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Research article

Breeding site fidelity in the concrete jungle: implications for the management of urban mallards

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Abstract

Understanding the selection of breeding sites in cities is key for the effective management of urban bird populations. We analysed 16 years of data collected within a relocation program for female mallards in Berlin (Germany), with the goal of (i) characterizing the breeding output and breeding sites in urban environments, (ii) identifying factors correlating with probabilities of individuals to return to previously used breeding sites (i.e. breeding site fidelity) and (iii) assessing the consequences of ongoing management strategies on the selection of breeding sites. Mallards using anthropogenic structures for breeding primarily chose balconies, roof terraces and courtyards. In 22.8% of cases, mallards selected the same sites in subsequent breeding events. Breeding site fidelity decreased with higher human population density at that location, and decreased as mallard families were relocated further away from the breeding site to a suitable water body. In contrast, return probabilities were higher for subsequent broods within the same breeding season than across two successive seasons. Above all, the identity of the breeding location and the identity of the female best predicted whether an individual would return to a given breeding site. We conclude that breeding site fidelity in urban mallards is strongly shaped by micro-scale location-specific properties (e.g. balcony characteristics), as well as individual variation due to an intrinsic propensity for site fidelity. We argue that adequate management for waterfowl in urban environments depends on why birds choose to breed on anthropogenic structures, on their conservation status and the availability of breeding sites around urban waters.

Keywords: breeding site; mallard duck; breeding ecology; managment; urban ecology

Introduction

The expansion of urban areas and the associated transformation of natural ecosystems is happening extensively around the world (United Nations, Department of Economic and Social Affairs PD 2015, Santangelo et al. 2018). For wildlife, urbanization represents a variety of challenges: it can affect fundamental environmental properties such as access to food sources (Reynolds et al. 2017), noise level (Sierro et al. 2017) and risk of predation (McKinney 2002, López-Flores et al. 2009). For birds in particular, the availability of suitable breeding habitat is one of the most critical factors limiting the successful colonization of urban environments (Reynolds et al. 2019). Urban birds must be able to nest near people, on anthropogenic structures, and away from traffic, which can cause high levels of noise and represents a serious risk of fatalities to them (Brown and Brown 2013, Mainwaring 2015, Liordos et al. 2021). Even for birds that can tolerate these sources of disturbance or cope with associated risks, the choice of breeding sites in urban landscapes may represent a so-called 'ecological trap' (Schlaepfer et al. 2002), whereby the response of organisms to novel environmental clues leads to a reduction in survival and/or reproduction (Sherley et al. 2017, Krams et al. 2021).

Here, we focus on the mallard (*Anas platyrhynchos*)—an emblematic species that, over the last century, has increasingly populated urban environments (Engel et al. 1988, Hallau and Otto 2005, Meissner et al. 2015, Yetter et al. 2018, Jarman 2019). Urban mallards are frequently observed breeding on anthropogenic structures, such as balconies or rooftop terraces (Rutschke 1990, Hallau and Otto 2005). In the absence of rescue interventions, the choice of such breeding sites is generally maladaptive and can therefore correspond to an ecological trap: once hatched, ducklings cannot escape breeding sites, exposing them to a high mortality risk due to starvation or predation (e.g. by crows, gulls or cats). For now, local animal conservation organizations in multiple large cities in Europe and North America try to alleviate the costs of these choices of breeding sites by providing guidance or service for relocating mallard families to an adequate body of water. These initiatives are often motivated by a desire to improve the mallards' welfare, but also contribute to mitigating human-wildlife conflicts and to ensuring the sustainability of urban mallard populations.

Recent research has focussed on the survival (Figley and VanDruff 1982, Engel et al. 1988, Yetter et al. 2018), behaviour (Hallau and Otto 2005, Baratti et al. 2009), physiology (Jarman et al. 2020), feeding ecology (Polakowski et al. 2010, Jarman 2019) and diseases (Meissner et al. 2015, Wille et al. 2017) of mallards

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in urban habitats. There is little research on their selection of breeding sites in such environments, the fitness consequences of alternative breeding sites and the effect of possible management strategies on the breeding fidelity of mallards. In other species, multiple factors have been identified to cause birds breeding on anthropogenic structures, including an increased access to anthropogenic food sources and protection from predators (Soh et al. 2002, Møller and Díaz 2018). Understanding which of the various incentives drive mallards to nest repeatedly on anthropogenic structures, what the consequences for offspring survival are and how interventions can influence breeding success should be the basis of efficient management of urban mallard populations.

In this paper, we aim to analyse data collected on 1199 breeding events from 795 ringed individuals over 16 years (2005–20), as part of an ongoing relocation and ringing program in Berlin, Germany. We focus on (i) characterizing the breeding outputs (clutch size and brood size) and breeding sites of this population, (ii) investigating whether breeding site fidelity of urban mallards is shaped by external factors of the breeding environment or internal properties and (iii) evaluating potential effects of ongoing management strategies performed by NABU Berlin on the breeding behaviour of urban mallards.

Materials and methods

Study background and data collection

Data on breeding mallard ducks were collected by employees of the wild bird rehabilitation centre of the NABU Berlin e.V. (Nature And Biodiversity Conservation Union) between 2005 and 2020 in the German metropole of Berlin (Germany, N52.50343–N53.53618, E13.40114–E13.41122). Berlin is the capital of Germany and has a growing human population (currently estimated at 3.87 million people) in an area of ca. 900 km^2. The city landscape is very heterogeneous, with highly urban areas as well as a large network of green habitat islands of parks and cemeteries. Water bodies and streams account for ca. 6% (5.415 ha) of the city's total area (www.statistik-berlin-brandenburg.de, 2020).

The NABU Berlin rehabilitation centre provides year-round telephone consultation and in-field services for wild bird related topics. Between April and July, a large proportion of the wild bird station's capacity is dedicated to the relocation of mallard families (adult female and ducklings) from breeding sites located on anthropogenic structures to a suitable natural water body in order to ensure their survival. The strategy consists of (i) centralizing the reports of breeding events on anthropogenic structures at NABU Berlin, (ii) educating citizens on the breeding ecology of mallards, explaining the predicament and advising them on how to handle the breeding duck, and (iii) relocating those mallard families to suitable water bodies. After the hatching of ducklings is reported by citizens, the adult female and ducklings are captured by hand at the breeding site within 24 h by employees of the wild bird station and transported to a suitable body of water for release. At that point, ducklings are mobile enough to follow the mother. The water body is usually chosen as the nearest suitable lake or river, taking factors such as shore vegetation, water area and potential predators into account. In many cases, citizens reported from which direction the ducks approached the breeding site, which further helps NABU Berlin to select the appropriate water for relocation.

Out of 1634 breeding events recorded in urban habitats during the study period, a total of 1199 events correspond to 795 ringed adult females. For each of these latter events, breeding parameters related to the brood location (e.g. coordinates, type of location), biology (e.g. clutch/brood size) and biometry of the adult female (e.g. wing length, body mass) were recorded whenever possible. Because data on the height of the nest (floor level) was available for only 6% ($n = 100$) of breeding events, we disregarded this piece of information. All identified adult females were ringed once around the tarsus at the first relocation event with individually coded metal rings (size JC, inner diameter 11 mm) provided by the ringing scheme 'Radolfzell' (Germany). Subsequent recaptures allowed us to collect and compare data on multiple consecutive breeding events of the same individuals. The beginning of incubation was calculated based on the hatching date reported by the citizens and assuming a mean incubation period of 27 days until hatching (Rutschke 1990).

Type of breeding site and site fidelity

In order to disentangle whether the decision of a mallard to return to a previously used breeding site was based on past experience of environmental features, its previous breeding success, its individual propensity for site fidelity or local environmental effects, we examined a series of generalized linear mixed-effects models (GLMMs). These GLMMs predict the breeding site fidelity, i.e. the probability that an adult female returned to its previous breeding site, based on multiple predictors related to the previous breeding event.

Since our goal is to estimate the probability that an adult female returned to a previous breeding site, all GLMMs were logistic regressions (binomial family) fitted on a subset of the original data that considered only individuals with a minimum of two breeding records, resulting in 632 breeding events from the 228 identified adult females. We further selected only observations corresponding to the same or two consecutive breeding seasons, resulting in discarding 91 breeding events and 42 individuals. Indeed, repeated observations separated by more than one breeding season widely differed in how far apart they were in time, and the sparsity of these data precluded the definition of a meaningful category to model how such durations have impacted the return probabilities. The presence of observations associated with missing values for at least one of the predictors used for modelling resulted in discarding all records associated with six ducks. The resulting dataset used to fit the GLMMs contained 301 rows, and encompassed records from 481 reproductive events—including 180 first captures and 301 recaptures—from 180 adult female mallards.

We considered seven different classes of predictor variables as fixed effects in our models (Table 1): one class to describe the habitat type, one for the habitat structure, one for the human disturbance, one for the breeding success, one for applied management strategies and one for the breeding season. All quantitative variables among these predictors were normalized prior to model fitting using z-scores. The maximum Pearson's correlation coefficient encountered between them was $|r| = 0.65$, suggesting acceptable levels of collinearity (Dormann et al. 2013). We classified the habitat type into five different categories according to the breeding sites chosen by the mallard: roof terrace, balcony, courtyard, other (e.g. sills, pathways or basement entries) and unknown.

We obtained aquatic habitat structures in the study region from the Copernicus online database (https://land.copernicus.eu), including the distance to the nearest body of water suitable for breeding (DNSW) and the presence of such (PSW) within two buffer zones of radii 1000 and 2000 m around the breeding site (Table 1). We considered all LBM-DE CORINE Land Cover (CLC)

Table 1. Fixed predictor variables used to model the breeding site fidelity.

Class	Predictor variable[a]	Description	Source
Habitat type	Habitat type (qualitative, 5 levels)	Roof terrace, balcony, courtyard, other, or unknown	NABU Berlin e.V.
Habitat structure	DNSW (quantitative)	Distance to the nearest suitable water body[b]	Copernicus (2018)
	PSW (qualitative, 2 levels)	Presence (0/1) of suitable water body[b] within 1000 and 2000 m radius	Copernicus (2018)
Human-related disturbance	Traffic volume (quantitative)	Average daily road traffic volume (vehicles/24 h) within 500, 1000 and 2000 m radius	Geoportal Berlin (2019)
	Human population density (quantitative)	Average human population density (inhabitants/ha) within 500, 1000 and 2000 m radius	Geoportal Berlin (2021)
Breeding success	Brood size (quantitative)	Number of successfully relocated juveniles	NABU Berlin e.V.
Breeding season	Delta season (qualitative, 2 levels)	Same or two consecutive breeding seasons	NABU Berlin e.V.
Management strategies	Relocation distance (quantitative)	Distance between breeding site and release location	NABU Berlin e.V.

[a] All variables refer to the previous breeding event during the same or previous breeding season.
[b] Considering water features with a total area ≥0.39 ha.

classes of group G (watercourses, waterbodies, mud flat) as bodies of water, using a digital land cover model for Germany (LBM-DE 2018, multitemporal RapidEye and Sentinel2 ESA satellite imagery; 10 m pixel resolution). We defined bodies of water to be suitable for breeding whenever their total area was larger than 0.39 ha. We derived this threshold from ornitho.de, a Europe-wide online database of individual sightings of birds. Specifically, we extracted from this database all reported sightings of mallard ducks with offspring at water bodies of classes C11 (active nest) and C12 (fledged juvenile) between first and 30th of July 2021 within the study area. Only sightings of these two classes represent reliable proof that mallard ducks successfully bred at a given water body. Out of these observations, we then calculated the average area of the five smallest water bodies in order to represent a minimal water area at which mallards potentially breed and rear young (Supplementary Table S1), resulting in the threshold of 0.39 ha.

We integrated human-related disturbance indices for urban environments by accessing data on traffic volume and human population density through the online database Geoportal for the state of Berlin (https://www.berlin.de/umweltatlas/). To account for potential scale-dependent effects, we averaged values for each breeding site in a buffer zone with a radius of 500, 1000 and 2000 m, respectively, using the open-source geographical information system QGIS (2024, version 3.36 *Maidenhead*).

We also included breeding success in the previous breeding event as the brood size (e.g. number of relocated juveniles) and whether two consecutive breeding events happened within the same or two successive breeding seasons. This allowed us to characterize the breeding status and breeding season of mallards, respectively.

To analyse the effect of ongoing relocation strategies, we used the relocation distance (m) from the breeding site to the site of release of the previously recorded breeding event as a fixed effect. All distances between two coordinates were computed as the shortest great circle distance using the 'st_distance' function from the *sf* R package (Pebesma and Bivand 2023).

Lastly, we included the ring number and the identity of the breeding site (using the coordinates and habitat type, i.e. treating two balconies in the same house independently) as random effects—termed, respectively, individual ID and location ID—to account for individual as well as spatial variability not captured by the fixed effect terms. We also attempted to account for continuous spatial autocorrelation by including an autocorrelated random effect with the Matérn correlation function (Matérn 1960), but these more complex models did not fit observations better than the original model fits according to the conditional Akaike information criterion (cAIC; Vaida and Blanchard 2005). For the sake of simplicity, we therefore chose not to retain such parametrization.

Using R standard notation, the formula for the full model considered was therefore:

$$\begin{aligned}\text{return} \sim\ & \text{habitat\_type} + \text{habitat\_structure\_previous} \\ & + \text{trafficvolume\_previous} + \text{populationdensity\_previous} \\ & + \text{brood\_size} + \text{delta\_season} + \text{relocation\_distance} \\ & + (1|\text{individual\_ID}) + (1|\text{location\_ID}),\end{aligned}$$

where the suffix '_previous' indicates that the predictors are defined by the characteristics of the breeding site during the previous capture (irrespective of whether or not the adult female returns to the same breeding site).

Statistical analysis

We fitted 27 GLMMs because we considered all possible combinations between three alternative predictors for habitat structure (DNSW, PSW1000, PSW2000), as well as three alternative predictors for both traffic volume and (human) population density as these variables can be defined at three different spatial scales (radius of 500, 1000 or 2000 m; see above). To identify predictors leading to the best goodness of fit among these 27 alternative representations of the full model, we selected the model fit yielding the highest likelihood. This procedure is appropriate given that the alternative models all shared the same number of parameters and were all fitted on the same data. All GLMMs were fitted using the function *fitme* from the R package *spaMM* (Rousset and Ferdy 2014) version 4.5.0 and setting the link function to 'logit' and the fitting method either to PQL/L or to PQL. The latter differs from the former by a form of restricted likelihood (REML) correction and is therefore more suitable for estimation and testing of random effect variances, while PQL/L must be used for fixed effects. We explored model assumptions by checking plots of residuals simulated via parametric bootstrapping using the R package *DHARMa* version 0.4.6 (Hartig 2022).

We tested the significance of variables in the selected full model using parametric bootstrap as implemented by the function *LRT* from *spaMM*. Specifically, we relied on 1000 bootstrap replicates to build the distribution of the test statistic of each Likelihood Ratio Test (LRT) under the null hypothesis. In one case, we increased the number of bootstrap replicates to 100,000 to obtain a more accurate estimate of the *P*-value. For each LRT reported below, we indicate if the underlying models were fitted using PQL or PQL/L using the abbreviation $\mathrm{LRT_{PQL}}$ or $\mathrm{LRT_{PQL/L}}$. We also compared the predictive power of nested models based on both the conditional and marginal AIC (cAIC and mAIC; Vaida and Blanchard 2005), as well as on Tjur's *D* (Tjur 2009). Tjur's *D* reflects the average difference between the predicted probabilities for individuals to return to the previously occupied breeding site between individuals that did return and individuals that did not. The predictive power increases with increasing *D* and can take values between 0 and 1. Tjur's *D* metric is simple to compute and interpret, but it evaluates the predictive power of a model based on the very data that was used to fit this model. Therefore, models overfitting the data can provide the illusion of having a strong predictive power in the light of this metric. The cAIC and the mAIC are more robust to overfitting by design. The mAIC is Akaike's original AIC. When applied on a mixed-effect model, it quantifies the ability of the model to predict future data depending on new realizations of the random effects. By contrast, the cAIC quantifies the predictive ability of future data conditional on the same realizations of the random effects as in the fitted data. The cAIC is thus a metric favoured when the goal is to identify the model best predicting the behaviour of already observed ducks given the already observed breeding sites. The mAIC is instead favoured when the goal is to identify the model best predicting the behaviour of new ducks in a landscape composed of new breeding sites. Wildlife management applications therefore fall somewhere in the middle of these two hypothetical scenarios, which is why we chose to rely on both metrics. To express the predictive power of the models based on the AIC metrics, we calculated ΔcAIC (ΔmAIC) as the difference of cAIC (mAIC) for each model and the model with lowest overall cAIC (mAIC).

Data processing and statistical analyses were all performed in R version 4.4.1 (R Core Team 2024). The data and code used in this publication are available in the form of a dedicated R package—mallaRd—which we created to promote transparency and reproducibility. The package is available on GitHub (www.github.com/courtiol/mallaRd) and Zenodo (https://zenodo.org/records/14397939). To summarize results, we used the 'gradual language of evidence' detailed in Muff et al. (2022).

Results

Breeding outputs

Between 2005 and 2020, NABU Berlin personnel relocated a total of 1634 mallard families (i.e. mothers and their ducklings) from inapt urban breeding sites to suitable waters in Berlin. The distribution of biometric parameters is displayed in Supplementary Fig. S1 and summarized in Table 2.

Table 2. Summary statistics for the biometric measurements from adult female mallards and breeding events observed in urban habitats between 2005 and 2020.

Biometric parameter[a]	Mean ± sd	Range (min–max)	Number of breeding events	Number of adult female mallards
Clutch size	8.65 ± 2.29	1–17	1238	711
Brood size	6.98 ± 3.13	1–15	1621	790
Body mass (g)	817 ± 66.1	520–1030	1140	754
Wing length (mm)	264 ± 7.61	226–287	1162	773
Hatching day (doy)	147 ± 23.4	61–207	1411	771

[a] The following biometric parameters were recorded: the number of eggs (*clutch size*), the number of ducklings (*brood size*), the body mass of the adult female mallard (*body mass*), the wing length of the adult female mallard (*wing length*), and the distribution of the hatching date as measured by the number of days between hatching and January first (*hatching day*).

Type of breeding site

Female mallards preferentially chose to build their nest in three different urban breeding habitats (Fig. 1): roof terraces (29.6%, $n_{\text{breeding events}} = 484$, $n_{\text{adult female mallards}} = 267$), balconies (32.7%, $n_{\text{breeding events}} = 535$, $n_{\text{adult female mallards}} = 319$) and courtyards (23.9%, $n_{\text{breeding events}} = 390$, $n_{\text{adult female mallards}} = 220$). Other types of breeding habitat, e.g. windowsills, pathways or basement entries accounted for only 4.4% ($n_{\text{breeding events}} = 72$, $n_{\text{adult female mallards}} = 37$) of all records. No data on the type of breeding habitats was available for 9.4% ($n_{\text{breeding events}} = 153$, $n_{\text{adult female mallards}} = 16$) of all breeding events.

Breeding site fidelity

Out of the 795 adult ringed female mallards recorded, 228 were observed multiple times, demonstrating that at least 28.7% of the ducks selecting anthropogenic structures as breeding sites did so more than once in their lives. The number of times ducks were recorded to breed in urban habitats ranged from 1 to 13 (mean ± SD = 1.51 ± 1.11; Fig. 2A). Among the 228 ducks recorded to have used anthropogenic structures as breeding sites more than once during the study period, 52 (i.e. 22.8%) of them were observed to have used the exact same breeding sites at least twice. The distribution of the maximum number of times each given female mallard reused the exact same breeding sites, within the same or the following breeding season, shows that some birds were particularly faithful in their breeding site selection (Fig. 2B). Out of the 863 breeding sites used by ringed individuals, 153 (i.e. 17.7%) breeding sites were used at least twice, and 64 have been occupied by at least two different adult female mallards.

To understand factors influencing the breeding site fidelity of adult female mallards, we ran 27 generalized linear mixed-effects models (GLMMs) predicting the probability that a mallard would return to a breeding site it previously occupied. These models do not differ in terms of number of parameters, only in terms of alternative proxies used to characterize predictors. For these alternative predictors, the model with the highest goodness of fit (hereafter referred to as *best full fit*), as measured by the likelihood (under a PQL/L fit), was one considering the presence of suitable water bodies within a 1000 m radius, the average daily road traffic volume within a 2000 m radius and the human population density within a 500 m radius (Supplementary Table S2). Most alternative parametrizations yielded a similar likelihood. Indeed, 19 out of the 27 models yielded a likelihood that did not significantly differ from the best full fit, as tested by a bootstrap procedure providing the distribution of likelihood ratios for samples simulated under each alternative model tested. In fact, all alternative parametrizations we considered were retained in at least one model within the set of best fitting models. This result demonstrates that the distinct proxies cannot be distinguished from those selected in the best full model on the basis of the

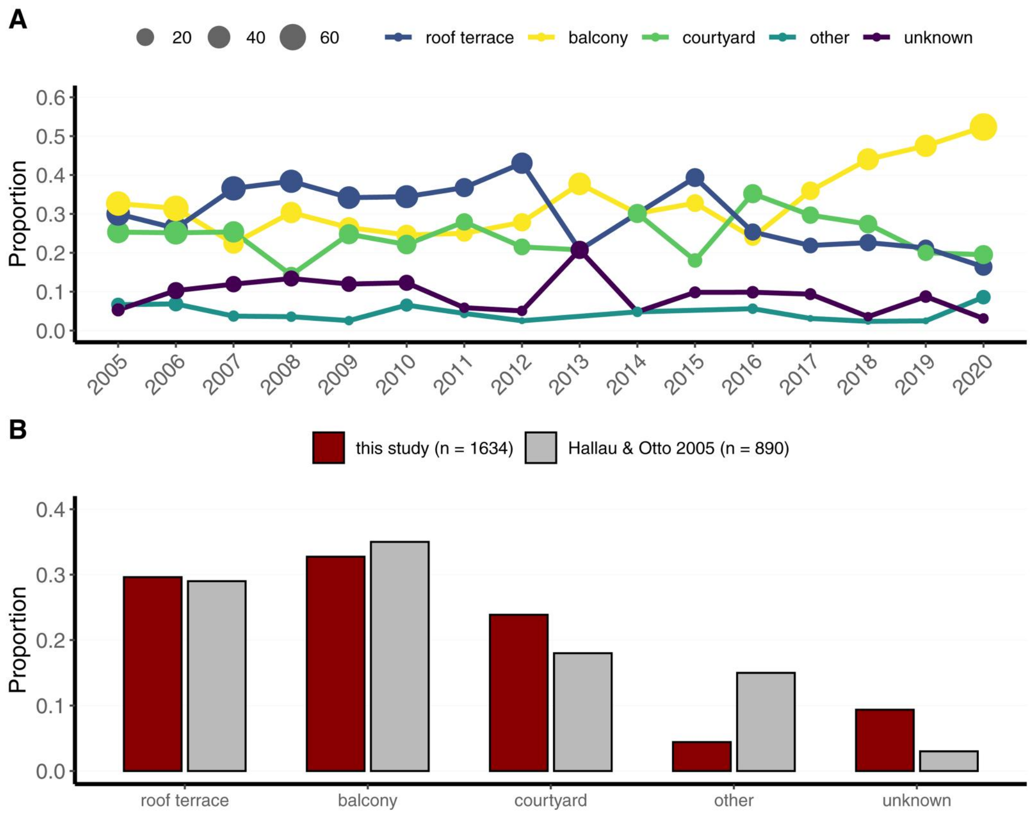

Figure 1. Usage of urban breeding habitats by adult female mallards. (A) Frequencies of types of urban breeding habitats selected by female mallards between 2005 and 2020. Colours depict the different types of habitats. Points depict the frequencies of observations within each year, with the diameter of each point being proportional to the number of observations for any particular year-habitat type combination. Lines connect points to help visualize temporal fluctuation. Data include 1634 breeding events from at least 795 different adult females. (B) Frequencies of types of urban breeding habitats from this study (2005–20, dark red) compared to a previous study in the same study region (1999–2005, light grey; Hallau and Otto 2005).

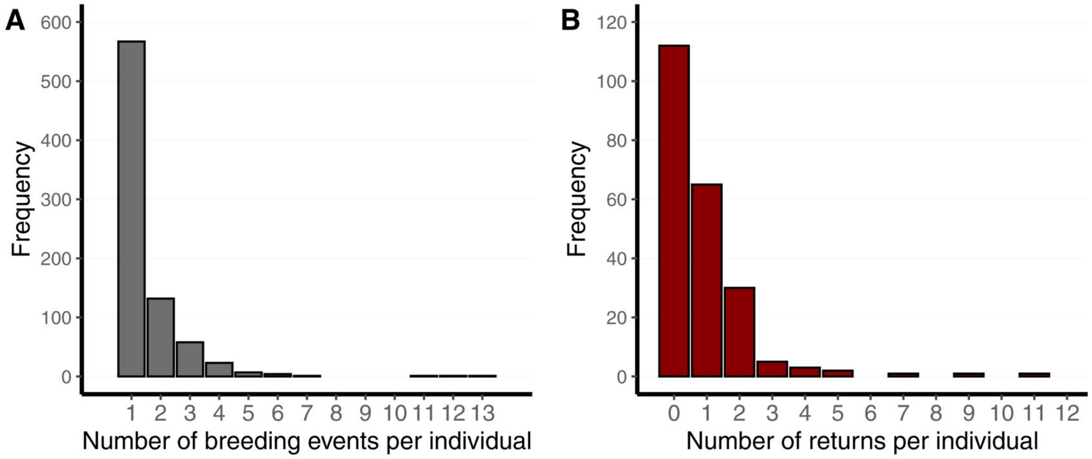

Figure 2. Distributions of captures and recaptures of adult female mallards breeding in urban habitats. (A) Frequencies of used anthropogenic structures selected per individual female mallards between 2005 and 2020. Data include 1194 breeding events at 863 identified breeding sites from 794 different ringed adult females with known breeding site locations. (B) Frequencies of returns to previously used breeding sites within the same or the following breeding season per individual female mallards between 2005 and 2020. For example, the value 3 on the x-axis corresponds to females that returned three times to their previously breeding site(s) during the study period. These three sites could correspond to the exact same location or to different ones. Data include 301 breeding events at 197 identified sites from 180 different adult females.

model predictions. The best full fit predicted breeding site fidelity significantly better than the fit of a model predicting the same probability of return for all breeding events (i.e. an intercept only model; LRT = 49, df = 11, $P < .001$). This was due to the improvement in likelihood stemming from both fixed effects ($\mathrm{LRT}_{\mathrm{PQL/L}} = 20$, df = 9, $P = .036$) and random effects ($\mathrm{LRT}_{\mathrm{PQL}} = 27$, df = 2, $P < .001$). All parameter estimates of the best full fit are provided in Table 3.

With respect to fixed effects, our best full fit revealed that two predictors were significantly negatively related to breeding site fidelity: the human population density within a 500 m radius ($\mathrm{LRT}_{\mathrm{PQL/L}} = 5.4$, df = 1, $P = .039$; Fig. 3A) and the relocation distance at the previous breeding event ($\text{LRT}_{\text{PQL/L}} = 4.3$, df = 1, $P = .043$; Fig. 3B). In the full dataset, human density around breeding sites varied between 0 and 295 humans per hectare (mean ± SD = 107 ± 62.6). In the reduced dataset used to fit the GLMMs, human density was similar and varied between 9 and 277 humans per hectare (mean ± SD = 109 ± 58.1). In the best full fit, each increase in human population density of 100 individuals per hectare resulted in the odds that an adult female mallard returns to the same breeding site to be multiplied by 0.479 ($\text{CI}_{95\%} = 0.311–0.739$).

Table 3. Model parameter estimates for the best full fit predicting breeding site fidelity of adult female mallards breeding in urban habitats.[a]

Fixed effects

Term[b]	**Estimate**[c]	**Cond. SE**[d]
Intercept[e]	0.235	0.441
Habitat type (courtyard)	−0.243	0.528
Habitat type (other)	−0.565	1.56
Habitat type (roof terrace)	0.0198	0.459
Presence of suitable water body (within 1000 m)	−0.0223	0.407
Traffic volume (within 2000 m)	−0.127	0.220
Human population density (within 500 m)	−0.427	0.221
Brood size	0.119	0.177
Delta season (same breeding season)	0.786	0.446
Relocation distance	−0.313	0.187

Random effects

Term	**Variance (λ)**
Individual ID	1.12
Location ID	13.3

[a] The model was fitted on a dataset including all required variables for 301 breeding events from 180 different adult females.

[b] All variables describe the context measured at the previous breeding event.

[c] Fixed effect estimates were obtained following a PQL/L fit and random effect variances following a PQL fit. All estimates are provided on the scale of the linear predictor. All predictors besides the habitat type were fitted after z-score transformation, so as to make estimates directly comparable across variables

[d] Standard errors for parameter estimates are displayed as conditional estimates.

[e] The intercept corresponds to the baseline where 'balcony' is the category for 'Habitat type', 'previous breeding season' is the value for 'Delta season' and 0 is the value for the other fixed effect predictors.

As a management strategy to ensure survival of the ducklings, families of ducks breeding in urban habitats were captured and relocated to a suitable natural breeding water. In the full dataset, relocation distances could be computed for 1192 breeding events. Such distances averaged 2.42 km (±3.74) and ranged between 31.0 m and 37.4 km. Most urban mallard broods (1072 or 90.0% of the total) were relocated within 5 km of the breeding site, and only a few broods (77 or 6.46%) were relocated more than 10 km away from the breeding site. The distribution of the subset of 301 relocation distances present in the reduced dataset used to fit the GLMMs was similar, with relocation distances recorded at previous breeding averaging 2.17 km (±3.30) and ranging between 82.1 m and 30.9 km. In total, 280 or 93.0% of urban mallard broods were relocated within 5 km of the breeding site and 14 or 4.65% relocated further away than 10 km. In the best full fit, each increase in the relocation distance at previous breeding of 5 km resulted in the odds that an adult female mallard returns to the same breeding site to be multiplied by 0.622 ($\text{CI}_{95\%} = 0.431–0.898$).

Beyond the effect of human population density and the relocation distance, there is also some evidence that breeding site fidelity increased when the focal breeding event followed a previous brood that happened during the same breeding season ($\text{LRT}_{\text{PQL/L}} = 4.0$, df = 1, $P = .045$; Fig. 3C). We found however no support for the influence of the habitat type ($\text{LRT}_{\text{PQL/L}} = 0.68$, df = 3, $P = .90$), the presence of suitable water bodies within a 1000 m radius ($\text{LRT}_{\text{PQL/L}} = 0.0013$, df = 1, $P = .97$), the average daily road traffic volume within a 2000 m radius ($\text{LRT}_{\text{PQL/L}} = 0.42$, df = 1, $P = .54$), or the breeding success in the previous breeding ($\text{LRT}_{\text{PQL/L}} = 0.69$, df = 1, $P = .42$).

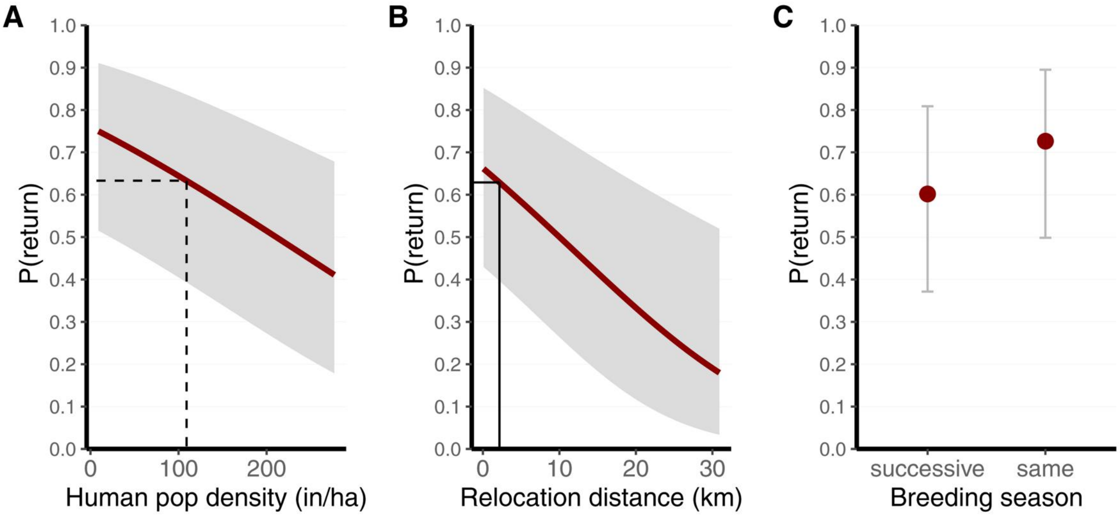

Figure 3. Effects of fixed effect predictors on the breeding site fidelity of adult female mallards breeding in urban habitats. Curves and points indicate model predictions for the effect of human population density (A), relocation distance (B) and breeding season (C). All predictions correspond to partial-dependence effects whereby the effect of a given fixed-effect variable is computed as the average of predicted values on the response scale, over the empirical distribution of all other fixed-effect variables in the data, and of inferred random effects. Grey areas and error bars indicate 67.45% intervals (expected to contain 50% of values, that is the so-called 'probable error') for such partial-dependence effects based on the prediction variance. Dotted lines mark predicted probabilities associated to the average value of the quantitative predictor variables in the dataset restricted to adult female mallards observed more than once. See Table 3 and its legend for details on model parameter estimates and sample sizes.

With respect to random effects, the best full fit revealed that the identity of the adult female duck ($\mathrm{LRT}_{\mathrm{PQL}} = 10.5$, df = 1, $P < .001$) and the identity of the urban breeding site ($\mathrm{LRT}_{\mathrm{PQL}} = 14.6$, df = 1, $P < .001$) have non-negligible variances. The comparison of the predictive power of alternative models nested within the full model described above showed the predictive power is highest when considering both fixed and random effects (Supplementary Table S2). Nevertheless, considering only the identity of the breeding site yielded a higher predictive power than the consideration of all the fixed effects mentioned above. This was true irrespective of the metric used to measure the predictive power (Tjur's *D*, mAIC or cAIC) and irrespective of the methods used to fit the mixed models (PQL or PQL/L). The consideration of the identity of the breeding site increased the predictive power more than the consideration of the identity of the adult female mallard (i.e. ring number), and models considering both random effects were generally superior to those only considering a single random effect.

Discussion

In this study, we describe the breeding outputs and breeding site selection, and analyse the determinants of breeding site fidelity for a population of mallards inhabiting a European metropolis. The study was motivated by the practical problem that, in Berlin, a large number of adult female mallards breed on anthropogenic structures which prompts NABU Berlin to organize and execute numerous rescue operations during the breeding period each year. This raised the question of why adult female mallards behave this way and whether the management of the urban mallard populations could be improved, as it requires NABU Berlin and other similar organizations worldwide to intervene at the cost of not being able to pursue other conservation-related activities. Moreover, not all breeding events on anthropogenic structures are observed and reported, and many ducklings probably die each year as the result of adult female mallards selecting such breeding sites. We discuss our results on breeding outputs, breeding site selection and breeding site fidelity, before drawing conclusion for the management of urban wildlife populations.

Breeding outputs

Mallard productivity is primarily dependent on two sequential events: the successful hatching of a clutch and the survival of ducklings until fledging (Amundson and Arnold 2011, Garrick 2015). Breeding at anthropogenic structures may affect these two components of the breeding success. Indeed, breeding on balconies and roof terraces might contribute to lower predation risk during incubation compared to breeding in natural sites, resulting in larger brood sizes (Roos et al. 2018, Holopainen et al. 2021, Wiegers et al. 2022). After hatching, on the other hand, the lack of access to a natural food supply or the inability to escape predators may lead to a higher mortality of juveniles (Chouinard and Arnold 2007, Amundson and Arnold 2011).

We found no comparable reports on average brood size for other urban mallard populations. However, according to our records, the average clutch size of mallards in Berlin is similar to those reported for an urban population in the USA (Oplinger 1977, Master and Oplinger 1984), but lower than that of semi-urban populations (Montgomery et al. 1975, Figley and VanDruff 1982, Supplementary Table S3). Compared to rural and natural habitats, our recorded clutch and brood sizes are also slightly lower than those reported for mallard populations in Europe (Eygenraam 1957, Master and Oplinger 1984, Wiegers et al. 2022), USA (Zicus et al. 2003) and New Zealand (Sheppard 2018). Unfortunately, data on the clutch and brood sizes of mallards breeding in natural habitats near our study area are lacking and we can not adequately assess the extent to which the breeding outputs are influenced by breeding in a natural vs. urban site within the same population.

Breeding site selection

In Berlin, adult female mallards select a diversity of anthropogenic structures for breeding, including balconies, roof terraces and courtyards. In general, the composition of these breeding sites does not seem to have changed for more than two decades, as the distribution of urban breeding sites we report for 2005–20 matches the one reported in a previous study for the same study region between 1999 and 2005 (Hallau and Otto 2005, see Fig. 1B). An exception is a recent increase in the number of breeding events recorded at balconies, which may reflect a change in breeding site availability related to the development of the city. The possibility that large numbers of adult female mallards also select anthropogenic breeding sites in other cities seems likely. Unfortunately, beyond a few reports of mallards breeding in ponds, tree trunks, wood piles and vegetation within towns and cities (Oplinger 1977, Figley and VanDruff 1982, Master and Oplinger 1984, Engel et al. 1988), studies addressing breeding site selection in urban mallards are lacking.

Breeding site fidelity

Despite, or perhaps because of, the close interaction between humans and ducks breeding on anthropogenic structures, our data reveal that many mallards reuse the same urban breeding site during their lives. The analysis of 301 recaptures provided very strong evidence for the role of individual and location specific effects, moderate evidence for the negative roles of the human population density and the distance between the breeding site and where mallard families were previously relocated, also moderate evidence for the role of the duration between two breeding events, and little or no evidence for all the other variables investigated (habitat type, habitat structure, traffic volume and previous breeding success).

The effect of human population density

We found that the higher the human population density around a breeding site, the less mallards were likely to return to it. This negative effect is likely related to an increased risk originating from human activities perceived by the mallards, as has been reported for other animals (Díaz et al. 2013, Møller 2015, Samia et al. 2015). Even in urban areas, birds may avoid close proximity to areas with a large number of humans and related disturbance, particularly during breeding season (Møller 2008). For example, as urbanization increases, magpies generally build their nests higher above the ground (Jerzak 2001, Wang et al. 2008). However, the negative effect of human population density may not be causal as it is also associated with other factors that might reduce the attractiveness of breeding sites in cities. For instance, mallards may not avoid humans *per se*, but rather cats and dogs.

The effect of the relocation distance

We also found that the further mallard families were relocated away from their breeding site, the less likely they were to return to it. The effect was small, however, and relocating birds over distances of only a few kilometres (in our study, most mallards were relocated within 5 km of their breeding site) appears insufficient to prevent them from returning to the same place. Preliminary findings for single mallard broods suggest however that relocation over longer distances (>10 km) may reduce breeding site fidelity (M. Engler, personal observations).

Effect of the identities of the duck and the anthropogenic breeding site

In addition to the effects of human population density and relocation distance, the identities of the duck and of the breeding site also shaped the return probability of female mallards. In fact, these random factors, which capture all unknown factors differing between individuals and breeding sites, exerted a larger influence on the predictive power of our statistical models than all the factors we considered.

The location-specific random effect captures small-scale properties that were not recorded but may strongly influence the attractiveness of breeding sites. Considering that the habitat type did not seem to influence the breeding site fidelity of mallards, we conclude that these location-specific properties may reflect the composition and availability of certain features at the breeding site, irrespective of the general type, e.g. balcony, roof terrace or courtyard. For example, mallards prefer elevated grounds (Roos et al. 2018, Holopainen et al. 2021) with high vegetation cover, e.g. balcony plants and flower beds (Oplinger 1977, Garrick 2015). In addition to the spatial characteristics of the breeding site, mallards may also prefer to return to a location where humans provided them with food and water ad libitum during the previous incubation period. In many cases, concerned citizens reported providing breeding females with a daily supply of carbohydrate-rich corn, mashed potatoes and lettuce leaves throughout the incubation period (M. Engler, pers. obs.).

Implication for the management of urban populations

How urban mallard populations are managed can potentially influence their welfare and conservation simultaneously. From the point of view of animal welfare, current management practices implemented by NABU Berlin are successful. In the absence of human interventions, the choice of anthropogenic breeding sites is highly maladaptive. In most situations the ducklings are unable to leave the anthropogenic structure (e.g. closed-off courtyard or impenetrable balcony barrier) in the first place, or they would fail to survive the trip to the water they need to reach after hatching. Yet, due to human interventions, rescued mallard families survive. The breeding output of the adult females remains high and neither these females nor their ducklings seem particularly stressed by these interventions. In fact, the same mallards often reuse the same breeding site multiple times in their life despite the required relocation interventions. The most striking example was that of one female (#JC69668) which was relocated 13 times, over 9 years, and which used the same site (a fully enclosed courtyard) 12 times and was only recorded once using a different breeding site.

Yet the rescue operations, however successful, have downsides. First, dealing with the logistics and the rescue operations require a significant amount of work from NABU Berlin, estimated at around 2.5 h per mallard family; time which could otherwise be spent on the protection of other populations of birds. Second, the practice may encourage ducks to repeat the same breeding behaviour which could eventually result in a high fitness cost. Indeed, an unknown proportion of birds using anthropogenic breeding sites is likely to not be observed or reported, leading to the death of the entire clutch. As breeding site fidelity is high for relocated ducks, but not total, birds can thereby be driven, due to their previous successful breeding experience, to new unmonitored locations which end up being a death trap for the ducklings. Furthermore, even if every single breeding attempt within anthropogenic structures were to be observed or reported, it is not guaranteed that conservation organizations like NABU Berlin would always have the means and personnel to cover all required relocations.

From the welfare point of view, if the choice of anthropogenic breeding site represents attractive ecological traps for urban mallards, a relevant research question is, ‘what actions could be taken to deter urban mallards from selecting anthropogenic structures for breeding without large (negative) consequences for breeding cost and population stability?’ The results we obtained suggest that the attractiveness of anthropogenic breeding sites is shaped by danger/disturbance (e.g. high human population density) and rewards (i.e. unknown factors influencing the attractiveness of certain breeding sites captured by the random variable ‘location ID’, probably related to better/safer breeding conditions as well as food provided to the ducks by people). Modifying the perception of danger therefore seems to be an appropriate mitigation strategy. This could be implemented by reducing the attractiveness of breeding sites, i.e. by removing flower boxes or deploying decoys of predators such as crows (Clucas amd Marzluff 2012). While the former heavily collides with the citizens’ interest, decoys are already used on balconies to deter birds like songbirds and pigeons. Unfortunately, evidence for their effectiveness is mixed and decoys may not present a long-lasting solution as birds can get used to them (Rensel and Wilder 2012, Micaelo et al. 2023). The perception of rewards could be reduced by encouraging humans not to feed the adult female mallards during the incubation period since these ducks can and do leave their eggs temporarily to forage elsewhere. Potential downsides of this approach include a decrease in the quality of human-wildlife interactions, but it is likely to be effective and potential drawbacks may be alleviated through effective communication campaigns.

Relocating mallard families far away might form a more effective prevention strategy. Opting for natural, high-quality bodies of water in rural environments around Berlin, without proximity to residential areas, could be a favourable choice for release. Two practical details would still need to be clarified: (i) how far the ducks must be relocated from their breeding site to effectively prevent their return, and (ii) whether this prompts mallards to cease using anthropogenic structures altogether or to continue using similarly inappropriate breeding sites, albeit in different locations.

Lowering the attractiveness of anthropogenic breeding sites has the potential to increase the welfare of mallards, but this should not be done at the expense of the conservation status of the local mallard population. So, before any program of deterrence is implemented, it will be necessary to identify: (i) whether there are sufficient natural breeding habitats in the vicinity that are available to support the mallard population, and (ii) whether even if such habitats are available, the population would remain largely sustained by the breeding output of mallards breeding in urban habitats (e.g. through the relocation program).

Studies in the UK, the USA and China have shown that the shortage of natural breeding spots alone may cause birds to use residential houses or other anthropogenic structures as breeding sites (Deng et al. 2005, Reynolds et al. 2019). Another important research question therefore becomes, ‘is the repeated occupation of anthropogenic breeding sites linked to a decline of available natural urban breeding sites?’ If this is the reason Berlin’s mallards choose to breed on anthropogenic structures, long-term population sustainability could be compromised, and the deterrence measures proposed above may not represent adequate solutions. Instead, management strategies aiming at increasing the availability of natural breeding sites would become the primary conservation target. Such an approach would also contribute to animal welfare by decreasing the incidence of breeding at inadequate anthropogenic sites. Measures reducing traffic and human related disturbance around water bodies are practical solutions, e.g. by designating urban water bodies as protected nature reserves or promoting dense vegetation in the shore area, thereby limiting access of humans to sensitive breeding habitat. Adding artificial structures such as 'nest rafts' in these locations could also help to increase the density of breeding sites in natural habitats (Brenner and Mondok 1979).

In sum, the need for the continuation of current relocation measures and investment in proposed extensions of (semi-) natural breeding sites depends on the conservation status of urban mallard populations. It is therefore crucial to monitor and evaluate occupancy and breeding success of mallards at natural water bodies in cities to determine if there is a shortage of natural breeding sites, and to determine the influence that this may have on the selection of anthropogenic structures as breeding sites. Benefits of a systematic application of management strategies should be critically evaluated in light of the objective. If animal welfare is the main concern, reducing the attractiveness of anthropogenic breeding sites, encouraging citizens not to feed mallards, and using long distance relocations may form reasonable options. However, if a lack of natural breeding sites in urban centres is the main driver forcing mallards to select alternative anthropogenic breeding sites, emphasis should be put on improving the general quality of natural urban water bodies, including the creation of structures appropriate for breeding and the reduction of human related disturbance. None of the proposed options are alternatives, and each should be rigorously tested before being deployed on a large scale.

Conclusion

To our knowledge, this study is one of the first to address the breeding site fidelity of mallards and study the effects of applied management strategies in a context of highly urban breeding environments. While our results show that location-specific properties exert a major influence on breeding site fidelity, the question remains why mallards elect to breed on anthropogenic structures in the first place. Clarifying the main cause behind the urban breeding behaviour of mallards should become a research priority since it impacts which wildlife management actions are likely to be most appropriate. To understand whether this originates from the attraction of such locations, we underline the need to record and study location specific properties of breeding sites. At the same time, future studies should monitor and evaluate occupancy and breeding success at natural water bodies in cities. We also suggest that relocation programs could be used as an experimental ground to test and refine management strategies. For example, one could (i) conduct a randomized trial on a small number of attractive anthropogenic breeding sites to test the effect of long-distance relocations on return rates or (ii) manipulate structure and appearance of breeding sites to reduce the attraction perceived by mallards. Not only could this kind of experiment be informative for the management and conservation of mallards and other bird species, but it could also bring fundamental insights into the reproductive biology of birds.

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Author contributions

Marc Engler (Conceptualization [equal], Data curation [equal], Formal analysis [supporting], Funding acquisition [lead], Methodology [equal], Project administration [lead], Resources [lead], Visualization [equal], Writing—original draft [lead], Writing—review & editing [equal]), Rubén Chavez (Formal analysis [supporting], Writing—review & editing [supporting]), Rebekka Sens (Data curation [supporting], Project administration [supporting], Writing—review & editing [supporting]), Maja Lundberg (Data curation [supporting], Writing—review & editing [supporting]), Alexandra Delor (Data curation [supporting], Writing—review & editing [supporting]), François Rousset (Formal analysis [supporting], Methodology [supporting], Writing—review & editing [supporting]), and Alexandre Courtiol (Conceptualization [equal], Data curation [equal], Formal analysis [lead], Methodology [equal], Supervision [lead], Visualization [equal], Writing—original draft [supporting], Writing—review & editing [equal])

Supplementary data

Supplementary data are available at *JUECOL* online.

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Data availability

The data and code used for the production of the result is available in the form of a dedicated R package—mallaRd—which we created to promote transparency and reproducibility. The package is available on GitHub (www.github.com/courtiol/mallaRd) and Zenodo (https://zenodo.org/records/14397939).

References

Amundson CL, Arnold TW. The role of predator removal, density-dependence, and environmental factors on mallard duckling survival in North Dakota. *J Wildl Manag* 2011;**75**:1330–9. https://doi.org/10.1002/jwmg.166

Baratti M, Cordaro M, Dessì-Fulgheri F *et al.* Molecular and ecological characterization of urban populations of the mallard (*Anas platyrhynchos* L.) in Italy. *Ital J Zool* 2009;**76**:330–9. https://doi.org/10.1080/11250000802566624

Brenner FJ, Mondok JJ. Waterfowl nesting rafts designed for fluctuating water levels. *J Wildl Manage* 1979;**43**:979–82.

Brown CR, Brown MB. Where has all the road kill gone? *Curr Biol* 2013;**23**:R233–4. https://doi.org/10.1016/j.cub.2013.02.023

Chouinard MP Jr, Arnold TW. Survival and habitat use of mallards (*Anas platyrhynchos*) broods in the San Joaquin Valley, California. *Auk* 2007;**124**:1305–16. https://doi.org/10.1093/auk/124.4.1305

Clucas B, Marzluff JM. Attitudes and actions toward birds in urban areas: human cultural differences influence bird behavior. *Auk* 2012;**129**:8–16. https://doi.org/10.1525/auk.2011.11121

Deng W, Zheng G, Zhang Z, Garson PJ, McGowan PJK. Providing artificial nest platforms for Cabot's tragopan *Tragopan caboti* (Aves: Galliformes): a useful conservation tool? *Oryx* 2005;**39**:158–63. https://doi.org/10.1017/S0030605305000396

Díaz M, Møller AP, Flensted-Jensen E *et al.* The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One* 2013;**8**:e64634. https://doi.org/10.1371/journal.pone.0064634

Dormann CF, Elith J, Bacher S *et al.* Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 2013;**36**:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Engel J, Keller M, Leszkowicz J *et al.* Synurbization of the mallard *Anas platyrhynchos* in Warsaw. *Acta Ornithol* 1988;**24**:9–28.

Eygenraam JA. The sex-ratio and the production of the mallard, (*Anas platyrhynchos* L.). *Ardea* 1957;**34**:117–43.

Figley WK, VanDruff LW. The ecology of urban mallards. *Wildl Monogr* 1982;**81**:3–39.

Garrick E. Duckling survival and habitat selection of brood-rearing mallard (*Anas platyrhynchos*) females in Southland, New Zealand. MSc thesis. Dunedin New Zealand: University of Otago, 2015.

Hallau A, Otto W. Brutplatzwahl der Berliner Stockenten (*Anas platyrhynchos*). *Berl Ornithol Ber* 2005;**15**:177–99.

Hartig F. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models (Version 0.4.6) [R Package]*. 2022. https://CRAN.R-project.org/package=DHARMa

Holopainen S, Väänänen V-M, Vehkaoja M *et al.* Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. *Biol Invasions* 2021;**23**:3795–807. https://doi.org/10.1007/s10530-021-02608-2

Jarman TE. Effects of urbanization on the feeding ecology and physiology of mallards (*Anas platyrhynchos*). MSc thesis. New Zealand: Massey University Palmerston North, 2019.

Jarman TE, Gartrell BD, Battley PF. Differences in body composition between urban and rural Mallards, *Anas platyrhynchos*. *J Urban Ecol* 2020;**6**:juaa011. https://doi.org/10.1093/jue/juaa011

Jerzak L. Synurbanization of the Magpie in the Palearctic. In: Marzluff J, Bowman R, Donnelly R (eds), *Avian Ecology and Conservation in an Urbanizing World*. Springer, 2001, 403–25.

Krams R, Krama T, Brūmelis G *et al.* Ecological traps: evidence of a fitness cost in a cavity-nesting bird. *Oecologia* 2021;**196**:735–45. https://doi.org/10.1007/s00442-021-04969-w

Liordos V, Jokimäki J, Kaisanlahti-Jokimäki M-L *et al.* Patch, matrix and disturbance variables negatively influence bird community structure in small-sized managed green spaces located in urban core areas. *Sci Total Environ* 2021;**801**:149617. https://doi.org/10.1016/j.scitotenv.2021.149617

López-Flores V, MacGregor-Fors I, Schondube JE. Artificial nest predation along a neotropical urban gradient. *Landsc Urban Plan* 2009;**92**:90–5. https://doi.org/10.1016/j.landurbplan.2009.03.001

Mainwaring MC. The use of man-made structures as nesting sites by birds: a review of the costs and benefits. *J Nat Conserv* 2015;**25**:17–22. https://doi.org/10.1016/j.jnc.2015.02.007

Master TL, Oplinger CS. Nesting and brood rearing ecology of an urban waterfowl population (*Anas platyrhynchos* and *Branta canadensis*) in Allentown, Pennsylvania. *Proc Pa Acad Sci* 1984;**58**:175–80.

Matérn B. *Spatial Variation—Stochastic Models and Their Applications to Some Problems in Forest Survey Sampling Investigations*, Vol. **49**. Report of the Forest Research Institute of Sweden, 1960, 1–144.

McKinney ML. Urbanization, biodiversity, and conservation. *BioScience* 2002;**52**:883–90. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

Meissner W, Rowinski P, Polakowski M *et al.* Impact of temperature on the number of mallards, *Anas platyrhynchos*, wintering in cities. *NwjZ* 2015;**11**:213–8.

Micaelo E, Lourenço L, Gaspar P *et al.* Bird deterrent solutions for crop protection: approaches, challenges, and opportunities. *Agriculture* 2023;**13**:774. https://doi.org/10.3390/agriculture13040774

Møller AP. Flight distance of urban birds, predation, and selection for urban life. *Behav Ecol Sociobiol* 2008;**63**:63–75. https://doi.org/10.1007/s00265-008-0636-y

Møller AP. The value of a mouthful: flight initiation distance as an opportunity cost. *Eur J Ecol* 2015;**1**:43–51.

Møller AP, Díaz M. Avian preference for close proximity to human habitation and its ecological consequences. *Curr Zool* 2018;**64**:623–30. https://doi.org/10.1093/cz/zox073

Montgomery RA, Oldenburg RC, Burger GV. Some aspects of the biology of an urban mallard population. In: *37th Midwest Fish & Wildlife Conference*. Toronto, Ontario, Canada: The Wildlife Society, 1975, 15.

Muff S, Nilsen EB, O'Hara RB *et al.* Rewriting results sections in the language of evidence. *Trends Ecol Evol* 2022;**37**:203–10. https://doi.org/10.1016/j.tree.2021.10.009

Oplinger CS. *Waterfowl Populations and Water Quality Relationships in the Allentown Park System*. PA Urban Observatory, 1977.

Pebesma E, Bivand R. *Spatial Data Science: With Applications in R*, 1st edn. Chapman and Hall/CRC, 2023. https://doi.org/10.1201/9780429459016

Polakowski M, Skierczyński M, Broniszewska M. Effect of urbanization and feeding intensity on the distribution of wintering Mallards *Anas platyrhynchos* in NE Poland. *Ornis Svec* 2010;**20**:76–80. https://doi.org/10.34080/os.v20.22636

R Core Team. *R: A Language and Environment for Statistical Computing [Computer Software]*. R Foundation for Statistical Computing, 2024. https://www.R-project.org/

Rensel L, Wilder J. The effects of owl decoys and non-threatening objects on bird feeding behavior. *Quercus Linfield J Undergrad Res* 2012;**1**:4.

Reynolds J, Galbraith JA, Smith JA *et al.* Garden bird feeding: insights and prospects from a North-South comparison of this global urban phenomenon. *Front Ecol Evol* 2017;**5**. https://doi.org/10.3389/fevo.2017.00024

Reynolds J, Ibáñez-Álamo JD, Sumasgutner P *et al.* Urbanisation and nest building in birds: a review of threats and opportunities. *J Ornithol* 2019;**160**:841–60. https://doi.org/10.1007/s10336-019-01657-8

Roos S, Smart J, Gibbons DW *et al.* A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. *Biol Rev Camb Philos Soc* 2018;**93**:1915–37. https://doi.org/10.1111/brv.12426

Rousset F, Ferdy J-B. Testing environmental and genetic effects in the presence of spatial autocorrelation. *Ecography* 2014;**37**:781–90. https://doi.org/10.1111/ecog.00566

Rutschke E. *Die Wildenten Europas*. AULA-Verlag GmbH, 1990.

Samia DSM, Nakagawa S, Nomura F *et al.* Increased tolerance to humans among disturbed wildlife. *Nat Commun* 2015;**6**:8877. https://doi.org/10.1038/ncomms9877

Santangelo JS, Rivkin LR, Johnson MTJ. The evolution of city life. *Proc R Soc B* 2018;**285**:20181529. https://doi.org/10.1098/rspb.2018.1529

Schlaepfer MA, Runge MC, Sherman PW. Ecological and evolutionary traps. *Trends Ecol Evol* 2002;**17**:474–80. https://doi.org/10.1016/S0169-5347(02)02580-6

Sheppard JL. Breeding ecology and productivity of Mallards and Mallard-grey duck hybrids in New Zealand. Doctoral thesis. 2018. New Zealand: University of Auckland, http://rgdoi.net/10.13140/RG.2.2.10591.36001

Sherley RB, Ludynia K, Dyer BM *et al*. Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. *Curr Biol* 2017;**27**:563–8. https://doi.org/10.1016/j.cub.2016.12.054

Sierro J, Schloesing E, Pavón I *et al*. European blackbirds exposed to aircraft noise advance their chorus, modify their song and spend more time singing. *Front Ecol Evol* 2017;**5**:68. https://doi.org/10.3389/fevo.2017.00068

Soh MCK, Sodhi NS, Seoh RKH *et al*. Nest site selection of the house crow (*Corvus splendens*), an urban invasive bird species in Singapore and implications for its management. *Landsc Urban Plan* 2002;**59**:217–26. https://doi.org/10.1016/S0169-2046(02)00047-6

Tjur T. Coefficients of determination in logistic regression models—a new proposal: the coefficient of discrimination. *Am Stat* 2009; **63**:366–72. https://doi.org/10.1198/tast.2009.08210

United Nations, Department of Economic and Social Affairs PD. *World Urbanization Prospects: The 2014 Revision*. New York, USA: United Nations publication, 2015.

Vaida F, Blanchard S. Conditional Akaike information for mixed-effects models. *Biometrika* 2005;**92**:351–70. https://doi.org/10.1093/biomet/92.2.351

Wang Y, Chen S, Jiang P *et al*. Black-billed Magpies (*Pica pica*) adjust nest characteristics to adapt to urbanization in Hangzhou, China. *Can J Zool* 2008;**86**:676–84. https://doi.org/10.1139/Z08-045

Wiegers JN, Jongejans E, van Turnhout CAM *et al*. Integrated population modeling identifies low duckling survival as a key driver of decline in a European population of the Mallard. *Ornithol Appl* 2022;**124**:1–12. https://doi.org/10.1093/ornithapp/duac020

Wille M, Lindqvist K, Muradrasoli S *et al*. Urbanization and the dynamics of RNA viruses in Mallards (*Anas platyrhynchos*). *Infect Genet Evol* 2017;**51**:89–97. https://doi.org/10.1016/j.meegid.2017.03.019

Yetter AP, Hagy HM, Horath MM *et al*. Mallard survival, movements, and habitat use during autumn in Illinois. *J Wildl Manag* 2018;**82**: 182–91. https://doi.org/10.1002/jwmg.21346

Zicus MC, Fieberg J, Rave DP. Does Mallard clutch size vary with landscape composition: a different view. *Wilson Bull* 2003; **115**:409–13.

Journal of Urban Ecology, 2025, 11, 1–11
https://doi.org/10.1093/jue/juae023
Research article