All-season space use by non-native resident Mandarin Ducks (*Aix galericulata*) in northeastern Germany

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Abstract
Patterns of space use are often subject to large temporal and individual-level variation, due to seasonality in behaviour and environmental conditions as well as age- or sex-specific needs. Especially in temperate regions, seasonality likely influences space use even in non-migratory birds. In waterfowl of the family *Anatidae*, however, few studies have analyzed space use of the same individuals across the full annual cycle. We used a resident population of Mandarin Ducks (*Aix galericulata*) in northeast Germany to study their year-round space use in relation to season, sex, and age. We marked 172 birds with colour rings and surveyed relevant water bodies for re-encounters for several years. As space-use patterns we derived home ranges from minimum convex polygons and the number of water bodies used by individual birds. Our analysis revealed that individuals shifted their space use between seasons, in particular extending their home ranges during the non-breeding season. Between years, in contrast, birds tended to show season-specific site fidelity. Sex differences were apparent during both breeding and non-breeding season, males consistently having larger home ranges and using slightly more water bodies. No difference was found between first-year and adult birds. Our study demonstrates that mark-resighting can provide valuable information about space use in species with suitable behaviour and readily accessible habitat. In such cases, it may be a valid alternative to more expensive GPS-tracking or short-term manual radio telemetry, particularly within citizen-science projects.

Keywords *Anatidae* · *Aix galericulata* · Home range · Site fidelity · Movement · Seasonality

Zusammenfassung
Ganzjährige Raumnutzung einer eingebürgerten Standvogel-Population der Mandarinente (*Aix galericulata*) in Nordostdeutschland.
Raumnutzungsmuster von Vögeln zeigen häufig große zeitliche und individuelle Variationen in Abhängigkeit vom saisonalen Verhalten und von Umweltbedingungen, aber auch alters- und geschlechtsspezifischen Ansprüchen. In gemäßigten Klimazonen können jahreszeitliche Einflussfaktoren die Raumnutzung auch von nicht ziehenden Arten bestimmen. Für Entenvögel (*Anatidae*) liegen bisher jedoch nur wenige Studien vor, die die Raumnutzung von Individuen über den gesamten Jahresverlauf hinweg betrachten. Wir untersuchten die ganzjährige Raumnutzung einer Standvogel-Population der Mandarinente (*Aix galericulata*) in Abhängigkeit von Jahreszeit, Geschlecht und Alter der Vögel. Wir markierten 172 Vögel mit Farbringen und kontrollierten mehrere Jahre lang die relevanten Gewässer, um Ringablesungen zu erzielen. Zur Analyse der Raumnutzung ermittelten wir Minimum-Convex-Polygone und die Anzahl der von den einzelnen Individuen genutzten Gewässer. Unsere Auswertung zeigte, dass die von den Vögeln genutzten Aktionsräume sich mit den Jahreszeiten veränderten. Insbesondere vergrößerte sich das besuchte Gebiet außerhalb der Brutzeit. Beim Vergleich mehrerer Jahre tendierten die Vögel zu einerURNSPEZIFISCHEN Gebietstreue. Geschlechterunterschiede zeigten sich sowohl innerhalb...
als auch außerhalb der Brutzeit, wobei die Männchen stets größere Gebiete und eine größere Zahl an Gewässern nutzten. Zwischen Vögeln im ersten Lebensjahr und Adulten wurden keine Unterschiede gefunden. Unsere Untersuchung zeigt, dass Farbberingungsprogramme wertvolle Informationen zur Raumnutzung bei Arten liefern können, deren Verhalten dafür geeignet ist und die in gut zugänglichen Lebensräumen vorkommen. In diesen Fällen kann die Farbberingung eine geeignete Alternative zur teureren GPS- oder manuellen Telemetrie sein, vor allem wenn die vereinte Kraft von Amateurornithologen in die Untersuchungen einbezogen werden kann.

**Introduction**

Birds’ space use and movement patterns are tightly linked to various aspects of their ecology and life history. Large-scale movement strategies, such as migration and residency, strongly affect survival, reproduction and recruitment (Grist et al. 2017; Buchan et al. 2020) and species interactions (Ahola et al. 2007). Also locally, space-use patterns arise from the behaviours that individuals express to survive and reproduce while interacting with their abiotic and biotic environments subject to their internal states. As such, emergent patterns such as home ranges and their characteristics can give insights, for example, into individual variation in fitness (Mack and Clark 2006) or spatiotemporal variation in habitat quality and population dynamics (Wang and Grimm 2007).

Typical factors that drive space use are in a broad sense resource availability as well as species-specific resource (including habitat) requirements and behaviours. However, species-specific patterns of space use may be subject to considerable individual-level and temporal variation, due to fluctuating environmental conditions (e.g. seasonally), species’ annual cycles of behaviour (e.g. reproduction and moulting), and age- or sex-specific needs. In waterfowl, most studies investigate space use either during the breeding season (Gilmer et al. 1975; Kirby et al. 1985; Mack et al. 2003) or during winter (Legagneux et al. 2009; Sauter et al. 2012). However, few studies report data across all seasons (but see Groeper et al. 2008; Sun et al. 2014; Pollander et al. 2019), possibly because many species of waterfowl are migratory and spend moulting season and winter in regions different from their breeding areas. Thus, our understanding of how waterfowl space use compares across seasons, possibly in interaction with sex or age, is limited.

Here, we present a study on year-round space use of Mandarin Ducks (*Aix galericulata*) in northeast Germany. Native to parts of eastern Asia, various wild populations of Mandarin Ducks established throughout Europe during the twentieth century from escapes or deliberate releases from private collections, parks, and zoos. One of these is a stable breeding population in the Berlin–Potsdam region, with an estimate of 140–215 breeding pairs by 2009 (Gedeon et al. 2014). While in their native range Mandarin Ducks are predominantly migratory (Lever 2013), German birds appear to be mostly resident but possibly undertake seasonal short-range movements within their breeding areas (Bairlein et al. 2014; Mädlow 2018a). The possibility of regular migration is discussed for some populations in southern Germany (Bezzel et al. 2005; Hölzinger et al. 2018). Mandarin Ducks are cavity nesters, and, therefore, their spatial distribution during the breeding season is likely driven by availability of nesting opportunities (Newton 1994). By contrast, in winter a limiting factor may be foraging opportunities and habitat suitability during colder weather conditions (Mädlow 2018a and references therein). Local counts of Mandarin Ducks in the Berlin–Potsdam region suggest seasonal shifts in space use within the region, but it is unclear to which extent such shifts and between-year site fidelity occur at the individual level. Another important aspect of space use is energy expenditure. To reduce energetic costs of movement, individuals may limit movement rates or distances in adverse conditions (Legagneux et al. 2009). However, little is known how this combines with other drivers of winter movements and how winter space use compares to other seasons.

Seasonal variation in space use may be intertwined with sex-related variation due to differences in mating and brood-care behaviour (Rolando 2002). In Mandarin Ducks, sex differences should occur mainly during the breeding season. As most males do not participate in offspring care, their bond to breeding sites is weaker, which should lead to greater mobility and home ranges compared to females. This may be exacerbated by a male-biased sex-ratio, as unpaired males tend to roam even further (Lever 2013; Sun et al. 2014; Mädlow 2018a). In contrast, sex differences are expected to be weaker during fall and especially winter, when ducks tend to be paired (Legagneux et al. 2009; Mädlow 2018a). Regarding age, home ranges of juvenile birds are often larger than those of adults, as young birds are less experienced and efficient in resource search and tend to undertake exploratory movements (Rolando 2002; Legagneux et al. 2009). Such a pattern may likely also hold for Mandarin Ducks.

Taking advantage of the prevalent residency of Mandarin Ducks in the Berlin–Potsdam area, we investigate their space use patterns across seasons, sexes and age classes, and compare this to a study on resident Mandarin Ducks in Taiwan, which are part of the most southern breeding populations in their natural range (Sun et al. 2014).
Methods

Study area, trapping, and survey

The study took place in the Berlin–Potsdam region in northeast Germany, which is dominated by urban and suburban land cover but also includes various green space and features a variety of water bodies (Fig. 1). In 2005, the total number of birds in the region was estimated to be 900–1000, with 140–215 breeding pairs.

Between December 2002 and June 2007, a total of 172 birds (92 males, 58 females, 12 unsexed) were captured in Potsdam with snares or nets and ringed. Individuals were sexed by coloration of plumage and bare parts. Fully grown juvenile birds were aged by tail feather structure until their first moult in late summer or autumn. Fifty-two of all birds were ringed as downy chicks. Birds were marked with a standard metal ring on one leg and a white plastic ring with a two-digit code on the other leg. The latter could be read with binoculars from a distance, as Mandarin Ducks often leave water to roost on the shore or on branches. In the years 2003–2010, all accessible water bodies with suitable Mandarin Duck habitat in Potsdam and the more important sites in neighbouring Berlin were regularly surveyed by several observers throughout the year, however, not following a fixed time schedule. The surveyed sites made up the majority of sites used by the Mandarin Duck population under study. There was no evidence (based on our own observations and a large community of ornithologists in the region) that the ducks regularly occupied sites in the surrounding hinterland. The surveys resulted in a total of approximately 4000 surveys of individual sites with more than 3500 ring re-encounters. A few irregular ring re-encounters during the years 2011–2015 were additionally included.

Statistical analysis

We omitted individuals that could not be unambiguously sexed. We further omitted all data from downy chicks because of their restricted mobility but retained their data after fledging. In the remaining data, age was classified as either juvenile (from August of first year to July of the following year) or adult, with unclear instances being omitted from age-related analyses but retained for other analyses. From ring encounters, we generated two sets of location data. A “fine” data set assigned encounters to their original survey sites. A “coarse” data set only distinguished between water bodies. For this, multiple survey sites at the same water body were merged and assigned one joint identifier when they were connected in the sense that ducks could access the various sites by swimming only. For example, in the coarse data set, we merged survey sites at the same lake but defined two separate water bodies on each side of a non-swimmable dam or weir. Long stretches of flowing waters (streams, rivers) were separated into a few disjoint sites according to duck core areas.

Home-range size

To estimate home-range size, we computed home ranges (HR) as 100% minimum convex polygons (MCP), using the fine data set. Computation of MCPs required at least

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**Fig. 1** Map of all sites at which ringed Mandarin Ducks were observed during the study. Both large and inset map (zooming in on central Potsdam) demonstrate the various water bodies that ducks inhabit, including the River Havel, lakes, streams, and ponds. Ringing took place only in the Potsdam region, not in Berlin.
five observations, of which at least four were distinct; birds that did not meet this condition in any of the below analyses were discarded from these specific analyses. We computed overall HRs, using only birds with observation period (starting with capture and ending with last re-encounter) of at least 1 year, and performed a sex comparison on these. For an age comparison, we took into account that birds were juveniles for at most 1 year, and required as minimum observation period for the juvenile age class 26 weeks and cut off all observations above 52 weeks in the adult age class to ensure comparability of HR estimates of the two age classes. To compare space use between different seasons, HRs were computed separately for breeding season (April–July) and non-breeding season (August–March), with no further requirements on the observation period in addition to MCP requirements. Because the non-breeding season was twice as long as the breeding season, the non-breeding season was further separated into two 4-month sub-periods fall (August–November; birds gather at traditional sites), and winter (December–March; birds move to ice-free waters during cold periods). Due to non-normality of the data, comparisons within groups were performed with non-parametric tests (Mann–Whitney rank sum test and Wilcoxon signed-rank test).

As Mandarin Ducks in our study area appeared to use multiple separate water bodies, we complemented the area-based MCP-method of home-range estimation by a second measure. For each individual, we computed the number of different water bodies (#WB) it used based on the coarse data set. For this, birds with data spanning at least 1 year were used. To test for differences between sexes and seasons, we further computed #WB separately for breeding and non-breeding season. In contrast to MCP area, #WB tended to increase with the number of times a bird was encountered. Therefore, we fitted a nonlinear model in form of a growth curve that reached an asymptote to #WB against number of encounters per bird (n) using the following formula:

\[
#WB = A \cdot (1 - e^{B \cdot n}),
\]

where A and B are parameters to be estimated. The parameter A is the asymptote of interest, which gives an estimate for the number of water bodies that birds on average use in the long term. To test for sex and season effects, including their interaction, we fitted multiple models, in which data were grouped and parameters A and B allowed to vary accordingly. Models were fitted via maximum likelihood estimation using Normal errors. For this, we implemented log-likelihood functions in R and found their maximum using function “optim” (R Core Team 2020). Parameter estimation was followed by information-theoretic model selection via AICc (Burnham et al. 2011).

Site fidelity

To further investigate seasonal space-use differences, we considered the overlap of home ranges (using both MCP area and water bodies) between seasons for all individuals with sufficient data in both seasons. We computed which percentage this overlap constituted of the breeding and non-breeding HRs, respectively. We contrasted this between-season comparison of HRs with a between-year comparison to estimate site fidelity between years. For all birds with data spanning at least 2 years and at least one encounter in each of the seasons, we computed how many water bodies were used in at least 2 years (e.g. in at least two breeding seasons). We performed the between-year comparison only for water bodies, due to the higher data requirements for MCPs computation that prevented to compute yearly MCPs.

For both seasonal and yearly analysis of water bodies, we again fitted asymptotic models for the quantities of interest to the total number of encounters per bird and report estimated asymptotes as resulting measures of interest. All analyses were performed in R (R Core Team 2020).

Results

After data cleanup, data of 160 (92 males, 68 females) individuals remained with a total of 3297 encounters (including ringing events and re-encounters). Although a few individuals were observed many times (max = 157), the central 50 percent of encounters per bird lay in the range 4–26, with a median of 10.5. Note that in the following, we do not report tests of group differences as binary (significant or not) but refer the reader to their p values, in line with contemporary recommendations (Wasserstein et al. 2019). In addition, we report effect sizes. Due to their suitability for non-parametric tests, we used rank biserial correlations, computed with R package “rcompanion” (Mangiafico 2021). The best way to interpret this measure is via the simple difference formula based on the common language effect size: as difference between the proportions of favourable and unfavourable evidence for a hypothesis contained in the data (Kerby 2014). A value of zero represents no evidence (the proportions of data speaking for and against the hypothesis are equal), while a value of 1 indicates strongest support. Negative values (ranging down to −1) indicate that the data are speaking against the hypothesis, e.g. supporting an opposite statement.

Home-range size

Considering MCP area, overall HR sizes were highly variable, ranging from 0.4 to 302 km² with a median of 11.9 km² (N = 76). Despite concomitant large variation in observation periods (56–437 weeks), HR size was related to neither
length of the observation period (linear model, $p = 0.42$, adjusted $R^2 = 0.005$) nor the number of observations per bird (linear model, $p = 0.29$, adjusted $R^2 = 0.002$), hence no further corrections with respect to these were required. Median HRs of males (13.7 km$^2$) were almost twice as large as HRs of females (7.1 km$^2$), and the comparison between sexes had an effect size of 0.22, which we consider a moderate size (Table 1, Fig S1). Note that although relatively more females than males were omitted from overall HR computation, this was mainly because fewer females met the requirement of a 1-year observation period probably due to higher mortality (Bellebaum and Mädlow 2015) and not because of fewer number of observations per se, precluding a bias in results due to the latter. When considering sex differences in HR size separately in breeding and non-breeding seasons, HRs of males remain to be larger in both seasons (Table 1, Fig S2). A higher $p$ value for the breeding-season comparison was likely due to smaller sample size, as effect size was even slightly larger.

For the HR comparison between age classes, few individuals met requirements for MCP computation in both age classes, precluding a paired test, and hence we treated all computed HRs as independent samples. Although median HR size was slightly larger in juveniles (5.8 km$^2$) than adults (4.5 km$^2$), a very small effect size of 0.06 indicates no difference between the age classes (Table 2, Fig S2).

Among all season-specific home ranges, those during the non-breeding season (median = 8.9 km$^2$) were larger than during the breeding season (median = 2.1 km$^2$), supported by an effect size of 0.55, which we consider a fairly large effect size given the nature of our data (Table 3, Fig S3). Non-breeding HR size decreased when considering a subset of individuals for which HRs could be computed for both seasons but remained still larger than breeding HR size (Table 3). When further separating the longer non-breeding season into two 4-month periods, fall (median = 4.1 km$^2$) and winter (median = 4.4 km$^2$) home ranges were smaller than the overall non-breeding HR, indicating that the difference between non-breeding and breeding period is somewhat, but not merely, due to the non-breeding season being longer. Both fall and winter HRs are still about twice as large as breeding HRs. When comparing sub-seasons, fall home ranges tended to be smaller than winter home ranges, yet the difference in median HR size was only subtle (Table 3).

Birds ($N=92$) used in total 47 different water bodies as defined by the coarse data set. For individual birds, #WB for the entire observation period ranged 1–11. When fitting #WB to number of encounters, model-selection support was largest for the model that separated data by season, with similar support for the model that additionally included a constant effect for sex (i.e. same effect in both seasons) (Table 4). According to the principle of parsimony, an even more complex model (the “full model”), in which the effect of sex was allowed to vary between seasons (e.g. larger effect

| Age class | Juvenile | Adult |
|-----------|----------|-------|
| Number of individuals | 18 | 36 |
| Median | 5.8 | 4.5 |
| 25% quantile | 3.0 | 2.1 |
| 75% quantile | 7.6 | 12.7 |
| Effect size | 0.06 | 0.066 |

We performed a Mann–Whitney rank sum test (alternative hypothesis: juvenile > adult), of which $p$ values are reported. Effect size is Glass rank biserial correlation. See Fig S2 for a plot of the detailed distribution of individual home-range sizes in each age class.
of sex during the breeding season) had considerably weaker support (empirical support for this model being only 1:25 compared to the best-fitting model with only the seasonal effect; Table 4). Therefore, we did not consider this model for any further interpretation. According to the estimated asymptote (representing expected long-term space use) of the best-fitting “season” model, birds used more water bodies during the non-breeding season ($A_{\text{non-breed}} = 5.2$, SE = 0.3) compared to the breeding season ($A_{\text{breed}} = 3.2$, SE = 0.25; Fig. 2). The additional effect of sex was small, male birds using 0.5 water bodies more than females.

### Site fidelity

HR overlap analysis revealed that individuals’ space use overlapped between breeding and non-breeding season but with an asymmetry between seasons. Considering MCPs, individuals reused fairly large parts (median = 73%) of their breeding HR during the non-breeding season, while only small parts (median = 17%) of the non-breeding HR were used during the breeding season (Fig. 3). There was large individual variation in the extent to which individuals reused their breeding HR during the non-breeding season, however, no sex difference was apparent. Results considering overlap in water bodies between seasons showed a similar trend. Individuals reused on average 72% of their breeding-season water bodies during the non-breeding season, while only 42% of the non-breeding-season water bodies were used during the breeding season (Fig S4).

In the comparison of between-season and between-year shared water bodies, we found that between-year overlap in water bodies within seasons was larger than between-season overlap. In contrast to 35% (33% when considering only birds with observation period ≥ 2 years) of their breeding HR during the non-breeding season, while only small parts (median = 17%) of the non-breeding HR were also used during the breeding season (Fig. 4). This showed a tendency in

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### Table 3

Comparisons of median home-range sizes (km²) based on 100% MCPs between seasons (breeding vs. non-breeding season) and the two sub-seasons fall and winter during the non-breeding season

|                     | Season (unpaired) | Season (paired) | Sub-season (unpaired) | Sub-season (paired) |
|---------------------|-------------------|-----------------|-----------------------|---------------------|
|                     | Non-breed Breed   | Non-breed Breed | Fall Winter           | Fall Winter         |
| Number of individuals | 77 24             | 24 24           | 36 51                 | 26 26               |
| Median              | 8.9 2.1           | 5.4 2.1         | 4.1 4.4               | 4.3 4.7             |
| 25% quantile        | 3.8 1.2           | 3.4 1.2         | 1.4 2.6               | 1.6 2.7             |
| 75% quantile        | 18.6 5.4          | 11.9 5.4        | 5.3 10.0              | 5.5 12.1            |
| Effect size         | 0.55              | 0.57            | −0.19a                | −0.19a              |
| p value             | <0.001            | 0.06            | 0.14                  | 0.14                |

For each comparison, we performed both an unpaired test (Mann–Whitney rank sum) and a paired test (Wilcoxon signed-rank) for those individuals that had sufficient data in both (sub-)seasons. For the comparison between seasons, we tested whether non-breeding home ranges were larger than breeding home ranges, whereas for the sub-season comparison, we did not have any prior expectation regarding the direction of the difference and applied a two-sided test. We computed effect sizes as Glass rank biserial correlation for unpaired tests and matched-pairs rank biserial correlation for paired tests. See Fig S3 for a plot of the detailed distribution of individual home-range sizes in the breeding and non-breeding season.

### Table 4

Model selection results for a nonlinear model fit of number of used water bodies (#WB) against number of encounters according to Eq. (1)

| Model              | No. par. | Log-Lb | AICc | ∆AICc | Evidence ratio |
|--------------------|----------|--------|------|-------|----------------|
| Season + sex       | 9        | −285.2 | 589.6| 6.4   | 25.1           |
| + season×sex       |          |        |      |       |                |
| Season             | 7        | −285.3 | 585.2| 2.1   | 2.8            |
| Sex                | 5        | −286.4 | 583.1| 0     | 0              |
| Joint              | 3        | −297.1 | 600.3| 17.2  | 21,833         |

To ensure comparability between models, we separated data between seasons (i.e. computing two season-specific values of #WB for all birds that had data in both seasons), even for models that did not include a season effect. Models with minimum $AIC_c$ were selected as best models (bold). Evidence ratios were computed as relative likelihood of each model compared to the best model (see e.g. Burnham et al. 2011).

Number of model parameters

Value of the log-likelihood function at the maximum likelihood estimate
birds to return to the same water bodies in the breeding/non-breeding season across years.

**Discussion**

We investigated space use of resident Mandarin Ducks in the Berlin–Potsdam region across seasons, sex, and age. We found that birds, despite their overall residency in the region, shifted their individual space use between seasons, in particular extending their home ranges during the non-breeding season. Between years, in contrast, birds tended to show season-specific site fidelity. Sex differences were apparent during both breeding and non-breeding season, males consistently having larger home ranges and using slightly more water bodies. Contrary to the common assumption that juveniles roam farther than adults, there was no clear difference in home-range size between first-year and adult birds.

**Large-scale mobility**

The population of Mandarin Ducks in our study is mainly resident. Although ring recoveries from earlier ringing campaigns revealed that individual birds from Berlin flew up to several hundred kilometers (Heinroth 1914, 1915), none of the birds that were ringed for this study were re-encountered or found outside the breeding range of Potsdam–Berlin. Additionally, out of 99 ringed birds that were observed for at least 1 year, 88 were present in winter (December–February) as well as during breeding time and in summer (April–September). Ten birds were seen only in winter and just one bird was seen only in summer. Although we cannot exclude that the ten winter birds originated from breeding areas away from Berlin/Potsdam, it is much more likely that they spent breeding time and summer in some remote parts of our study area that could not be controlled regularly, especially in the city of Berlin. Occasional observations of unringed Mandarin Ducks outside the breeding area in the wider surroundings of Berlin (Mädlow 2018a) probably refer to some of the Berlin–Potsdam birds, but there are no hints of regular movements of the Potsdam birds to any other area. Several references on ring recoveries of European birds present similar results (Wernham et al. 2002; Bairlein et al. 2014; Majoor 2014; Robinson et al. 2018). However, Bezzel et al. (2005) and Hölzinger et al. (2018) suggested that some Mandarin Duck populations in southern Germany may show regular migration to unknown wintering sites, as they were not observed in their breeding areas during winter. Mikule (2020) also discussed the possibility that wintering birds in the Central Bohemian Region (Czech Republic) originated from breeding populations in Germany. Although ring recoveries from our study do not indicate any regular migrations of the Berlin/Potsdam birds, fully ascertaining the residency status of the population would require much greater observer effort with systematic observations at sites outside of the Berlin–Potsdam region, which was out of scope for our study.

**Home ranges**

We found highly variable individual home-range sizes, ranging between 0.4 and 302 km². This fits with results of...
other studies in ducks that report seasonal home ranges and space use. Both breeding and winter home ranges have been found to range over similar orders of magnitude in studies of mallards Anas platyrhynchos (Kirby et al. 1985; Mack et al. 2003; Legagneux et al. 2009; Sauter et al. 2012), Eurasian teal A. crecca and northern pintail A. acuta (Legagneux et al. 2009), and mottled ducks A. fulvigula (Pollander et al. 2019). Such large variability in home-range size may be a result of individuals utilizing a full gradient of habitat quality and a heterogeneous distribution of water bodies (Kirby et al. 1985). In our study, while some birds remained within close clusters of water bodies in the Potsdam area, others utilized sites in both Potsdam and Berlin. In addition, many duck species use roosting sites different from foraging sites, so that home ranges are influenced by daily flights between these sites (Johnson et al. 2014). Although this behaviour was observed in Mandarin Ducks in Berlin occasionally in earlier years (Ornithologische Arbeitsgruppe Berlin (West) 1990), observations during the present study did not indicate commingling behaviour. A formal test of daily mobility patterns was not possible, however, as re-encounters of birds were not frequent enough.

Space use was more extensive during the non-breeding than during the breeding season, considering both MCP-based home ranges and number of water bodies. The large difference in home-range size (median of 2.1 km² versus 8.9 km²) may partly be explained by the non-breeding season (August–March) being twice as long as the breeding season (April–July). However, when accounting for this by estimating Fall (August–November) and Winter (December–March) home ranges separately, both of these were still twice as large as breeding home ranges. This may be related to ducks utilizing a wider range of sites and water bodies. Fall home ranges may include different sites used for moulting, foraging in autumn (e.g. fruits of beeches and oaks) and the beginning of wintering. In winter, rather than reducing movement rates per se, ducks have to be mobile to find ice-free water bodies and sites with food supply by humans. The same pattern was observed in Taiwan, where non-breeding home ranges of Mandarin Ducks were also larger than breeding home ranges (Sun et al. 2014). In contrast, breeding season home ranges of, e.g., mottled ducks were larger than seasonal home ranges in summer, fall and winter (Pollander et al. 2019). This may be partly due to the breeding season being defined as a 5-month period (February–June) in this study, while the other seasons were shorter. When considering only individuals with enough data for computing home ranges in both seasons for the paired seasonal test, 53 birds (30 males, 23 females) had to be omitted, because they did not have sufficient data during the breeding season. Resulting median home ranges for the non-breeding season dropped from 8.9 to 5.4 km². Possibly, omitted birds tended to be those with not only greater mobility during non-breeding but also greater overall mobility, resulting in less re-encounters during the breeding season. At that time of year, it is much more difficult to find birds that use small ponds or streams aside from the regularly visited sites. Possibly, some of these birds were not involved in any breeding behaviour. Whether larger home ranges also translate into greater mobility (i.e. more frequent moves between sites or water bodies) remains open. This could best be addressed by means of automated tracking (e.g. via GPS transmitters) that yields more regular and frequent localizations of individuals.

Home ranges of males were considerably larger than those of females during both seasons, although moderate
effect sizes, especially for the non-breeding season, suggest that the difference between sexes arose from a limited number of individuals. Larger home ranges of males were expected for the breeding season and confirms results of Mandarin Ducks in their native breeding range in Taiwan, where mean home-range size of male Mandarin Ducks during breeding was nearly twice as high as females (Sun et al. 2014). Such large sex difference is not apparent in all ducks, for example mean breeding-season home ranges of male mallards in Canada were found to be only slightly larger than those of females (Gilmer et al. 1975; Kirby et al. 1985). In our study this may be explained by a strong sex difference in breeding behaviour. As only 3.2% of males cared for their offspring (Mädlow 2018b), males were more independent from breeding sites and began to gather in male assemblies during May (Mädlow 2018a). In addition, because of the male-biased sex ratio (65% males, Bellebaum and Mädlow 2015) at least one third of the males were not involved in any breeding behaviour.

Larger male home ranges during the non-breeding season were unexpected, as males and females tend to be paired in winter. A study on teal, mallard, and pintail did not find any sex-related differences in winter home ranges (Legagneux et al. 2009). Likely, the larger male home ranges of our Mandarin Ducks were due to some bachelor males roaming about. This differs from the behaviour of Mandarin Ducks in Taiwan, where no difference of non-breeding home ranges between males and females was found, although there was a similar male-biased sex ratio as in Potsdam (Sun et al. 2014). A possible explanation is a different configuration of habitat. In Taiwan, habitat is mainly linear along a river, and during the non-breeding season all birds flew to several sites and reservoirs downstream of the breeding sites. In contrast, a distribution of various water bodies in the Potsdam and Berlin region (Fig. 1) provides more heterogenous and spatially scattered sites for moulting and overwintering. Future studies may consider the influence of habitat more explicitly to better understand how size and quality of water bodies influences HR sizes (Kleyheeg et al. 2017). We assume that the observed sex differences in HR sizes resulted from true behaviour and not an inherent methodological bias towards observing males. Excepting the period that females spend breeding on their nests, no behavioural differences were apparent that may have led to different probabilities in ring re-encounters between males and females. However, ideally one would confirm this in a rigorous analysis of re-encounter probabilities based on supplementary data.

There was no clear difference in home ranges of first-year and adult birds. The same was found in mallards, teals, and pintails (Mack et al. 2003, Mack and Clarck 2006, Legagneux et al. 2009), whereas in wintering black ducks *Anas rubripes*, home ranges of juvenile females where several fold larger than those of adult females (Morton et al. 1989). The latter was explained by choice of better and more constant habitat and dominant behaviour of adults. In other bird species than waterfowl, different influences of age on home ranges have been found, with the majority of studies showing larger home ranges in juvenile birds (Rolando 2002). Statistically, our unclear result may be due to small sample

**Fig. 4** Fraction of water bodies shared between seasons (left), between years within the breeding season (middle), and between years within the non-breeding season (right). For the between-year, within-season analysis, water bodies were defined as shared when they were used in at least two different years. Data of individual birds (points; \(N=53\)) were fitted with asymptotic curves (solid lines). The asymptote reached (numbers on top of lines) represent the average values expected given sufficient number of encounters for all individuals.
size in juveniles. Following a similar argument as for the seasonal comparison, juveniles with greater mobility may have easier escaped observation, precluding MCP computation and thus possibly biasing results.

Note that in our analysis of home-range size, we used all locations for MCP computation instead of the more common approach to discard the 5% greatest outliers (i.e. computing 95% MCPs) for two reasons. First, sample size per birds was on average small and re-encounters of birds generally infrequent (compared to, e.g., telemetry studies). Second, during our study not all water bodies possibly used by Mandarin Ducks could be surveyed regularly, especially some sites in the city of Berlin. Thus, each encounter had the potential to add important information about an individual’s space use. Based on similar reasoning, we also included opportunistic encounters from sites that were less often surveyed. Testing 95% MCPs naturally decreased absolute values of home-range size, however, our choice of using 100% MCPs did not influence our results qualitatively. In fact, given the above reasons, true home ranges may even be larger than reported here. However, even if absolute estimates of home-range size include some uncertainty, there were no indications that this may have influenced the comparability of home ranges between seasons, sexes, or age classes. We encourage future studies to implement a more rigorous sampling scheme that covers an even greater range of possibly occupied sites.

Site fidelity

Count data on Mandarin Ducks in the Berlin–Potsdam area as well as in other regions of the European range showed that they prefer specific sites at certain times of the year and that these preferred sites remain stable for at least several years (Erdmann 1992; Saemann and Flöter 2015; Mädlow 2018a). Our results confirm this at the individual level: the estimated between-year overlap of used water bodies by individual birds was considerably larger (54% and 61% for breeding and non-breeding season, respectively) than the between-season-overlap (35%), showing that individual birds tended to visit the same sites in the same season across multiple years. This fits with the notion on the benefits of familiarity with the environment and long-term spatial memory (Spencer 2012; Fagan et al. 2013). The overlap patterns suggest that on the one hand, individuals showed some preference for familiar sites, as large parts of the breeding home ranges were also used during the non-breeding season. On the other hand, individuals greatly increased their space use during the non-breeding season, indicating that they searched for sites that met fall and winter needs not only in proximity of their immediate breeding home-range. The relatively large between-year, within-season overlap suggests that throughout their annual cycles of varying needs, individual Mandarin Ducks remembered and revisited sites that met season-specific needs, for example tree cavities for breeding, protection during moult when they cannot fly, and food availability during tree masting and in ice-free waters in winter. However, individual ring recoveries also showed that some birds combined site fidelity with less regular and explorative space use in the greater vicinity of their core areas.

Conclusion

Year-round data on occurrences of Mandarin Ducks allowed us to analyze individual space use across the full annual cycle. Our study shows that despite apparent residency of Mandarin Ducks in our study region, different seasonal needs lead to small-scale seasonal shifts in space use, while individuals show site fidelity within seasons, across years. Our data further revealed that sex differences in home-range size (males’ being larger) carried on from breeding to non-breeding season, an unexpected result that suggests that habitat configuration (here configuration of water bodies within the urban/suburban matrix) is a strong driver of space use, especially bachelor males likely making use of habitat heterogeneity. Although data on waterfowl space use can best be acquired from automatic tracking devices attached to birds (e.g. GPS transmitters), especially in terms of spatial and temporal resolution, our study demonstrates that mark-resighting can also provide valuable information especially on longer-term space use. Facilitated by the fact that Mandarin Ducks regularly leave the water for roosting and the accessibility of many water bodies for surveying, we were able to collect data over many years and on many individuals to gain rare insights into waterfowl space use across all seasons. Thus, we suggest that mark-resighting via colour rings may for certain species still be a valid alternative to much more expensive GPS-tracking or short-term manual radio telemetry and particularly applicable within citizen-science projects.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-021-01932-7.

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Declarations

Conflict of interest  None declared.

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