with relatively high breeding densities. We suggest that conducting experimental studies may help to make more informed methodological choices. A field experimental study that investigates the additional mobbing effect of heterospecifics on nest survival would help in deciding whether to include or exclude other meadow bird species in the analysis (Møller et al., 2018). Furthermore, we know that oystercatchers protect neighbours nesting up to 50-100m in an island population with high densities (Bailey et al., 2017). Experimental studies would be helpful in understanding how the protective effect of mobbing varies at different breeding densities (mobbing behaviour could be density-dependent), not only with artificial but also with natural nests (Major & Kendal, 1996).

Changes in the Dutch landscape have led to increasing numbers of predators over the last 40 years (Roodbergen & Teunissen, 2019), and it is known that predation levels can fluctuate among years (Teunissen et al., 2008), probably due to varying predator abundance, alternative prey species (Nolet et al., 2013) or mesopredator release (Ritchie & Johnson, 2009). For our relatively short study period (of 10 years), we do not have any evidence of extreme changes in population numbers of the avian predator species (Figure S3). For studies conducted on a larger temporal scale or with more fluctuations in the number of predators, it would be wise to consider predator maps that vary on temporal scale.

To conclude, the results show that there is no consistent positive effect of density on nest survival across populations. This emphasizes the risk of generalizing results from a single local population for management decisions and population modelling. Therefore, we encourage researchers across different study systems to set up studies at large spatial scale, if possible. In addition, we would like to emphasize with this study that taking into account possible density-dependent effects in relation to the whole predator community, rather than to one specific predator species, can be important in identifying causes of population regulation and decline and making appropriate conservation decisions.

CONFLICTS OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data files and R code to reproduce the results are publicly available on zenodo and can be accessed via https://doi.org/10.5281/zenodo.5718466 (Frauendorf et al., 2021).

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BIOSKETCH

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