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Occurrence of rats and their impacts on colonial waterbirds in a Danish fjord

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Human development around the globe has led to great expansion of the Brown Rat (*Rattus norvegicus*), which has implications for local wildlife and especially ground-breeding birds. In this study, we analyse the colonisation and persistence of rats on small islets important to breeding waterbirds in a Danish fjord, and investigate the effect of rat presence on the number of breeding pairs of eight waterbird species. The islets had an annual rat colonisation probability of 6% and an annual rat population persistence rate of 65% (equalling an annual population survival rate of 62% when adjusting for re-colonisations upon extinctions). Contrary to our hypotheses, rat colonisation and persistence was uncorrelated with islet size, distance from the mainland and the presence of shrub cover. Rat presence had a significant negative effect on the number of breeding pairs of four waterbird species, including Avocet (*Recurvirostra avosetta*, reduced to 30% compared to years without rats), Black-headed Gull (*Chroicocephalus ridibundus*, reduced to 45%) and Common Tern (*Sterna hirundo*, reduced to 52%). The smaller bird species in particular seemed to be affected by the presence of rats, and control efforts aimed at reducing rat presence on important breeding bird islets may consequently have a positive effect on the occurrence and breeding success of these species. We found no evidence of birds acting on a memory of where rats had been present in the previous year, and further research is needed to investigate the precise mechanisms behind the recorded negative effects in the contemporary year, *i.e.* how do prospecting as well as settled breeders detect and behaviourally respond to the presence of rats.

1. Introduction

Anthropogenic expansion to every part of the world has led to severe secondary effects in the form of introductions of commensal species such as Cats (*Felis catus*), Pigs (*Sus domesticus*) and rats (*Rattus* sp.) (Mack *et al.* 2000, Doherty *et al.* 2016). The invasive behaviour of these species threatens avian biodiversity worldwide, and rats have had a major impact on bird populations around the globe (BirdLife International 2008, Jones *et al.* 2008). The Brown Rat (*Rattus* *norvegicus*) originates from eastern Asia, and began to spread worldwide, including Western Europe, during the 18th and 19th centuries (Puckett *et al.* 2016). Since then, rats have demonstrated an exceptional ability to benefit from an increasing human population (Barnett 2002, van Adrichem *et al.* 2013), to the extent that they are now distributed all over Europe as one of the most numerous contemporary species. The increasing human presence in rural areas has led to an expansion of rats in natural habitats, which has again led to increased exposure of native species to rats (Barnett 2002, Banks & Hughes 2012). The growing exposure to rats (*Rattus* spp.) has been shown to have adverse effects on distribution, survival and reproduction for a number of different native taxa around the world, in the form of increased competition, spreading of diseases and direct predation (Jones *et al.* 2008, Chiba 2010, Smith & Banks 2014, Wolf *et al.* 2018).

Among the groups most susceptible to exposure to rats are ground-breeding waterbirds (Atkinson 1985, Jones *et al.* 2008). These birds generally rely on small islands or islets isolated from the mainland as suitable breeding habitats, exploiting the fact that these are largely inaccessible to most native mammalian predators. However, the proximity of their nests to water, in combination with the easy access to eggs and chicks on the ground, render this group especially vulnerable to a mammalian predator with good swimming capabilities such as the Brown Rat (Møller 1983). Due to their generalist feeding strategy and high adaptive capability to new environments (Lee 2002), rats pose an important threat to several coastal waterbird species. Consequently, a number of studies have found rats to be serious predators of adults, eggs and chicks of seabirds and ground nesting colonial waterbirds (*e.g.* Møller 1983, Bertram & Nagorsen 1995, Major *et al.* 2007). The impact is especially severe when affected species are characterised by low annual reproductive output (Martin *et al.* 2000, Owens & Bennett 2000). The many documented examples of negative impacts of rats on coastal-breeding birds have led to management initiatives trying to limit rat abundance in these habitats (Taylor *et al.* 2000, Duron *et al.* 2017).

Ground breeding birds have been under selection to assess and avoid microhabitats exposed to predation from mammalian predators. Birds prospecting for breeding sites on the ground are therefore expected to obtain information about presence/absence of mammalian predators by use of visual, auditory and olfactory cues as well as through presence/absence of conspecifics (Amo *et al.* 2011, Zidar & Løvlie 2012, Stanbury & Briskie 2015). The ability of the birds to detect that rats are present on the islet where they intend to settle to breed is, however, likely to be affected by factors such as the density and/or detectability of rats, which in turn may depend on the diurnal activity patterns of the rats as well as the microhabitat features such as vegetation cover.

During the last couple of decades, coastal-breeding waterbirds have been declining in most of northern Europe, including Denmark (Stroud *et al.* 2006, Laursen & Thorup 2009). The decline seems to result mainly from the effects of loss and degradation of wetland habitats, with knock-on effects on survival and reproduction from increased predation pressure (Stroud *et al.* 2006, MacDonald & Bolton 2008, Rickenbach *et al.* 2011). Larger mammals such as Red Fox (*Vulpes vulpes*) and mustelids (family *Mustelidae*) and avian predators such as corvids (family *Corvidae*) comprise a role as main native predators on eggs and chicks of coastal birds, but increasing exposure to rats may make this invasive predator very important as well – especially given their ability to swim, enabling them to exploit otherwise predator-free islands and islets. Although negative effects of rats on coastal birds have been well documented, most studies have focused on single islands and/or single species, and an actual quantification of the effects has seldom been extracted (Igual *et al.* 2006).

In this study, we analyse the occurrence and abundance patterns of rats and their impacts on numbers of breeding pairs of eight different species of coastal ground-breeding waterbirds across 25 different islets in a Danish fjord (Roskilde Fjord), comprising an important breeding area for these species. We explored the effect of rats on numbers of breeding pairs on individual islets, and investigated whether the extent of negative effects increased with increasing abundance of rats. Furthermore, we examined whether different structural factors of the individual islets (area, distance to mainland and presence of shrub cover) and environmental factors related to weather (average winter temperature and occurrence of ice winters) affected colonization probability of rats. Based on current knowledge, we hypothesized that breeding numbers of smaller species would be negatively affected by the abundance of rats on islets (Avocet *Recurvirostra avosetta*, Common Gull *Larus canus*, Black-headed Gull *Chroicocephalus ridibundus*, Common Tern *Sterna hirundo,* and Arctic Tern *S. paradisaea*), and that larger species would not be affected (Mute Swan *Cygnus olor*, Common Eider *Somateria mollissima*, and Herring Gull *L. argentatus*). We further hypothesized that the number of breeding pairs would be affected by rat abundance in the current year as well as by rat abundance in the previous year. Our reasoning was that:

A) At the time of prospecting and settling, the birds would to some extent be able to detect presence of rats on potential breeding islets, at least if rats occurred in high densities, which would trigger avoidance.

B) The birds would sometimes fail in detecting presence of rats during the time of pre-laying, especially if rats occurred at low density on larger islets covered by vegetation. If this was the case, we anticipated that birds were likely to detect the presence of rats during the incubation or chick rearing period, and that this would lead to avoidance of that specific islet in the following year (a memory effect).

Finally, we modelled the frequency by which rats colonised islets (taken as being recorded one year having not been recorded the previous year) and went extinct (not recorded on an islet having been recorded the year before). We furthermore tested whether these events correlated with islet size, distance to the mainland and winter conditions. The probability of colonisation by rats was hypothesised to correlate negatively with distance to the mainland and positively with the number of days with sea ice cover the preceding winter, as both factors were expected to ease the crossing of open water. Persistence probabilities (*i.e.* opposite of extinction) were hypothesized to relate positively to islet size, presence of shrub cover and rat abundance score the previous year. In the same manner, we expected a negative effect of winter severity on the rats' persistence.

2. Material and methods

2.1. Study area and focal species

Roskilde Fjord (55°48'N, 12°03'E) is situated in the northern part of the island of Zealand in Denmark. The fjord extends 36 km southwards from its mouth to the middle of Zealand, forming an enclosed area with the narrow mouth being the only connection to the open sea of Kattegat (Fig. S1). The fjord depth is generally 0–5 m, but can reach depths up to 30 m. Roskilde Fjord is an important breeding area for substantial numbers of coastal-breeding birds. In particular, Avocet, Common Gull, Black-headed Gull, Common Tern, Arctic Tern, Mute Swan and Herring Gull occupy the area in large numbers (see Tables S3–S10). Several of these species are listed on the EU Birds directive, prompting international obligations to ensure the future of this area as suitable coastal breeding habitat.

In the fjord there are 25 small islets of variable size (range: 0.03–139 ha, median = 0.8, Table S1) and structure, where up to approximately 10,000–20,000 pairs of breeding birds covering 25–30 different species have been breeding every year (Andersen-Harild 2003). The first occurrences of Brown Rats on the islets in Roskilde Fjord were recorded in the late 1980s (E. Hansen & P. Andersen-Harild, pers. obs.), where they were observed to predate on eggs as well as adults of Black-headed Gulls and terns. Since 1989 rat control initiatives (poisoning) were applied whenever rats were detected, but due to the inaccessibility of islets, and to minimize disturbance of breeding birds, there was no systematic data available on the efficacy of control efforts.

2.2. Surveys of breeding birds and rat presence

The breeding populations of waterbirds on islets in Roskilde Fjord were surveyed annually during 1978–2021, and the occurrence of rats was recorded systematically in the years 1988–2009, following the first observation of rats in 1987. In all years included in the present study the surveys of breeding waterbirds were undertaken by the same two experienced observers (E. Hansen &

P. Andersen-Harild), and in the entire period each of the 25 islets were (with few exceptions) visited annually at least once or twice. The most important visit took place between the last week of May and the first week of June during which all the breeding birds present (except for passerines) were recorded. The observers walked over each of the islets, except for a few tiny and low-lying islets, which could be covered by observing from the boat. The two observers attempted to keep disturbance at a minimum. From observation points as well as while walking over the islets the observers estimated the number of breeding pairs of each species either based on counts of all nests found and/or based on counts of the individuals that apparently were involved in breeding activities. In this study, we focus on the species Avocet, Common Gull, Black-headed Gull, Common Tern, Arctic Tern, Mute Swan, Common Eider and Herring Gull. Owing to the small size of the islets, and the high detectability of the breeding colonies, the probability of not detecting the study species included here was very low. The number of annual breeding pairs of all species recorded on the individual islets is given in Table S2–S9.

Surveys of rat occurrence were conducted during the monitoring of breeding waterbirds. Based on these visits, each islet was given a semi-quantitative score for rat abundance representing the situation in the incubation phase of the breeding season. The score ranged from 0 to 3 using the following definitions: 0 = no evidence of rats, 1 = one direct observation of rats and/or other evidence that rats were present in low abundance, 2 = several observations of rats in more than one location on the islet, and/or signs of moderately high numbers of rats, 3 = rats observed several times and many signs of a high abundance of rats. The score was systematically registered on all islets by direct observations of the number of rats, tracks and holes observed as well as the abundance of excrements and carcasses from birds apparently killed by rats. The score was given by the same two persons across all years in this study. The observers knew how to distinguish the signs of presence of European water vole (*Arvicola terrestris*) on the islets from signs of presence of rats. Islets on which rats had been recorded present in May–June were usually revisited in September–October and again in late winter or early spring when rat poison was administered. The persistence of rats in consecutive years is considered most likely to reflect a situation where rats persisted despite management efforts, although we cannot completely rule out the possibility of successful eradication and followed by reinvasion.

2.3. Factors affecting colonization and persistence probability of rats

To investigate whether structural factors at the individual islets affected colonization probability of rats, we collated data on islet size, distance of the islets to the mainland and presence of shrub cover (Table S1). Areas, distances and presence of shrub cover was measured and assessed from orthophotos from spring 2018. Although the extent of shrub cover did change somewhat during the long study period, this variable is useful to distinguish between islets subject to recurrent flooding and islets with persistent vegetation that could make them more attractive to rats and maybe more conducive to persistence of rat populations locally. To explore the importance of winter conditions, we collated data on average winter temperature and occurrence of ice winters during the study period (Table S10). Average winter temperature (December–January) was calculated from data acquired from the Danish Meteorological Institute (DMI), and the occurrence of ice winters in Roskilde Fjord was extracted from annual surveys of local ice cover completed by the Defence Command Denmark (https://www2.forsvaret.dk/omos/organisation/sovarnet/organisation/marinestaben/istjenesten/Pages/Om-Istjenesten.aspx).

2.4. Statistical analyses

2.4.1. Colonisation and extinction rates of rats on islets

The probability of rat colonization on individual islets in individual years was modelled as either 0 (no rats present) or 1 (rats present) for all islet-years, 1989–2009, with a rat score at 0 the previous year in a generalised linear mixed model (GLMM: Glimmix procedure in SAS 9.4) with a logit link function and binomial error distribution. To account for random variation between year and between islets, we stated year and islet as random effects. In this model, we tested the fixed effects of area, distance to mainland and presence of shrubs on individual islets, as well as average winter temperature and days with sea ice the previous winter. All models had a generalised chi-square / df -ratio ranging from 0.48–1.01 (a ratio of 1 indicates a perfect fit), indicating no signs of variance inflation. Models that accounted for spatial autocorrelation generally provided similar predictions as models that did not address spatial autocorrelation, but reached less robust predictions as their estimated G matrix was usually not positive infinite (suggesting less reliable solutions due to overly complex model structure) if converging at all. The same phenomenon occurred when modelling annual variation in rhe number of breeding pairs per islet per year (see below). For these computational (overfitting) as well as biological reasons (the islets were generally closer to the mainland than to each other, so we consider the annual variation in rat presence and bird numbers in reality to be independent between neighbouring islets), we did not incorporate spatial autocorrelation in any of the statistical models to which we refer.

We modelled the general persistence time of rat populations (once established), 1988–2009, as a Kaplan-Meier-survival function (Lifetest procedure in SAS), with the number of consecutive years with rats present as a response variable. Hence, an event where rats were found in a single year only was scored as survival time of 0, whereas an event where rats persisted for four years in a row was scored as survival time of 3. Four rat islet populations still present in 2009 were right-censored. Since the survival curve suggested that annual persistence probability was independent of population age, we subsequently modelled the annual persistence probability as per islet per year (1989–2008) as either 0 (no rats left the following year) or 1 (rats still present the following year) in a GLMM. In the GLMM, islet and year were stated as random effects, and islet area, distance to mainland, presence of shrubs, average winter temperature and days with sea ice as fixed effects. All models had a generalised chi-square / df -ratio ranging from 1.00–1.08 (a ratio of 1 indicates a perfect fit), indicating no signs of variance inflation.

Since the presence of rats on an islet in two subsequent years could be the result of the population surviving as well as a new colonisation event, the annual rat population survival rate (s) was $s = (p - c)/(1 - c)$, where p is the probability that rats would be present from one year to the next and c is the probability that rats would colonise a rat-free islet. The confidence limits of s was estimated from 100,000 bootstrap estimates drawn on the probability distributions of the estimates of p and c.

3.4.2. Effect of rat abundance on numbers of breeding pairs

We modelled the variation in the number of breeding pairs per islet using a GLIMMIX with a log link function and a negative binomial distributed error term). In a few cases (Black-headed Gull data) when models would not converge, we instead used a Poisson distributed error term and corrected for overdispersion (‘random _residual_’ statement: these models provided similar predictions as those with negative binomial distributed error terms in the other species). We tested for the effect of rat presence and rat abundance score, and included year and islet as random effects. The apparent effects of either rat presence or rat abundance on number of breeding pairs (adjusted for year and islet variation) was modelled as $\exp(B)$, where B was the model coefficient of rat presence (relative to rat absence) or rat abundance (difference between succeeding levels of rat abundance score from 0 to 3). For those species where we found significant effects of rats on the number of breeding pairs, we also conducted post-hoc estimates of the differences between rat score 0 (no rats) and rat scores 1, 2 and 3, respectively. We investigated whether the number of breeding pairs was affected by rat presence in the contemporary year as well as by the presence of rats in the preceding year (a memory effect). We therefore analysed for the effect of rat abundance in the same year as the birds were counted (t) as well as in the previous year (t–1: for the case birds should express a delayed response to rat presence). However, because no cases of delayed effects of rat presence were apparent after we had corrected for effects of immediate presence (same year), while immediate effects persisted even adjusted for effects of rat presence the previous year, we only present results of same-year-effects.

3. Results

3.1. Colonisation and extinction rates of rats on islets

The 25 islets in Roskilde Fjord were not equally likely to be populated by rats (Fig. 1). For example, rats were recorded present on Langholm (Lejre Vig) and Kølholm in eight and 13 (respectively) of the 22 study years, whereas 13 of the other islets never had rats (Table S11). In 15 of the 31 instances where rats had immigrated to an islet before the birds settled to breed, the rats had apparently disappeared again before the start of the following breeding season. However, on five islets rats were present without interruption for at least 4–7 years in a row, despite attempts to eradicate them by use of anticoagulant poison (Table S11).

From 1988 through 2009, rats were registered as present on 66 of 493 islet years (13%, Table S11). From 1989 to 2009 we registered 30 colonisation events by rats out of 399 islet years with no rat presence the previous year, equalling an annual colonisation probability of 8% (95% confidence interval: 0.06–0.11) if estimated with plain logistic regression and 6% (95% confidence interval: 0.03–0.12) if adjusting for year and islet ID as random effects. Of 27 islet populations of rats registered for the first time between 1988–2008, 12 (45%) had apparently

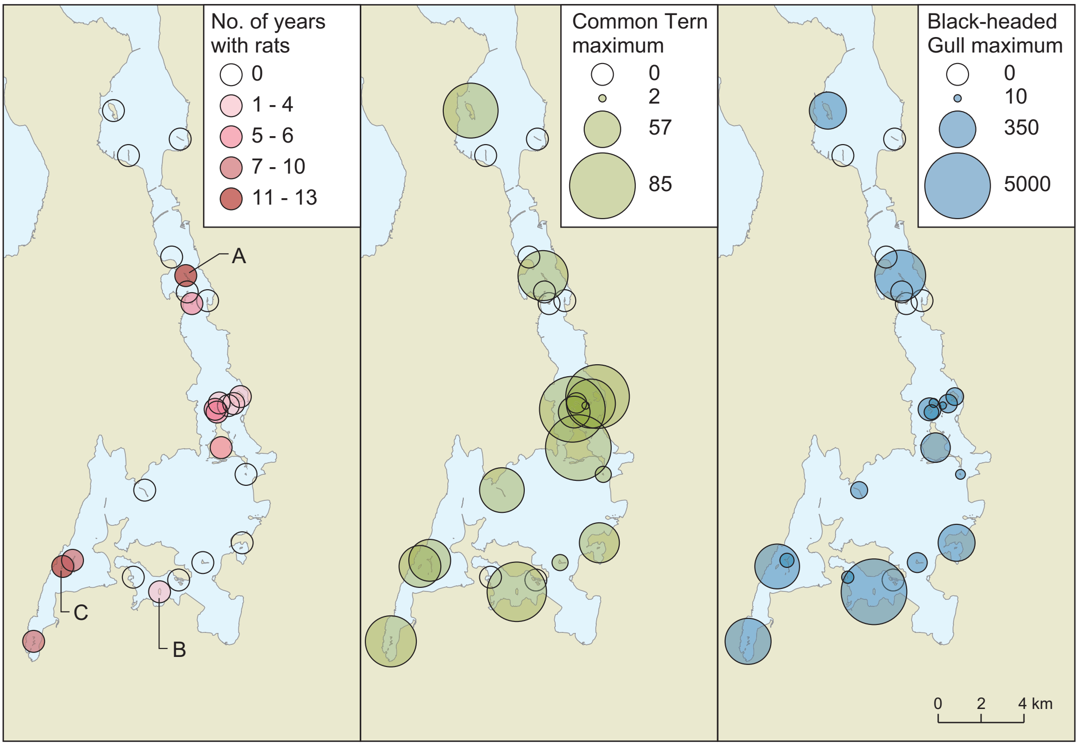

Fig. 1. Distribution of rats and of breeding Common Terns and Black-headed Gulls in Roskilde Fjord 1988–2009. For rats, circles denote the number of years where rats were recorded present during the study period. For birds, circles denote the maximum number of breeding pairs recorded on each islet (note that the scales for the circles differ between the species). The letters A, B and C in the left figure indicate the locations of the islets Kølholm, Ringøen and Hyldeholm for which histograms are shown in Fig. 3.

gone extinct the following year after being registered (Fig. 2). The log-linear shape of the Kaplan-Meier survival curve strongly indicated that the annual persistence probability was constant regardless of population age (Fig. 2). From logistic regression, the annual persistence rate was estimated at 60% (95% confidence interval: 0.47–0.72) in a model without predictor variables, and to 65% (0.45–0.81) if including islet and year as random effects. If adjusting for some apparent persistence observation being due to new colonisations, the latter estimate corresponded to an annual survival probability of 63% (95% confidence interval: 41–82%) for rat populations.

Colonisation, as well as extinction rates, were independent of islet size, distance to mainland, presence of shrubs and winter severity (days with ice cover)(all *P*-values > 0.2).

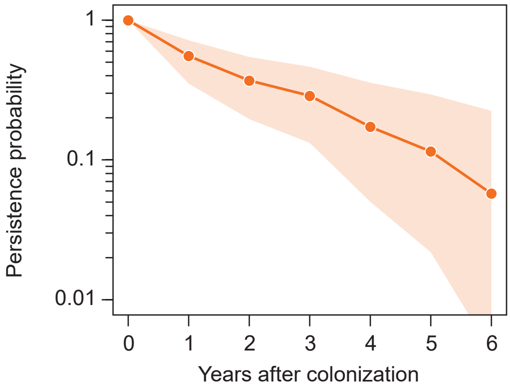

Fig. 2. Survivorship of 27 rat populations established on islets in Roskilde Fjord expressed as a Kaplan-Meier survival function (thin lines indicate 95% confidence zones).

3.2. Observations of rat impacts

The distribution of rats among islets in the fjord greatly overlapped with the distribution of islets holding large numbers of breeding waterbirds (for examples, see Fig. 1). The most dramatic impact of the presence of rats was recorded in 1989 when rats occurred on five of the islets holding colonies of Black-headed Gulls and Common Terns. Rats were particularly abundant on the three islets with the highest numbers of breeding pairs of Black-headed Gulls (*c.* 1,100-1,800 pairs on each islet; the islet 'Ringøen' held approx. 5,000 pairs the year before, see Fig. 3). Based on collection and counts of dead gulls and terns, it was estimated that 500–1,000 adults had been bitten to death and approx. 10,000 eggs and chicks had been lost, eaten or killed. The first adults found bitten to death were recorded before egg-laying had been initiated. Up to 25 corpses of Black-headed Gulls were found at each of the recorded rat holes. The species of breeding birds that had been killed by rats on the five islets included Black-headed Gulls (by far, the most commonly killed species), Common Gulls, Common Terns and Arctic Terns. Later in the season, the rats continued predating eggs and chicks which in several cases led to complete breeding failure for these four gull and tern species. There were no clear documentation of rats predating eggs of Herring Gulls, but there were instances where chicks of this species apparently had been killed and partly eaten by the rats. Eggs of Mallard (*Anas platyrhynchos*) and Tufted Duck (*Aythya fuligula*) were found predated by rats on a few of the islets.

The incidents in the late 1980s with predation from rats in the four largest colonies of Black-headed Gulls in the fjord (5,640 pairs in total) may explain why their numbers declined massively on some of the islets (examples in Fig. 3) and in total declined from approx. 15,000 pairs in the fjord in 1983–1988 to 6,000–8,000 pairs in 1989–1998. Common Tern numbers had increased in the fjord (from 160 pairs in 1978 to 496 pairs in 1988; the largest concentration of breeders of the species in Denmark) but declined almost annually thereafter to just 26 pairs in 2009. Some of the serious incidents with rats probably triggered local population declines, by means of avoidance, increased adult mortality as well as failure in producing new potential recruits. There is some evidence from ringing and counts of other colonies that some of the terns and Black-headed Gulls emigrated to alternative breeding sites in the neighbouring fjord, to lakes on the mainland and to more distant breeding localities.

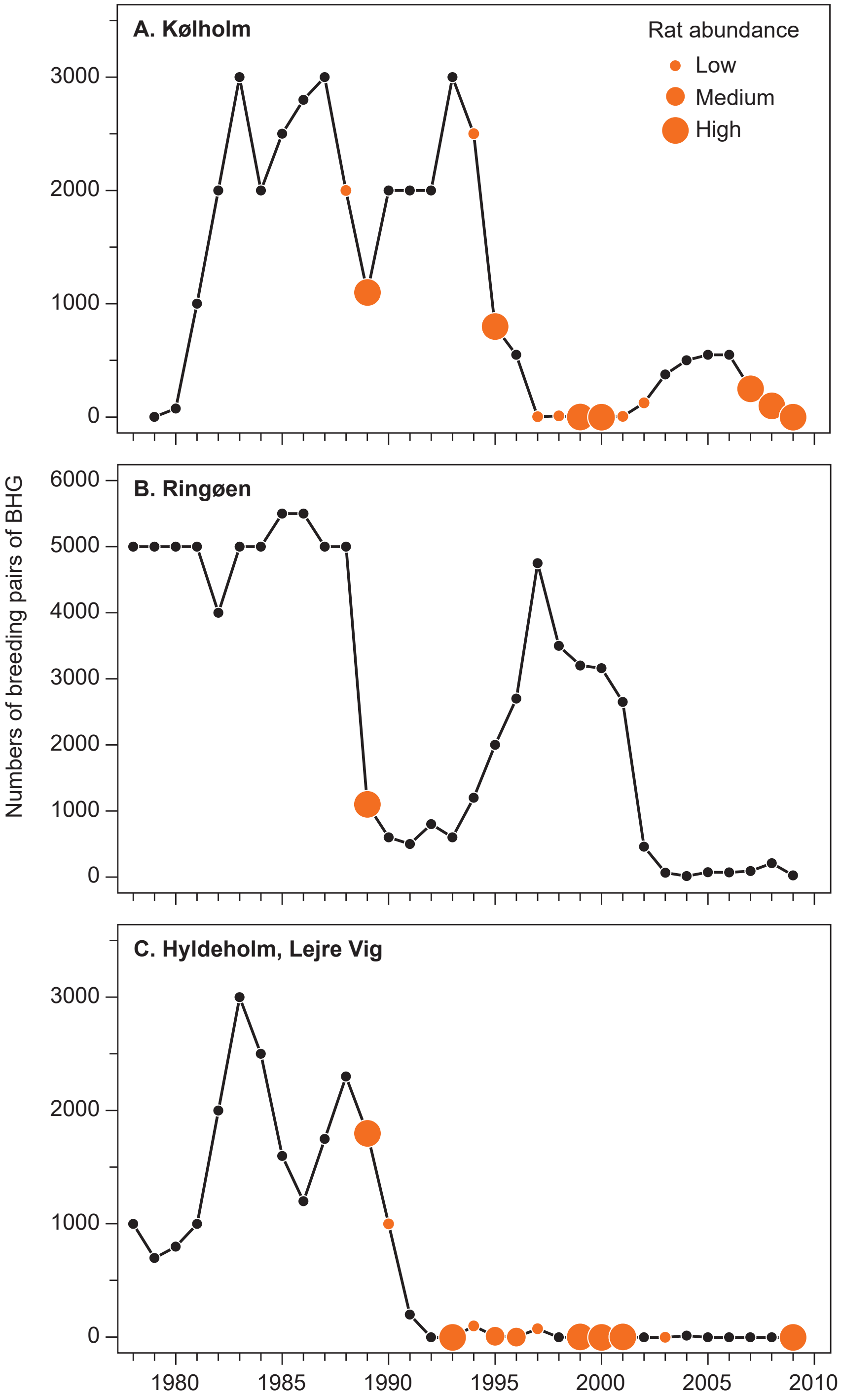

Fig. 3. Examples of the development of numbers of breeding pairs of Black-headed Gulls (BHG) 1978-2009 at three islets in Roskilde Fjord, colonized by rats in the late 1980s. The estimated sizes of the local rat populations are denoted by the three sizes of circles. Note that only two of the y-axes are drawn to the same scale.

3.3. Breeding bird numbers modelled as a function of rat presence and rat abundance

Numbers of breeding pairs of Common Tern, Mute Swan, Avocet and Black-headed Gull correlated negatively with rat presence or abundance (Table 1, Fig. 4). Avocets appeared to be the species most negatively affected by rat presence with an estimated reduction to 30% (95% confidence limits: 16–58%) compared to years without rats, followed by Black-headed Gull (reduced to 45%; 95% confidence limits: 33–60%) and Common Tern (reduced to 52%; 95% confidence limits: 31–89%). Mute Swan numbers were reduced to 81% (95% confidence limits: 60–95%) of the numbers observed in years without rats. Altogether, seven of eight species expressed negative responses to rat presence, and the overall species' response was significantly negatively different from 0 (Table 1: average coefficient = –0.40, $SE = 0.15$, $df = 7$, $P = 0.028$). Analyses of breeding numbers modelled as linear functions of rat score yielded similar results as responses to presence-absence (Table 1). However, post hoc examinations of responses specified to rat score level, suggested that only Common Tern responded more negatively the more rats were present whereas Avocet, Mute Swan and Black-headed Gull responded equally negative no matter whether few or many rats were present (Fig. 4).

4. Discussion

Our findings indicate a clear negative effect of rats on numbers of ground-breeding waterbirds on small islets. This finding supports earlier studies reporting negative impacts of rats on both waterfowl and seabirds (Bertram & Nagorsen 1995, Taylor *et al.* 2000, Angelici *et al.* 2012), and emphasizes that the presence of rats might compromise the availability of suitable breeding sites as well as breeding success among several groups of avifauna. In accordance with our hypothesis, especially the smaller species (Common Tern, Black-headed Gull and Avocet) seemed to be affected by the presence of rats. This relationship has previously been suggested by Martin *et al.* (2000), and may relate to the smaller species' inability to fend off attacks from the approaching predator. The higher impact on small-bodied species was further supported by the finding of adult individuals of Common Terns and Black-headed Gulls that had been killed by rats. We presume that most kills of adult terns and Black-headed Gulls took place at night and that the rats attacked the birds while they were incubating eggs. Following the introduction of infrared cameras on the islets we now know that the rats become particularly active above ground after sunset. For a small but relatively long-lived species like the Common Tern, this adult mortality

Table 1. Effects of presence and abundance of rats on the number of breeding pairs of waterbirds on islets in Roskilde fjord, 1988–2009. The coefficients (B) indicate loge-odds ratios of number of breeding pairs as function of rat presence vs. absence or increasing rat abundance score. Relative difference in numbers as function of more rates are thus derived as exp(B). Statistical significance levels: °: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; ****: $P < 0.0001$.

	Presence vs. absence of rats					Rat score tested as covariate (0–3)				
	B	Exp(B)	SE(B)	t_{446}	P	B	Exp(B)	SE(B)	t_{446}	P
Common Tern	–0.65	0.52	0.27	–2.43	*	–0.51	0.60	0.13	–3.81	°
Arctic Tern	–0.09	0.91	0.24	–0.38		–0.20	0.82	0.13	–1.56	
Mute Swan	–0.21	0.81	0.08	–2.60	**	–0.07	0.93	0.04	–1.78	°
Avocet	–1.20	0.30	0.33	–3.60	***	–0.67	0.51	0.17	–3.88	***
Common Eider	0.09	1.10	0.19	0.49		0.08	1.08	0.09	0.92	
Common Gull	–0.14	0.87	0.13	–1.10		–0.09	0.92	0.06	–1.40	
Herring Gull	–0.20	0.82	0.12	–1.71	°	–0.11	0.90	0.06	–1.91	°
Black-headed Gull	–0.80	0.45	0.15	–5.39	****	–0.38	0.68	0.08	–4.90	****

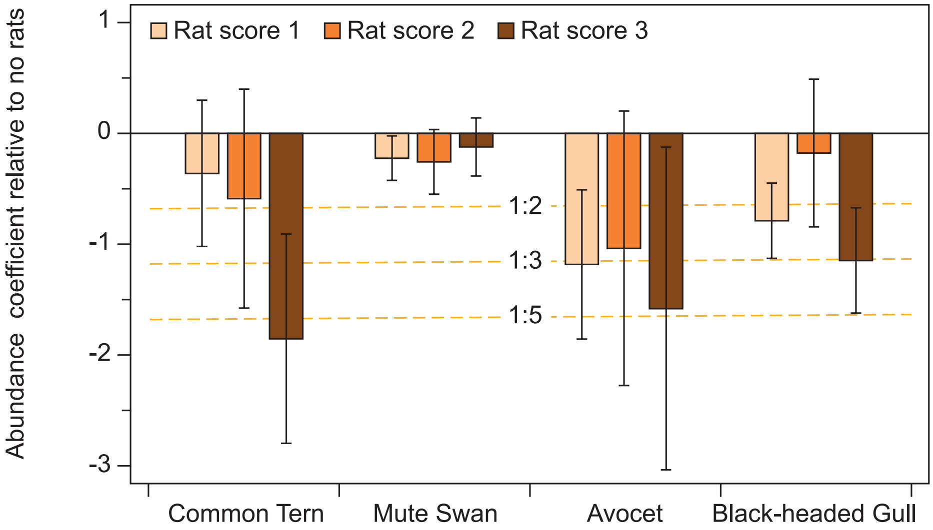

Fig. 4. Differences (with 95% confidence intervals) in number of breeding pairs at different rat abundance levels (score 1–3 from few to many rats) relative to no rats being present in the four bird species that responded negatively to rat presence (Table 1). The horizontal, stippled lines indicate odds-ratios of the difference in breeding pairs relative to no rats being present (1:2 indicate a halving of the number of breeding pairs compared to no rats being present).

is likely to have a large negative impact on population dynamics (Lebreton 2005, Cabot & Nisbet 2013). Our analysis also indicated a negative effect of rats on the number of breeding Mute Swans on individual islets, suggesting that even birds more than 20 times the size of rats were impacted. It is also known from other islets in Denmark that even though rats do not attack incubating birds of the size of Herring Gulls they may predate heavily on their chicks causing a more or less complete breeding failure in an entire colony (own observations). We find it noteworthy that even Mute Swans appeared to avoid nesting on islets with rats. Rats have been observed crawling up on nests of Mute Swans but being repelled repeatedly by the incubating parent that remained lying on the nest (Davies 2020). Our results could thus be an indication that the mere stress caused by rat harassment is sufficient to drive ground-nesting birds away from their breeding grounds.

Only Common Tern expressed a clear negative relation between numbers of breeding pairs and rat abundance. This may indicate that for some species of breeding birds the presence or absence of rats is more crucial than actual rat numbers. The birds' experience of rat presence may also have differed from the perception of the observers in the present study, *i.e.* observers and birds do not necessarily use the same cues and may interpret these differently when 'estimating' rat abundance.

We found an immediate negative effect of presence of rats on the numbers of breeding pairs of the smaller species (Avocets, Common Terns and Black-headed Gulls), *i.e.* breeding numbers dropped significantly in the year when rats had immigrated before the birds settled to breed. This immediate response may appear because potential breeders detect rats when prospecting prior to egg-laying and/or because birds experience that rats are present after they have settled and initiated breeding and then decide to abandon the islet before the monitoring of breeding birds took place. We find it likely that most of the colonial coastal birds such as the terns and gulls did try to prospect for presence of predators at the time of settling (*cf.* Cabot & Nisbet 2013), and probably some individuals experienced that rats were present and consequently gave up their first choice and instead selected another islet in the fjord or maybe even outside the fjord. Rats are normally not very active above the ground during day-time (which was also the case in our study area), and this may make it difficult for prospecting breeding birds to detect presence of rats and other nocturnal predators during the time of pre-laying (*cf.* Ratcliffe *et al.* 2008), especially if the rats occur at low density and the islet is covered by vegetation and is fairly large. It is unclear to what extent birds are able to detect the presence of rats, and what environmental cues or sensory perceptions might trigger abandonment of a breeding site. Several studies have documented that visual and auditory signals aid birds to detect potential predators (*e.g.* Quinn *et al.* 2006, Fernandez-Juricic 2012), and a study by Stanbury and Briskie (2015) report indications that Common Starlings (*Sturnus vulgaris*) are able to detect rats by means of olfactory cues. We find it likely that it commonly occurred that individuals were unaware of the presence of rats at the time of settling, maybe because they used the presence of already settled breeders as a cue for safety or were site faithful to previous breeding sites. Subsequently, rats might have become attracted to the specific site where the birds were nesting, whereby the incubating birds experienced that they and their eggs were at a real risk of being predated, and this then triggered abandonment of the islet, in some cases before the breeding survey took place. Overall, the results clearly indicate that the birds' ability to avoid rats was not super-efficient, given that there are several documented cases of birds breeding on islets with rats despite availability of rat-free and apparently suitable islets nearby.

Taken together, the collective impact of rats on numbers of ground-breeding birds is considered likely to have arisen both because some birds responded to rat presence by leaving the islet entirely and by the increased vulnerability of the birds that decided to stay or failed to detect rats and consequently were at risk of being killed during incubation as well as by losing their eggs and/or young due to predation from the rats.

We anticipated that a significant proportion of the breeding birds would avoid returning to and settling on islets where rats had been present in the previous breeding season. There were certainly instances where Black-headed Gulls and Common Terns apparently abstained from returning to breed on an islet where rats had been numerous in the previous year or over several previous years (examples in Fig. 3). However, overall we did not find significant evidence to support the hypothesis that birds would skip an islet as a breeding site if rats had been present in the previous year. Based on the clumped distribution of the breeding birds present inside the fjord, we find it very likely that many of the individuals that settled to breed on an islet on which rats had been present in the previous year were site faithful individuals which had nested on the same islet the year before. It was a surprising finding that birds reappeared on islets which had rats the previous year, especially considering that the species covered by this study – in almost all instances – had opportunities to settle on other islets free of rats. Other studies have demonstrated how islands and islets are skipped completely as breeding sites in years following immigration of predators (Nordström & Korpimäki 2004, Hilton & Cuthbert 2010), but there are also studies documenting how colonial coastal birds may continue for years to return to specific islets despite deteriorating breeding conditions that are linked to the islet itself and despite availability of suitable alternative islets (*e.g.* Heinänen *et al.* 2008). The recorded behaviour of breeding birds returning to islets in our study area which had been populated by rats in the previous year (as well as in the current year) is likely to have amplified the negative impact of the rats on the overall breeding populations of the smaller species of colonial waterbirds in the fjord. It is unknown whether the observed 'tolerance' of rat presence reflect that the historical selection pressures for strong behavioural avoidance of sites populated by this species of rodent has been fairly weak despite the coexistence of the species for almost 2000 years.

Contrary to our expectations, colonisation rate of rats on individual islets seemed unrelated to distance to the mainland and winter severity. We expected that shorter distances to the mainland and the presence of ice cover would increase the probability of colonisation. Acknowledging that the power of the analysis is limited (30 colonisation events), absence of any effects of winter severity could indicate that the rats primarily reached the islets by swimming. The absence of a relationship with distance from the mainland may indicate that, within distances of 875 m from the mainland (maximum distance among all the included islets), rats are fully capable of colonizing islets under most circumstances – at least in a relatively protected water body like Roskilde Fjord. Lodal (2008) report that rats are capable of swimming at least 750 m, and that they are able to survive for 3 days in water, and Russell *et al.* (2008b) found rats to regularly swim up to 1 km. This demonstrates that most, if not all, islets in Roskilde Fjord are probably within colonization distance. To this end, the distances between several of the individual islets were substantially less than the distance to the mainland, and rats may therefore have used the islands and islets as stepping-stones when colonizing new areas. Periods with low water levels are likely to increase movements to other islets, as rats have been observed running across the mudflats between the islets (S. Christensen, H. Jørgensen & H. Aare pers. comm.). Interestingly, Møller (1983) also found no effects of island size and distance to the mainland, but suggested that the presence (and size) of larid colonies might increase the probability of an island being occupied by rats. As such, the mere presence of terns and gulls on specific islets in Roskilde Fjord might have been a driver of rat colonisation events. The presence of birds might also have affected rat persistence locally, but the larid colonies are only present during the breeding season in spring and early summer, whereas the bottleneck in terms of rat food availability (and hence persistence) is likely to be in winter. In addition, the colonization with rats of islets in Roskilde Fjord is certainly not limited to the period when terns and gulls are present, and the birds are therefore unlikely to be the sole driver of rat presence. In our data set, there is a high risk that eradication efforts on the individual islets obscured the possible positive effect that the presence of breeding birds might have had on local rat populations, and the data we have available are therefore unsuitable to shed further light on the importance of birds as drivers for local rat population dynamics.

The persistence of rats was unaffected by the size of individual islets, presence of shrubs and winter severity. While this may lead to the conclusion that rats can survive on even very small and bare islets under most conditions in this area, it may also reflect that most colonisation events of rats on small islands are relatively short-lived (see Møller 1983). In all cases, the potential population regulatory effects of these factors may well have been obfuscated by the systematic implementation of control measures upon the detection of rats on an islet. Hence, persistence should not be interpreted as ‘natural’, but rather as the ability to persist despite control efforts. Although rats were generally subject to control whenever detected, there were no systematic data available to evaluate the efficacy of these initiatives.

In terms of management implications, it is clear that some species of waterbirds suffer from the presence of rats on their breeding islets. Consequently, eradication of rats is likely to have a positive effect on breeding numbers if successful. Currently, pest control of rats in Roskilde Fjord is severely hampered by a national ban since 2016 on the use of poison to kill rats in natural habitats. The current methods applied on the islets in the Roskilde Fjord include use of traps and trained dogs as well as shooting of rats by use of a rimfire rifle combined with a night vision scope. These methods have turned out to be far less efficient and very time consuming compared with the former use of poison. The recently developed automatic self-resetting Goodnature A24 rat traps were also in use, and these were not costly in use in terms of time and man power. However, they were effective only in a few cases, apparently because the rats were difficult to attract to the traps, possibly because the rats had easy access to alternative food resources. Consequently, the control of rats on the islets has become increasingly ineffective. Nonetheless the most sensitive species being terns and Black-headed Gulls are still breeding on a few of the islets but now in far lower numbers than they used to (T. Bregnballe, P. Andersen-Harild & E. Mandrup-Jacobsen in prep.).

In all cases, the recurring problem with rats on the islets in Roskilde Fjord clearly indicate that sustained eradication will be very challenging. Some of the lessons learned during the ‘control to zero’ campaigns on islands in New Zealand include that for control to zero density to be feasible, the following three rules must be met: (1) all pest animals must be put at risk; (2) pests must be removed faster than they reproduce; and (3) immigration must be stopped or new invaders captured before they reproduce (Anderson *et al.* 2014). In an environment like Roskilde Fjord, near-shore pest management will be regularly counteracted by reinvasion from the mainland. So, effective pest control may require multiple different control measures, including a simultaneous effort in mainland source populations and frequent surveillance in the islets (*cf.* Russell *et al.* 2008a, 2008b).

To conclude, the presence of rats on breeding islets can have substantial negative effects on their value as breeding sites for colonial waterbirds. Although the effects were most pronounced for the smaller species, our findings indicate that even large species of waterbirds might potentially be affected. Our analysis suggested that the presence or absence of rats was more important than rat abundance and that, at least in sheltered waters like bays and fjords, rats were able to colonise islets irrespective of their size, the extent of vegetation cover and their distance to the mainland.

Förekomst av råttor och deras påverkan påkoloniala vattenfåglar i en dansk fjord

Människans verksamhet har lett till en omfattande global utbredning av brunråttan (*Rattus norvegicus*) med konsekvenser för djurlivet, speciellt för markhäckande fåglar. I denna studie analyserar vi kolonisering och fortlevande av brunråttor på små öar i en Dansk fjord som är av stor betydelse för häckande vattenfåglar. Sannolikheten att öarna kolonsierades av brunråttor var 6% och sannolikheten att de fortlevde på öarna var 65% (motsvarande en 62% årlig överlevnad när återkolonisering efter utdöende beaktas). I motsats till våra hypoteser var brunråttans kolonisering oberoende av öarnas storlek, deras distans från fastlandet eller förekomsten av buskvegetation på öarna. Brunråttans närvaro hade en signifikant negativ effekt på antalet häckande par hos fyra vattenfågelarter. Antalet häckande skärfläckor (*Recurvirostra avosetta*) minskade till 30% under år med brunråttor, skrattmåsar (*Chroicocephalus ridibundus*) minskade till 45% och fisktärnor (*Sterna hirundo*) minskade till 52%. Främst de mindre vattenfågelarterna påverkades negativt av brunråttans närvaro. Kontrolleringsinsatser för att minska brunråttans närvaro på de viktigaste häckningsöarna kan ha en positiv effekt på fågelarternas förekomst och häckningsframgång. Vi fann inga bevis för att fåglarna skulle utnyttja sitt minne för att veta var brunråttorna fanns året innan. Mera forskning behövs för att undersöka beteendemekanismerna bakom de omedelbara negativa effekterna i fågelpopulationerna samma år som råttorna observerades, med andra ord, hur iakttar och reagerar prospekterande och etablerade häckande individer på närvaro av brunråttor.

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Online supplementary material

Supplementary material available in the online version includes Tables S1–S3 and Fig. S1.