Urban Ecosystems (2023) 26:1355–1366
https://doi.org/10.1007/s11252-023-01372-6

The lure of the big city: smaller Danish rookeries are increasingly associated with urban land cover

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Accepted: 5 May 2023 / Published online: 2 June 2023

Abstract

Rooks *Corvus frugilegus* are common and widespread in urban and agricultural habitats in Denmark. Large numbers are killed annually by derogation shooting to control population growth to reduce noise near populated areas and prevent agricultural damage. Responding to increasing public complaints about noise nuisance from urban rookeries, we investigated changes in extent of urban and agricultural habitats within 500 m, 1000 m and 2000 m of all known breeding rook colonies (rookeries) in eastern Jutland, Denmark in 1991 compared to 2021 based on open access land cover GIS layers in 1990 and 2019. Numbers of rookeries increased by 40% from 95 (1991) to 133 (2021) but nest abundance increased only by 6% from 10,299 to 10,887 due to more and significantly smaller rookeries, increasingly associated with urban sites. In both years, the proportion of urban area within distance classes of rookeries was significantly higher, and the area of agriculture significantly lower, than at randomly chosen points in the same region. The proportion of urban area around each rookery decreased with increasing distance, whereas the proportion of agricultural land cover increased. The proportional area of urban land use within the distance classes increased between 1991 and 2021 whereas agricultural land cover decreased. Given no simultaneous major change in overall land use, our results indicate an increasing selection by rooks for smaller urban rookeries over agricultural landscapes, where rookeries have declined. We consider these trends, especially the proliferation of smaller rookeries in urban areas, as a potential explanation for the upsurge in public complaints about rookery noise in residential areas. We urge further research to explain the causes behind these trends before we can provide science-based solutions to resolve such conflicts effectively.

Keywords Agriculture · Breeding distribution · Colony size · Conflict · *Corvus frugilegus* · Habitat shift · Noise nuisance · Rook · Urban

Introduction

Human impacts on natural ecosystems are causing global declines and mass extinction of species (Pimm et al. 2014). However, some species show behavioural, ecological and dietary plasticity to adapt to new, artificial environments, including urban landscapes (e.g. Lowry et al. 2013; Sol et al. 2013). Human-wildlife interactions, especially in urban environments, are also increasingly promoted as being positive for human health and well-being (e.g. Douglas 2012), although some species may come to be regarded as a "nuisance" or "pests" by human urban dwellers (Soulsbury and White 2015). Such human-wildlife interactions in urban areas have stimulated an upsurge in interest in such research, seeking mechanisms for conflict resolution and mitigation (e.g. Magle et al. 2012, 2019)

Wildlife noise effects on human residents may seem trivial compared to damage and injury caused by some animals (e.g. road collisions and damage to property, crops and infrastructure). However, noise from raucous colonial nesting birds, such as the rook *Corvus frugilegus* is loud, variable and persistent throughout nest-building and the rearing

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of young, extending from before sunrise to after sunset (Røskaft and Espmark 1982; Frankhauser 1995). Despite urban rookery noise levels (mean 64 dBA (a-weighting) re. 20 µPa root-mean-square) being lower than from traffic and ambient noise (74 dB), it is continuous and particularly disruptive during early mornings and into the evening, causing particular distress for local residents (Frankhauser 1995).

In Denmark, growing conflict between rookeries and local residents is reflected in increasing numbers of newspaper articles concerning rooks and noise, especially in the last ten years (see Fig. 1). This has put increasing pressure on authorities to find solutions to what is considered a problem. However, we lack basic knowledge about the nature of the conflict upon which to base mitigation mechanisms and develop effective management strategies to reduce conflict between urban wildlife and human residents. For instance, if Danish rooks increasingly abandon rural, agricultural areas but are increasing in urban and suburban areas (as suggested by Moshøj et al. 2018), this inevitably results in the exposure of more human residents to effects of noise from rookeries.

The rook is a common and widespread mostly resident breeding species in Denmark (Bønløkke et al. 2006) numbering *c.*85,000 pairs (Fredshavn et al. 2019), stable since *c.*1990 (Eskildsen et al. 2021). Comparing national breeding bird atlas surveys in 1993-1996 with 2014-2017 revealed a *c.*26% increase in distribution, occupying 43% of all 5 x 5 km grid squares (Vikstrøm and Moshøj 2020). Despite no hunting season for rooks in Denmark since 1982 (because rooks are not designated as huntable on Annex II of the Birds Directive), *c.*75,000 birds (mainly fledglings)

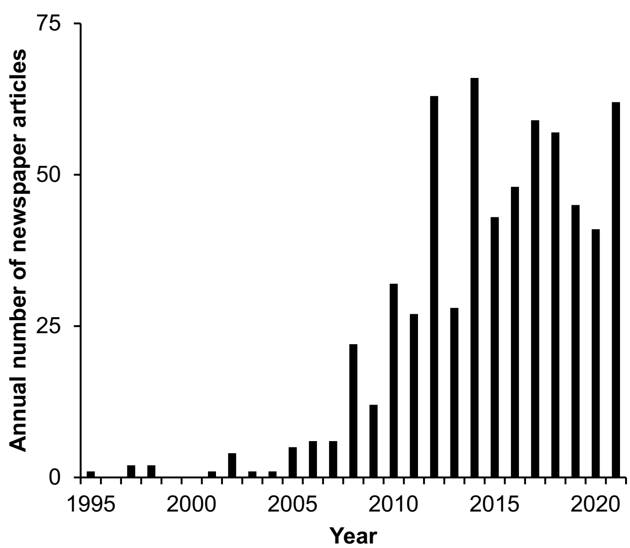

Fig. 1 Histogram showing the annual number of newspaper articles found using the search words "råger" (rooks) and "støj" (noise) in the Danish national media from 1 January 1995 to 31 December 2021, searching the Infomedia database of national and local newspaper articles (https://library.au.dk/en/resources/newspapers)

are shot annually under derogation (Article 9 of the Birds Directive), permitted on non-huntable species where there is no other satisfactory solution to the significant problems they cause (e.g. to flora and fauna, human health and safety or to crops). Such measures are motivated to control population growth to reduce noise near populated areas and prevent agricultural damage. The details of each case of control are not fully documented, although the numbers killed are usually registered locally (Madsen et al. 2021).

Despite a perception as a farmland breeding bird in western Europe, a rookery reported from Gray's Inn in central London from the sixteenth century was abandoned as late as 1915 (Nicholson 1951), suggesting a long established adaptation of rooks to urban living. Some studies suggest declines in urban nesting rooks result from increasing urbanisation that denied them local access to agricultural land, specifically pasture, which they require for feeding in proximity to the nesting site, as in Edinburgh, Scotland (Munro 1970) and Norway, where declines in urban rookeries were linked to persecution and loss of nearby pasture (Reppe 2020). Elsewhere, rooks are reported declining in rural areas while increasing in urban areas (e.g. in Bern, Switzerland; Frankhauser 1995 and Poland; Orłowski and Czapulak 2007). Praus (2015) reported the disappearance of all known Czech Silesian rural rookeries in the late 1980s, due to destruction by hunters and/or worsening feeding conditions caused by changes in agriculture, while rookeries expanding in urban areas benefitted from more stable food resources and better protection from destruction of nests and birds.

Anecdotal evidence from Denmark suggests that in recent years, rooks have increasingly shifted from constructing their rookeries in agricultural areas to nesting in urban areas, a pattern reflected in other countries (see above), with several theories about why this may be the case. One of these is in response to persecution; it was always more common to shoot at rookeries in rural areas. Another posits loss of grassland in agricultural land compared to urban areas where rooks are increasingly feeding on the short-mown grass of garden lawns, parks, playing fields and recreation grounds associated with built up areas. Before we can effectively investigate the causes of this change, we need to be convinced that this rural to urban transition has genuinely occurred and how it has been manifested. Given conflicting evidence for rookeries shifting from rural to urban landscapes in Europe, first we need to establish a recent distributional change in Danish rookeries between urban versus agricultural landscapes and assess whether the extent of habitat types within foraging distance of rookeries has changed over that time.

Here, we use national land cover data in areas surrounding rookeries in an extensive area of east Jutland in Denmark censused in 1991 and 2021. We concentrate on the proportions

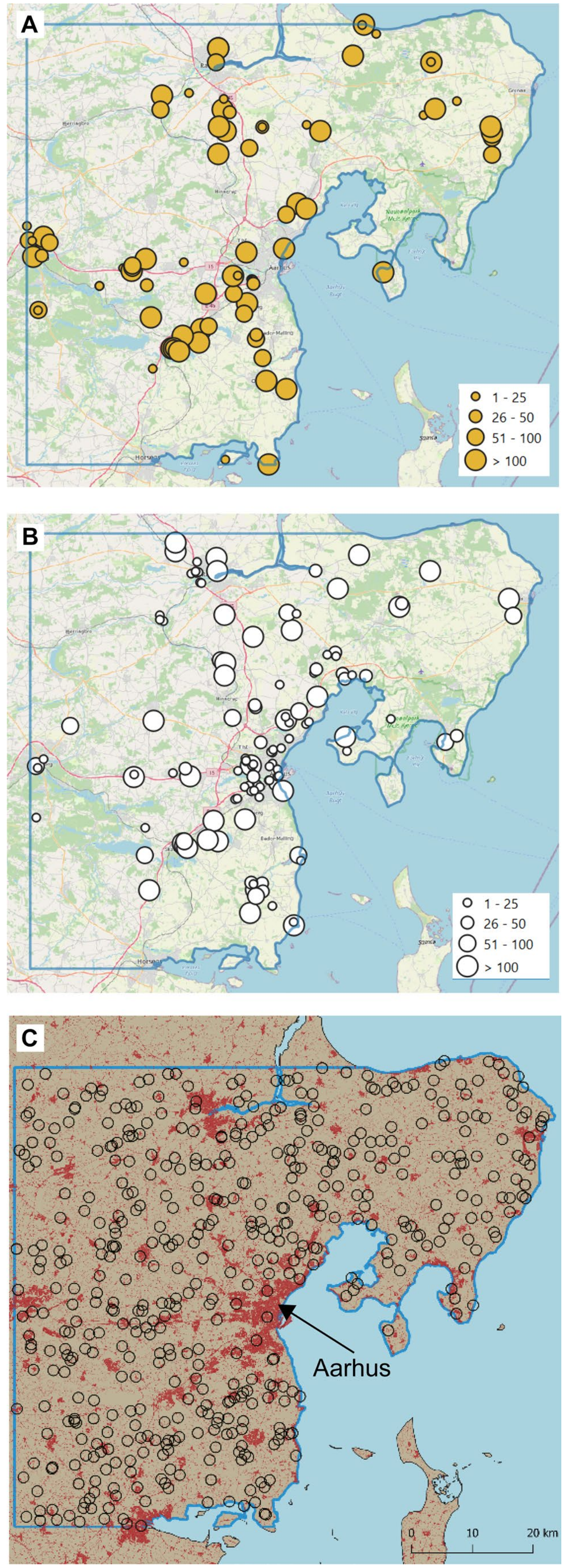

Fig. 2 Locations and size of all rookeries found in East Jutland study area (defined by pale blue outline) during 1991 (**A**) and 2021 (**B**). (**C**) illustrates the locations of the 500 generated random points used in the analysis overlaid on the map showing extent of urban land cover (shown in red) and shows the location of Aarhus city

of city, urban and suburban (the built environment, combined as "Urban") and agricultural ("Agriculture") land cover to assess the past and present distribution and size of rookeries in relation to mapped landscaped features in 1990 and 2019 respectively. Here, (1) we assess the evidence for the anecdotal impression that rookeries are becoming smaller over time, which adds to the problem in Urban areas (by increasing numbers of more fragmented smaller loci of noise) and investigate whether this tendency may be linked to Urban versus Agriculture land cover. Subsequently, we (2) compare the extent of land cover types within foraging distance of rookeries in 1991 compared to 2021 to see if, on average, the proportion of Urban area has increased, and Agriculture decreased across all rookeries. We (3) compare the extent of land cover types within a given distance of rookeries with those from random points to test whether rooks select for Urban areas and avoid Agriculture and for differences between the two periods. Furthermore, (4) if rooks specifically select Urban sites within the landscape to construct rookeries, we would expect declining Urban land cover and increasing Agriculture land cover with increasing distance from rookeries, whereas we predict there should be no such change with distance among random samples. Because rooks nest in tree blocks and in the edges of woodland rather than being associated with dense extensive Forest, we predict (5) that rooks avoid areas with extensive forest at all times and select for their favoured foraging habitat Grass (despite its rarity in the landscape) but show little other selection/avoidance.

Methods

Counts and study sites

Surveys of the former county of Aarhus (Eastern Jutland, Denmark, 56°3'N, 10°3'E, an administrative unit that existed until 2007) were undertaken to locate all rookeries in 1991 and 2021 (Fig. 2A, B). A citizen science survey was conducted in 1989-1991 by the local branch of DOF-BirdLife Denmark to determine the total number and georeferenced distribution of rookeries and number of nests at each site, with best coverage achieved in 1991 (Kahlert 1991; Kahlert and Jensen 1991). A repeat 2021 survey covered the same area with the same methods with the aim of comparing numbers of nests and distribution of rookeries, involving some of the same fieldworkers in 1991, with support from other local ornithologists. The georeferenced centre of gravity for each rookery position and counted numbers of nests were entered into the publicly accessible Danish bird portal DOFbasen (www.dofbasen.dk) for both years. Some loosely structured rookeries have nests some distance apart, often related to local lack of suitable trees, so we treated rookeries with nests > 100 m apart as two separate rookeries, during recording and data handling, after Sage and Vernon (1978) and Jensen (1980). Because rooks are active and noisy in and around rookeries in spring, they are generally easily detected, but inevitably, we cannot exclude the possibility that some rookeries were overlooked and that potential bias arises from the fact that smaller rookeries could likely be overlooked more often than larger ones. Nests are normally situated in deciduous trees in this study area (Janniche 1992), so active nests are most easily detected and countable before the last days of April before developing foliage makes this difficult (which coincides with hatching).

Land cover data

To relate rookery locations to the mosaic of habitats that surround them, we used the nationwide map of land use and land cover for Denmark known as Basemap available for the years 1990 (Levin 2014) and 2019 (Levin 2019). This map combines all existing thematic geographic information into one land use/land cover map for Denmark, publicly available since 2019. The land area within the study area fell into 553 habitat codes for 2019 data, which we then grouped to seven main land cover classification: Agriculture, Forest, Grass, Lake, Sea, Urban and "Other" land cover, relevant for describing the landscape around the rookeries and in the study area in relation to our hypotheses (see Supplementary Materials Table S1 for details). Sea and Lake areas were not considered relevant for foraging rooks and were omitted from the further analysis. We compared land coverage in the immediate vicinity of each rookery in 1990 with 2019 and rookery size and distribution in 1991 with 2021. Unfortunately, the 1990 land cover definitions were slightly coarser than in 2019, so some areas shown as Grass in 2019 were merged with surrounding habitats in 1990. This means that our estimates for the extent of Grass available in the vicinity of rookeries in 1990 was not reliable compared to those in 2019. We compared the land cover within 500 m, 1000 m and 2000 m of rookeries detected in the two survey years (locations shown in Fig. 2A, B) with that within the same distance classes from 500 randomly selected points across the study area (Fig. 2C). We chose these three distance intervals on the basis of unpublished GPS tracking data from rooks in the study area that suggest that well over 60% of foraging in the breeding season occurs within 500 m of rookeries and almost all within 1000 m (Heldbjerg et al. 2023) including land cover out to 2000 m to test for effects at longer distances.

Statistical analyses

(1) We tested for changes in the distribution of rookery size in the study area between the two years using two-tailed Mann-Whitney U (performed as Wilcoxon rank sum test) and χ^2 tests to assess differences in the size class distribution of rookery size between years and with regard to the surrounding land cover types. We then tested for differences between the arc sine square root of the proportional area of the different land use category types within 500 m, 1000 m and 2000 m of the rookeries and of the generated random points in the two survey years using ANOVA and generalised linear mixed models to perform an analysis of the relationship between land cover around rookeries (response variable) and distance class, year, colony size (pairs) and colony-id (explanatory variables). (2) The percentage Urban and Agriculture land covers were inversely correlated ($r = -0.49$ in 1991; $r = -0.69$ in 2021), suggesting some statistical (linear) dependency between the two. Hence, we compared the extent of Urban and Agriculture within the distance categories in separate generalised linear mixed models to test whether the extent of Urban had increased and that of Agriculture decreased around rookeries between 1991 and 2021. We entered distance, year and colony size as fixed effects and colony-id as random effect into the models. The interaction between distance class and year was insignificant for all habitats and therefore omitted in the final models and no multicollinearity among the explanatory variables were detected (variance inflation factors were far below 5 *sensu* O'Brien (2007)). (3) We compared the extent of Urban and Agriculture within the distance categories with those of random points to test whether rooks selected for Urban and avoided Agriculture and for differences between 1991 and 2021. (4) We compared the extent of Urban and Agriculture with increasing distance to rookeries to test for selection for Urban and Agriculture against the expectation that Urban would decrease with increasing distance from rookeries and Agriculture would increase if rooks select for Urban and avoid Agriculture, while there should be no difference in these properties with distance from random points. (5) Finally, we compared the extent of Forest and Grass within the distance categories from rookeries to test whether rooks selected for Grass (despite its rarity in the landscape) and avoided Forest as we predict, but show little other selection/avoidance

We used R version 4-2-1 (R Core Team 2022) and lme4 (Bates et al. 2015) and lmertest (Kuznetsova et al. 2017) for the mixed model analyses.

Table 1 Overall changes in number of rookeries and in the total numbers of nests counted in the East Jutland study area in 1991 and 2021

	1991	2021	% Difference
Number of rookeries	95	133	40
Number of nests	10,299	10,887	6
Median colony size (Inter Quartile range)	70 (163.5)	25 (93)	-64

Results

(1) Overall, the total number of rook nests detected in the two years increased by 6% from 10,299 in 1991 to 10,887 in 2021. In 2021, breeding birds were distributed between many more, inevitably smaller, rookeries than in 1991 (Table 1; Fig. 3). There was a significant difference in rookery size class distribution between 1991 (Median (Inter Quartile range) = 70 (163.5)) nests and 2021 (25 (93); $W = 8055.5$, $P < 0.001$) and the rookery size class distribution differed significantly between the two years ($\chi^2_3 = 38.0$, N = 230, $P < 0.001$), due to greater numbers of small (1-25 and 26-50 nests) rookeries in 2021, and fewer rookeries of 51-100 nests (Fig. 3).

(2) The generalised linear mixed model fit showed that the proportion of Agriculture land cover around rookeries varied significantly with distance, year and rookery size. This supported the hypothesis that there was less Agriculture within the various distance classes from rookeries in 2021 than in 1991; in both years, Agriculture increased with increasing distance from rookeries (Fig. 4, Table 2). Likewise, the model fit for the proportion of Urban land cover varied significantly with distance, year and rookery size. This supports the hypothesis that there was more Urban within the various distance classes from rookeries in 2021 than in 1991 but in both years, Urban decreased with increasing distance from rookeries (Fig. 4; Table 2). There were no significant differences between the proportions of Urban and Agriculture with increasing distance from the random points (Fig. 4). (3) Comparing the extent of land cover types within a given distance of rookeries with those from random points showed that in 1991 rooks selected for Urban and tended to avoid Agriculture and Forest relative to that expected by chance (Fig. 4; Table 3 and see Supplementary Material Table S2 for full statistical support). This difference was even greater in 2021. Rooks significantly selected Grass over its availability in 2021. The lack of a similar relationship in 1991 is likely to be an effect of the reduced resolution of Grass in the land cover data from 1991. (4) The proportion of Urban area increased and that of Agriculture decreased significantly with increasing distance from the rookeries in both years. In contrast, there were no differences between distance categories among random points for Urban (ANOVA $F_{2,1497}$ = 2.78, $P > 0.05$) nor Agriculture ($F_{2,1497} = 0.38$, $P >$ 0.05; see Fig. 4, Tables 2 and S3 for full statistical report).

(5) Rooks avoided nesting in Forest in 2021, but only within 2000 m in 1991 (Table 3); they also selected for more Grass than expected by chance (Table 3) in 2021 and the proportion of Grass declined significantly from 500 m out to 2000 m around rookeries in that year (Table S2). However, because of the problems of Grass classified as other habitats in 1991, we cannot draw any firm conclusions for that year (Tables 3 and S1). Statistical comparisons between the percentage cover of all land cover types (excepting Grass because of the underestimation of this area in 1991) showed significant increases in the area of Urban and significant decreases in Agriculture within 500 m of rookeries located in rookeries of 1-25 nests between 1991 and 2021. There was also significantly more cover of Other land cover among rookeries of 51-100 nests and less Forest among rookeries of 26-50 nests compared to expected, while no other comparisons attained statistical significance (Fig. 5; see Table S4 for data and statistical tests).

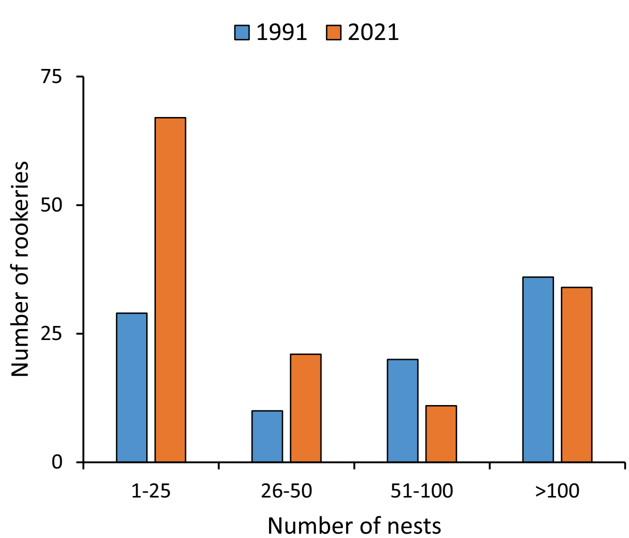

Fig. 3 Rookery size (number of nests) frequency distribution as recorded in the study area in 1991 (n=95) and 2021 (n=133)

Discussion

In our east Jutland study area, overall nest numbers increased by only 6% from 1991 to 2021, but rookeries numbers increased by 40%, because of the increase in numbers of small rookeries in urban areas. In another study covering Aarhus Municipality (the area with the largest city in this study, Fig. 2C) the mean number of nests per rookery halved from 90 in 1984/85 (Ettrup 1986; Tofft 1986) to 43 nests per rookery in 2021, while the number of rookeries

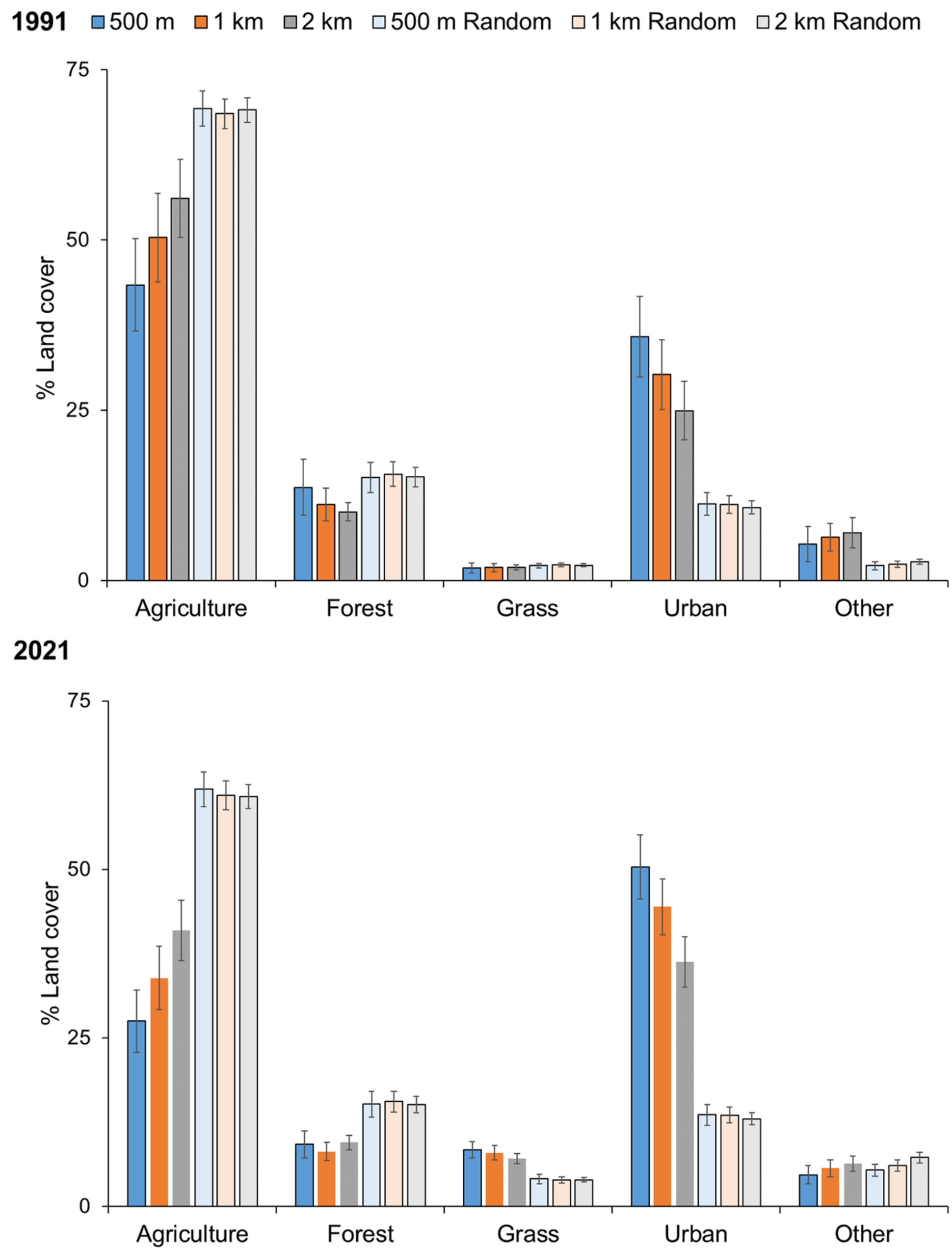

Fig. 4 Mean percentage land cover area of the five main land cover types (in % ± 95% CI) within 500 m, 1000 m and 2000 m radius around colonies in 1991 (upper) and 2021 (lower) compared to the same values generated from 500 random points within the study area within the same radii

increased from 13 to 49 in the same period This result alone implies an increase in the potential nuisance levels in urban areas close to newly established rookeries, just by virtue of more rookeries, despite only a modest increase in overall total number of nests. We also showed that the proportion of urban land cover within 500 m of rookeries

Table 2 Result table for generalised linear mixed models fitted to rookery data showing the relationship between the arcsine square root transformed proportions of land cover around rookeries and distance class, year and colony size. Data for other land cover types are provided in Supplementary Material Table S3

Land cover type	Explanatory variable	Estimate ± Std.Err	t-value (df)	Pr(>|t|)
Agriculture	(Intercept)	0.569 ± 0.034	16831 (414.1)	<0.001
	Distance	0.0001 ± 0.000007	14808 (462.6)	<0.001
	Year2021	-0.145 ± 0.030	-4890 (674.2)	<0.001
	Pairs	0.0004 ± 0.0002	2616 (343.9)	0.009
Urban	(Intercept)	0.716 ± 0.029	24923 (411.1)	<0.001
	Distance	-0.00009 ± 0.000009	-10212 (460.2)	<0.001
	Year2021	0.106 ± 0.028	3855 (518.4)	<0.001
	Pairs	-0.0004 ± 0.0001	-3215 (272.7)	0.001

Table 3 Comparison of the direction and statistical significance of comparing the percentage extent of each land cover type within an area 500 m, 1000 m and 2000 m out from all rook colonies compared to those within the same distance out from random points. "Less" indicates less of the land cover type within each given distance from the rookeries compared to random points; "More" indicates the opposite. *** indicates significant differences based on ANOVA tests between the population means at $P < 0.001$, * at $P < 0.05$ and ns indicates not significantly different. Full details of all tests are provided in Supplementary Material Table S4

Distance from rookery/random point	Year	Statistical comparisons between means of each of the land cover types within 500 m, 1000 m and 2000 m of rookeries and those of randomly selected points				
		Agri	Forest	Grass	Urban	Other
500m	**1991**	less***	ns	ns	more***	more***
1000 m	**1991**	less***	ns	ns	more***	more***
2000 m	**1991**	less***	less*	ns	more***	more***
500 m	**2021**	less***	less*	more***	more***	ns
1000 m	**2021**	less***	less***	more***	more***	ns
2000 m	**2021**	less***	less***	more***	more***	ns

increased and agricultural land decreased across all rookeries between 1991 and 2021. This was not the result of increased urbanisation of agricultural land, although this will have contributed on a very minor scale (agricultural land area within 2 km of the random points fell by 8.3%, while the area of urban increased by 2.1% between the two

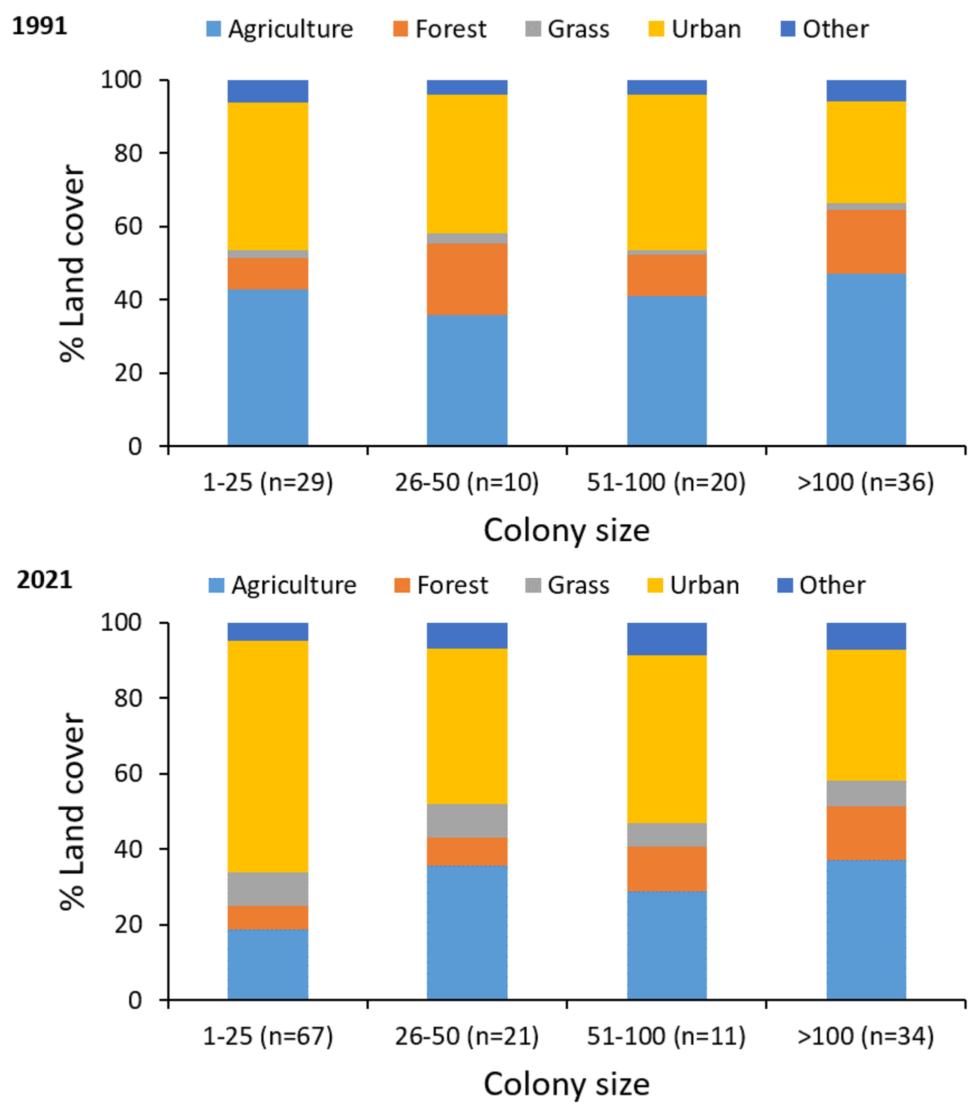

Fig. 5 Percentage of land cover types within a radius of 500m from rookeries in East Jutland in 1991 (upper) and 2021 (lower) for different colony size classes. Note that the percentage of Grass is not comparable between years because the classification of this category was less rigorous in 1991 compared to 2021

periods). Rather, this change resulted from rooks actively abandoning rural rookeries and moving to smaller rookeries in urban habitats (as clearly visible around Aarhus city and surrounding suburban area, compare the very centre of the coverage in Fig. 2A, B). Compared to land use within the same distance of random points, rooks selected for urban land cover and avoided agricultural land in both years, showing an increasing selection for urban areas and a decreasing use of agricultural land between the two periods. Furthermore, we found declining urban land cover and increasing agricultural land cover with increasing distance from rookeries out to 2000 m, whereas there was no change with distance among random samples. We found limited support for our prediction that rooks avoided constructing rookeries in forests at all times. Because of difficulties associated with differences in grassland classification in 1990, we cannot assess changes between years in this land cover in relation to rookeries in that year. However, in 2021, rooks showed selection for grass over its availability based on random points and showed declining cover with increasing distance from rookeries, indicating selection for this land cover type (despite its rarity in the landscape).

In interpreting these results, it is important to remember that smaller rookeries are more likely to be overlooked than the larger ones, so we cannot reject the suggestion that this may have led to underestimation of true numbers of rookeries and breeding pairs. However, to our best judgement there was no difference between 1991 and 2021 in the risk of having overlooked rookeries (since some authors and several volunteers took part in both survey years).

Despite these minor concerns, we remain confident that during 1991-2021, when public complaints and publicity about rookery noise in Denmark have markedly increased, nesting rooks increasingly moved from rural into urban areas in east Jutland, a trend reported from many other areas of Europe since the 1970s (e.g. Glutz von Blotzheim and Bauer 1993, Heckenroth and Zang 2009, Chmielewski et al. 2017). In Lower Saxony, this has been blamed on continued illegal persecution of nesting rooks in the countryside in a way not possible in built-up areas (Krüger et al. 2020). In our study (1991 to 2021), rooks in urban areas built more rookeries of smaller average size than formerly the case in rural areas. The trend for more, smaller rookeries in urban areas and fewer colonies on agricultural land has been identified in many other countries, thought to result from persecution on agricultural land which "splits" nesting birds displaced from disrupted rookeries into colonising more new sites elsewhere (see Fallet 1978; Porter et al. 2008; Kitowski 2013; Chmielewski et al. 2017; Krüger et al. 2020). In our study area, whatever their cause, these two processes resulted in more people being affected by the noise (due to proximity of more rookeries in residential areas) and smaller rookery size, implying greater breeding fragmentation that expands the geographical impact and overall frequency of conflict. In addition, Rooks have been spectacularly successful in adapting to exploit feeding opportunities presented by the extensive availability of short grassland available in urban environments that provide their invertebrate food (e.g. Jadczyk and Drzeniecka-Osiadacz 2013), especially during the breeding season (Benmazouz et al. 2021), which has undoubtedly contributed to the success of colonising these novel areas.

So why the shift in nesting distribution from countryside to city? Obviously, there are likely multiple fitness benefits to the individual from making the transition, but the relative importance of deteriorating conditions in the rural environment versus increased benefits associated with breeding in urban areas is likely to vary from site to site. Many authors have speculated on these factors, summarised for many Corvid species by Benmazouz et al. (2021), most of which can be gathered under the following headings:

Human proximity Differential disturbance levels (especially human persecution and hunting pressure) inside and outside urban areas could potentially influence settlement in an area, rookery size, rookery fate, as well as individual breeding success and survival (Sorace 2001, Vuorisalo et al. 2003; Kövér et al. 2018). In the Netherlands, for example, in the five years up to 2004, stable population size did not stop an increase in numbers of rookeries (inevitably of smaller size), attributed specifically to illegal disturbance at large rookeries causing the establishment of smaller satellite rookeries in the neighbourhood (Schoppers 2004). Declines in the Dutch national breeding population are also attributed to renewed persecution of the species there (SOVON 2018). "Unrestrained" persecution (shooting, poisoning, destruction of nests and clutches) explained a 93% decline in rook abundance between 1898 and 1976 in NW Germany and the recovery since that time under legal protection (Krüger et al. 2020). As discussed above, active persecution of nesting rooks has also been blamed in many countries for the movement of rookeries from the countryside into urban areas and for the fragmentation of fewer large rookeries into more, smaller rookeries (see Praus 2015; Krüger et al. 2020).

Declining availability of short grazed grass in agricultural land landscapes Rooks habitually select for feeding on fertile short grassland across Europe, especially in summer (e.g. Reid 1984; Rolando et al. 1998; Mason and Macdonald 2004; Gimona and Brewer 2006). Declines and fragmentation in the overall area of this habitat in the agricultural mosaic are frequently cited as contributing to declines in local rook nesting abundance (e.g. Orłowski and Czapulak 2007). In eastern Poland, breeding success of rooks increased with area of spring cereals, meadows and pastures in the vicinity of rookeries, but decreased with winter cereal and root crop extent (Kasprzykowski 2007). In Denmark, the area of spring cereals declined dramatically between 1975 and 1995 with the switch to winter cereals, while permanent grassland has been declining since the 1960s as more cattle are kept indoors, rather than grazing outside (Fox 2004; Heldbjerg et al. 2016). These trends coincide with the changes in relative habitat use (declining agricultural use, increasing urban use) during 1976-1995 by rooks during the breeding period. Since 1995, the relative habitat use has been stable (Common Bird Monitoring programme; Daniel Palm Eskildsen in litt.). In contrast, urban areas often provide a rich mosaic of habitats that include continuously managed fertilized short grass (in the form of football fields, road grass verges, garden lawns, etc.), perfect for foraging rooks (Pithon et al. 2021). The complex and fragmented mosaic of grassland presented by urban landscapes could also potentially favour the development of smaller rookeries, which have their own advantages (see below).

Differential breeding success between rookeries in urban and agricultural areas Reproductive output may be greater in urban habitats compared to that in rural areas, although the causes of this are not clear and could vary between rookeries (e.g. Frankhauser 1995). Unfortunately, this aspect would be impossible to investigate at most Danish rookeries, given that a very large (but unknown) proportion of these are subject to regulation by shooting.

More and diverse nesting sites in urban environments Although the highly diverse agricultural landscapes of Europe are often characterized by extensive areas of open fields dedicated to grass or other crop production, they are inevitably broken up by field boundaries, copses, wood edges and farmyards, where trees can establish and offer nest sites for rooks. However, urban and semi-urban environments offer as many if not more dense, varied and complex nesting opportunities through the network of parks, cemeteries, wood lots, allotments, avenues and single trees provided in close proximity to grasslands (Vuorisalo et al. 2003; Benmazouz et al. 2021). Rooks have also learned to exploit extraordinary novel nesting sites in urban areas, such as electricity pylons at a city power station (Chmielewski et al. 2017) and church towers (Cramp and Simmons 1994).

Fewer predators/parasites in urban areas Some individual large birds of prey such as Eurasian Eagle Owl *Bubo bubo* and Northern Goshawk *Accipiter gentilis* specialize on taking rooks in the breeding season (e.g. Laursen 1999; Hoy et al. 2017; analysis of pellets from an Eurasian Eagle Owl nest in central Jutland Denmark was composed almost exclusively of rooks, P. Sunde pers. comm.). While Northern Goshawk is not a common species of suburban and urban areas, Eurasian Eagle Owl can occasionally breed in built-up areas (including the town of Grenå within this study area; Vikstrøm and Moshøj 2020), potentially negating benefits of reduced predation in urban areas. Red Squirrels *Sciurus vulgaris* which can be a serious and persistent predator of rook eggs (Reppe 2020) are more common in forest than in urban areas, but less numerous in agricultural land in Denmark. Disease and parasite transmission are also considered as potential disadvantages of colonial nesting (Vuorisalo et al. 2003; Benmazouz et al. 2021). Very high losses of young rooks in the week after hatching in some years (not considered due to predation/cannibalism) is not thought due to parasite infestation or disease, even in large dense rookeries (e.g. Lockie 1955), but are rather thought to be caused by variations in other food items (Owen 1959, Holyoak 1967, Purchas 1979). We therefore lack evidence that there are benefits to avoiding predators, disease and/or parasites to be gained from moving into urban areas, but this remains a possibility.

It is assumed that rooks gain advantage from nesting in close proximity in dense colonies, because the earliest breeders (generally those most experienced, Patterson and Grace 1984) chose to nest highest in trees with most (old) nests (Rytkönen et al. 1993). Clutch size also correlates with tree nest density, although with no effect on numbers of young produced (Rytkönen et al. 1993). However, it may be the case that the transition from larger to smaller rookeries also has potential fitness costs and/or benefits. Factors potentially affecting the decision to move from large dense rookeries to smaller often more dispersed rookeries include:

Lack of available suitable nesting trees Lack of trees or suitable nest sites in urban areas could potentially limit rookery size, despite the advantages of colonial breeding, e.g. if the only nesting trees available are avenues of individual trees close to foraging areas, these may be acceptable as nest sites in the absence of anything else.

Avoiding competition In urban situations with a highly fragmented food supply, it may be advantageous to nest at lower densities thereby reducing the risk that breeders in some periods of the breeding cycle are forced to travel far to find suitable foraging sites.

Founder effects Despite the tendency to natal site fidelity, rookery attractiveness seems to affect rates of return between years (Patterson and Grace 1984). Younger rooks are restricted to the periphery of established rookeries and lay later, smaller clutches and hatch fewer nestlings than older birds (Røskaft et al. 1983). Smaller, less stable rookeries may have been founded by young inexperienced individuals, but there is little evidence in the literature to support this hypothesis.

Avoiding costs of high nesting densities Smaller rookeries may enable individuals to escape consequences of high nesting densities (e.g. high parasite/disease transmission rates, interference from neighbours, cannibalism and/or predation) associated with large rookeries.

Clearly, many of these factors could act in isolation or in concert to affect the shift from large rural rookeries to increasingly more, smaller urban rookeries. However, we consider that it will take further investigation of the individual responses of rooks from colonies of different size and along the gradient from urban to rural landscapes to determine their importance. We are also in the process of analysing long term data relating to annual rookery size in smaller study areas to look more closely at the flux of establishment of new rookeries balanced against the extinction of other rookeries on an annual basis in well-studied areas to establish potential causes of these changes. We also wish to embark on studies of how site-specific persecution of rookeries can affect subsequent dispersal rates to colonise new rookeries in the vicinity, potentially including monitoring of manipulated control at observed rookeries with marked individuals to see how rooks react at the individual and rookery level to targeted disruption.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11252-023-01372-6.

Acknowledgements We thank all the volunteers who supported this project with fieldwork for their major contribution by counting rookeries in 1991 and 2021, especially to Allan Janniche for his enormous contribution, to DOF (the Danish BirdLife International Partner) for their partnership in the project, and an anonymous referee for valuable comments and suggestions.

Authors contributions OTH secured the funding for the project and with HH, TB and ADF conceived the study. CLP carried out all GIS analyses, HE, JK, TB and TV all organised and participated in data collection, HH carried out the statistical analyses, ADF led on writing the manuscript aided by HH, which was read and improved by all co-authors, all of whom gave final approval for publication.

Funding Open access funding provided by Royal Danish Library. This project was co-funded by the Danish Environmental Protection Agency and Aarhus University, neither of which had any influence over the work or the conclusions flowing from the study and support the publication of the results in this form.

Data availability The datasets and R scripts generated and analysed here are available on reasonable request from the corresponding author.

Declarations

Conflicts of interest We declare we have no conflicts of interest and no competing interests.

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