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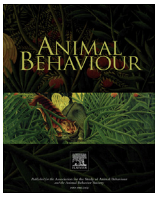

Dispersal behaviour and settlement in an invasive bird: dispersers prefer their natal habitat

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Habitat selection has profound consequences for individual fitness, but how do animals decide where to settle? The natal habitat preference induction (NHPI) hypothesis proposes that individuals choose habitats that exhibit similar environmental cues to those experienced in early life. In this study, we first examined juvenile movements and dispersal and then tested the NHPI hypothesis in the monk parakeet, *Myiopsitta monachus*, an invasive species that nests primarily in pine or palm trees in our study site. Juveniles were observed ranging extensively, but we found no relationship between ranging distances prior to dispersal and subsequent natal dispersal behaviour. As predicted by NHPI, we found that dispersed individuals displayed a significant preference for nesting in their natal tree type in their first year, irrespective of tree availability. The probability of changing tree type was not influenced by individual dispersal distance, the proportion of the natal tree type available or natal tree type. We found that adult birds undertaking breeding dispersal also showed a preference for the same tree type they dispersed from when making nest site selections, demonstrating that preferences can be maintained by adults during breeding dispersal movements. Finally, conspecific breeding success did not differ between palm and pine tree nests, and so did not provide a useful source of public information regarding the suitability of the two nesting substrates. These results contribute to our understanding of the drivers of habitat selection in both adults and juveniles and have implications for our understanding of dispersal patterns and range expansion in this worldwide invasive species.

Habitat selection can have a profound influence on individual fitness and a multitude of ecological interactions (Hale et al., 2015; Huey, 1991; Thomson et al., 2006), so understanding the causes and the ecological and evolutionary consequences of individual variation in habitat selection is important (Davis & Stamps, 2004; Piper et al., 2013; Selonen et al., 2007; Tonnis et al., 2005). One potential cause of individual variation in habitat choices is natal habitat preference induction (NHPI), which occurs when individuals demonstrate a propensity to select habitats that exhibit similar environmental cues to their natal habitat (Davis & Stamps, 2004; Stamps & Davis, 2006). NHPI influences habitat selection in several taxa including insects (Lhomme et al., 2018), fish (Arvedlund et al., 1999), amphibians (Hepper & Waldman, 1992), reptiles (Roe et al., 2010), mammals (Haughland & Larsen, 2004; Merrick & Koprowski, 2016) and birds (Piper et al., 2013). NHPI has been implicated as a mechanism driving reproductive isolation and speciation (Tonnis et al., 2005; Beltman & Metz, 2005; Bolnick et al., 2009; Qvarnström & Vallin, 2011), and maladaptive habitat selection (Piper et al., 2013); it may also have conservation implications (Kleinstäuber et al., 2018; Roe et al., 2010). However, conclusive demonstrations of NHPI in nature are few, perhaps due to the difficulty of assessing habitat availability in order to demonstrate a preference (e.g. Tordoff et al., 1998).

In addition to their personal natal experience, individuals may use intentional or unintentional cues from other individuals (social information) to select suitable territories or breeding sites (Boulinier & Danchin, 1997; Frederiksen & Bregnballe, 2001). Public information, a form of unintentional social information, regarding the breeding success of conspecifics can influence the decisions that determine habitat choice (Boulinier & Danchin, 1997; Danchin et al., 1998; Doligez et al., 2002; Parejo et al., 2007). For instance, in collared flycatchers, *Ficedula albicollis*, both settlement and

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departure decisions were influenced by conspecific breeding success (Doligez et al., 2002), and experimental indicators of conspecific reproductive success affected breeding-site selection by black-throated blue warblers, *Dendroica caerulescens* (Betts et al., 2008). In contrast, experimental manipulation of social information about reproductive success did not affect nest site choice by female wood ducks, *Aix sponsa*; instead, personal information about habitat structure appeared to drive decisions (Berg & Eadie, 2020). The accessibility and reliability of information and the costs associated with obtaining it may influence the use of information from different sources (Danchin et al., 2004; Kendal et al., 2005; Dunlap et al., 2016; Van Bergen et al., 2004). For example, public information may be more accessible in species that breed at high densities (Danchin et al., 1998), or may be of particular importance for naïve individuals with no personal breeding experience (Nordell & Valone, 1998). However, such information is likely to be more ephemeral than external habitat cues and therefore may be available to individuals over more limited timescales (Berg & Eadie, 2020).

Dispersal and choice of a habitat in which to breed is not necessarily a discrete event in an individual's lifetime. Habitat selection may be influenced by predispersal exploratory behaviour that determines the habitats that individuals can sample before deciding where to settle. Dispersal and associated habitat selection may also occur at various life stages and on multiple occasions across an individual's life span; natal dispersal is defined as the first movement of an individual from its natal area to a new location that is potentially suitable for reproduction, while breeding dispersal is the movement of an individual between consecutive breeding sites (Greenwood & Harvey, 1982). Whenever it occurs, dispersal is inherently difficult to study in open populations (Koenig et al., 1996). Moreover, studies routinely include dispersal outcomes but often report little regarding predispersal exploration due to methodological constraints. Nevertheless, several studies have shown that exploratory behaviour typically occurs prior to dispersal (Cox & Kesler, 2012; Debeffe et al., 2013), and such forays may be related to subsequent dispersal (Haughland & Larsen, 2004; Debeffe et al., 2013). For example, patterns of sex-biased dispersal reflect sex differences in exploratory behaviour in Florida scrub-jays, *Aphelocoma coerulescens*, (Sherer, 2019; Fitzpatrick et al., 1999; Woolfenden & Fitzpatrick, 1984). However, the movement of predispersal juveniles remains an understudied area of dispersal ecology and the potential ecological and evolutionary consequences warrant further investigation.

In this study, we used detailed field observations to investigate ranging behaviour, dispersal and the drivers of habitat selection in juvenile and adult monk parakeets, *Myiopsitta monachus,* an invasive parrot species native to South America (Forshaw, 1989), that has been introduced world-wide mainly through escapes from the pet trade (Bush et al., 2014; Lever, 2005; Postigo et al., 2019; Russello et al., 2008). Unusually among parrots, monk parakeets are not cavity-nesters; instead they construct large stick nests that can contain many separate chambers and are used year-round for roosting and breeding (Eberhard, 1998; Forshaw, 1989; Spreyer & Bucher, 1998). Multiple nests are often aggregated within trees (Bucher et al., 1990; Eberhard, 1998). Monk parakeets are non-territorial but defend their nests from predators and conspecifics (Dawson Pell, 2022). Previous investigations into dispersal behaviour revealed that natal dispersal is female biased and dispersal occurs over relatively short distances in the urban environment (Dawson Pell et al., 2021); natal philopatry has also been observed in both sexes (Dawson Pell et al., 2021). However, little is known about movements by juveniles prior to natal dispersal or regarding the factors driving nest site selection in this species. Understanding patterns of habitat selection is particularly important for our understanding of invasion dynamics in the monk parakeet. Clear preferences for certain nesting substrates are shown in different locations around the world, despite the availability of suitable alternatives (e.g. Di Santo et al., 2017; Roviralta & Garc, 2001). In addition, preference for certain substrate types has been linked to large-scale range expansion in this species; for example, the widespread planting of eucalyptus trees in Argentina was cited as a key factor favouring range expansions of the monk parakeet in South America (Bucher & Aramburú, 2014). Therefore, understanding the drivers of nesting substrate preference during habitat selection by monk parakeets may help to predict dispersal and range expansions, key aspects of biological invasions.

As habitat selection can be influenced by exploratory and dispersal behaviour, we first investigated movements by recently fledged monk parakeets in the months postfledging, testing whether ranging distances were related to whether an individual was philopatric in their first year postfledging or dispersed, or to the sex of the individual. We also examined whether ranging distances were related to subsequent natal dispersal distances. We then examined evidence for NHPI and investigated the factors that may influence changes in nesting tree type. To our knowledge, this is the first study to investigate NHPI in an invasive bird. In addition, we examined nesting tree type preferences following breeding dispersal by adult monk parakeets to determine whether preferences are maintained through breeding dispersal movements. Finally, we compared reproductive parameters in different tree types to examine whether conspecific productivity may be a useful source of public information regarding the suitability or quality of nesting tree types.

METHODS

Study Site and Species

The field study was conducted in Barcelona, Spain (41.39°N, 2.17°E) on the northeast coast of the Iberian Peninsula. The metropolitan area of Barcelona is approximately 102 km^2, comprising a highly developed urban environment with numerous parks containing both native and exotic vegetation. Barcelona has one of the highest densities of monk parakeets in Europe and the population is expanding exponentially (Postigo et al., 2019) with an estimated 5000 birds in 2015 (Molina et al., 2016; Senar et al., 2017). Monk parakeet nests were first recorded in Barcelona in Ciutadella Park in palm trees, *Phoenix dactylifera*, in 1975 (Batllori & Nos, 1985) and in 1992 the first pine tree, *Pinus halepensis*, nests were detected (Sol et al., 1997). The vast majority of current nests in Barcelona are in palm (68%) or pine (19%) trees, the focus of this study, with a small minority in other tree types (11%); nests in artificial structures (e.g. pylons; Newman et al., 2008, pp. 355–363) are reported elsewhere, but in Barcelona there are very few such nests (2%; Senar, 2015).

Sample Collection

Monk parakeet chicks were ringed during the breeding seasons (March–August) in 2003, 2017 and 2018, using a cherry picker to access nests. In 2003, chicks were ringed in Ciutadella Park, Passeig de Lluís Companys, Plaça de Tetuan and Jardins de Magalí. The same locations excluding Jardins de Magalí were used in 2017, and in 2018 nests were accessed only in Ciutadella Park and Passeig de Lluís Companys. Natal nesting tree type was recorded for each individual. For ringing, nestlings more than ca. 21 days old were removed briefly from nests and marked with aluminium leg rings and a unique medal on a neck collar (Senar et al., 2012). Blood samples (maximum 50 μl) were extracted from either the jugular or brachial vein for genetic sex typing. For details of blood sample storage, DNA extraction and PCR protocols see Dawson Pell et al. (2020). Blood samples were unavailable for the juveniles that fledged in 2003, but all other ringed juveniles included in analyses ($N = 56$) were sexed using a sex marker, Z002B (Dawson, 2007), previously confirmed to sex monk parakeets successfully (Dawson Pell et al., 2020).

Ethical Note

Monk parakeets were handled and blood samples extracted with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. J.C.S. received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07.

Juvenile Movements

To investigate the potential for habitat sampling by juvenile monk parakeets prior to dispersal, we collected location data of individually marked birds in the months following fledging (June–September) in 2017 and 2018. These data were collected in three ways: by observations conducted for approximately 3 h every week at an artificial food source (containing sunflower seeds and peanuts) set up on the roof of the Museu de Ciències Naturals de Barcelona within Ciutadella Park, by opportunistic recording of the location of individuals encountered during surveys of the core field site in Ciutadella Park, or by surveys across Barcelona. Most individuals were observed during surveys of Ciutadella Park, but surveys of sites up to 6 km from the main study area were also conducted. Monk parakeets are nonterritorial, so for this study we defined ranging movements as any movements away from the nesting tree by recently fledged individuals. Therefore, the ranging movements recorded in this study may include foraging trips as well as more exploratory forays to assess habitat prior to dispersal.

We calculated distances travelled by juveniles using the GPS coordinates of the sighting location and the natal tree and the distGeo function in the geosphere package (Hijmans et al., 2019). In analyses of ranging behaviour, we included birds that were philopatric and those that dispersed for their first breeding season. Here and elsewhere, we define philopatric birds as those that remained nesting in their natal tree for their first breeding season postfledging; birds that nested any distance from their natal tree, even if they moved to a neighbouring tree, were considered to have dispersed. We observed 67/73 (92%) of the birds with GPS locations away from their natal tree in the months following fledging with a mean of 7.6 ± 6.1 SD sightings per individual (total = 509 locations, range 1–27 per bird).

To examine whether mean or maximum observed ranging distance was influenced by the sex or number of observations of each bird we constructed separate generalized linear models (GLM) with Gaussian error distributions in R version 3.5.0 (R Core Team, 2018). We checked model assumptions and transformed data where required. The response variables, mean and maximum distance from the natal tree, were log-transformed and square-root transformed, respectively, and we included sex and the number of observations per individual as predictor variables. We considered terms significant at $P < 0.05$. We also tested for differences in the mean and maximum ranging distances of individuals that dispersed or were philopatric in their first year postfledging using a Wilcoxon rank sum test and a t test on square-root-transformed data, respectively. To examine the relationship between dispersal distances and either the mean or maximum ranging distance we conducted separate linear regressions. We also determined whether either dispersal or maximum recorded ranging distance was further for each individual.

Nesting Tree Selection Following Natal Dispersal

The nest locations of marked monk parakeets were recorded in the breeding season of their first year postfledging (2004, 2018 or 2019) during surveys of nests in Ciutadella Park and nest sites elsewhere across Barcelona. Over 640 h were spent surveying the main nest sites across Barcelona, up to 6 km from Ciutadella Park (2004: 260 h, Carrillo-Ortiz, 2009, 2018 and 2019: 387 h). When marked birds were located, the tree type and GPS coordinates of the nest were recorded. Monk parakeet nests are often spatially clustered in groups occupying the same or neighbouring trees; these aggregations are sometimes referred to as colonies (Bucher et al., 1990; Eberhard, 1998). However, due to a lack of clear delimitations between monk parakeet colonies we instead used nesting tree location without assigning birds a 'colony' location. Individuals were recorded as nest occupants only if they were seen either in a nest chamber or delivering nest material; birds observed only perched in a tree containing a nest were not assumed to occupy a nest in that tree. All statistical analyses were performed in R version 3.5.0 (R Core Team, 2018). Dispersal distances were calculated using the distGeo function in the geosphere package (Hijmans et al., 2019) using GPS coordinates of natal and first-year nesting trees.

The nests of 103 birds we ringed as nestlings were located during the study. A number of birds were excluded from the data set; seven birds were first located during their second breeding season and were excluded because experience during their first breeding season may have influenced subsequent nest location. Three birds that nested in tree species other than palms or pines were also excluded. Twenty-one birds (nine dyads, one trio) built nests with siblings and could not be considered independent, so one bird from each dyad and two birds from the trio were removed before analyses. Thirty-three of the 1-year-old birds nested in their natal tree; five of these (two males, three females) remained in a nest chamber with at least one parent bird and were excluded for not having chosen where to place their own nest. The other 28 philopatric birds (four females, 21 males, three unknown sex) had paired and built their own nests in their natal tree and were not excluded from initial analyses. Some birds fell into more than one exclusion category.

We first examined whether birds were more likely to be philopatric when fledging from a pine or palm tree using a chi-square test of independence. For this analysis we had 78 individuals, but to be conservative, we excluded any philopatric birds from the analysis of NHPI, because philopatry may have dictated their nest tree choice. Following these strict exclusion criteria, there were 56 birds (24 males, 18 females, 14 unknown sex) in a conservative data set for analyses of NHPI.

The availability of tree types for nesting was determined using the tree inventory managed by Barcelona City Council containing data from the entire city (Open Data Barcelona, https://opendata-ajuntament.barcelona.cat/en/ and https://ajuntament.barcelona.cat/ecologiaurbana/en/about-us/companies-and-independent-bodies/municipal-institute-of-parks-an; accessed 2021). Mean dispersal distances for juveniles was 386 m when philopatric birds were excluded (see Results), and we used this distance as a proxy for average search distance to determine the numbers of each tree type likely to be encountered by individuals. This distance was well within the maximum observed ranging distances of individuals (see Results). Using QGIS version 3.4.14 (QGIS Development Team, 2018) we created 'search areas' for each individual as circles with a radius of 386 m with the natal tree at the centre of the circle and determined the number of each tree type available within this search radius. Included in the palm tree count are *P. dactylifera* and *Phoenix* *canariensis,* both of which are used by monk parakeets for breeding, and pine trees included *Pinus brutia, P. halepensis, Pinus nigra, Pinus pinaster, Pinus pinea and Pinus roxburghii*, all of which may be used by parakeets for nesting. All but three birds had both pine and palm trees available to them within the exploration radius. Three birds that fledged in 2003 had only palms available, having fledged from palm nests that were 595 m, 624 m and 657 m from their nearest pine tree. The number of palms available to birds within the search radius ranged from 12 to 150 (mean ± SD = 120 ± 39) and the number of pines ranged from 0 to 251 (mean ± SD = 52 ± 48). For each individual we calculated the proportion of available pines and palms within the 386 m radius. All trees were assumed to be available for nesting because many nests can be constructed in a single tree; therefore, occupied trees are still available for settlement by newcomers.

In our assessment of tree availability we used a fixed search radius; however, as individual differences in dispersal distances have the potential to alter the habitat available to dispersers (Mabry & Stamps, 2007), we also examined whether the dispersal distance of an individual influenced the probability of an individual changing tree type. We ran a binary logistic regression GLM with a logit-link function including the binary response variable of whether an individual changed tree type or not. Using this model, we investigated the possibility that the proportion of the natal tree type available within the assigned search radius (386 m), the natal tree type, the interaction between the natal tree type and the proportion of the natal tree type available, the dispersal distance of an individual, or the interaction between natal tree type and dispersal distance influenced the probability that an individual changed tree type. We checked model assumptions and transformed data where necessary. We conducted model reduction through stepwise backwards elimination (Crawley, 2005); comparisons of models were conducted using likelihood ratio tests and terms were removed by order of least significance. *P* values for removed terms were calculated by comparisons between the minimal model without the term included and a model including the term. Final significance values for retained terms were obtained by comparing the minimal model with a model from which the term of interest was removed.

Nesting Tree Selection Following Breeding Dispersal

We examined whether adult birds ($N = 25$) that undertook breeding dispersal preferred to nest in the same tree type they had previously used following dispersal movements. All birds observed making breeding dispersal movements dispersed from pine trees (for details of surveys see Dawson Pell et al., 2021) and for each event we recorded nesting tree type following breeding dispersal. Using the same search distance (386 m) we applied for juveniles, we assessed the available vegetation for each bird that underwent breeding dispersal. This distance is within reported home range sizes (radius 300–400 m) for adult monk parakeets (Carrillo-Ortiz, 2009; Senar et al., 2021) and also within recorded breeding dispersal distances at our study site (maximum 464 m; Dawson Pell et al., 2021). As with birds in the natal dispersal analysis, for each individual we calculated the proportion of available pines and palms within a 386 m search radius. Mean proportion of palm trees when including data for all birds was 0.76 (range 0.49–0.89) and the mean proportion of pines was 0.24 (range 0.1–0.51). Because numbers in one category were small, we were unable to perform a binary logistic regression as above as this prevented model convergence. Alternatively, we applied two chi-square tests, one test assuming the most abundant tree within each individual's assigned search radius was selected to generate expected numbers of individuals selecting each tree type and one test using the mean tree abundance to generate expected numbers.

Breeding Success

In addition to, or instead of, personal information, individuals may use public information regarding conspecific breeding success in the process of nest site selection. To assess the potential for this to occur we compared reproductive success in pine and palm tree nests at our study site. We monitored breeding activity from April to June (first broods) 2017 in Ciutadella Park and the Passeig de Lluís Companys, accessing nests with a cherry picker. During each nest chamber check, we recorded whether it was being used for breeding, the clutch size, and the number and age (estimated from known monk parakeets' growth rates; Carrillo-Ortiz, 2009) of any chicks present. Each active nest was visited two or three times over the course of the first brood and we assumed that any chicks that attained ringing age (> ~21 days) fledged successfully. Approximately half of monk parakeet pairs in Barcelona attempt a second brood, but clutch size and fledging success are significantly lower in second broods (Senar et al., 2019). Here we focus only on reproductive success in first broods because we did not monitor second broods. We used Wilcoxon rank sum tests to investigate whether clutch size or the number of fledglings differed between nests in pine and palm trees.

RESULTS

Juvenile Movements

Juveniles were observed ranging a mean distance of 148 m ± 151 SD (range 3–994 m) and a maximum distance of 305 m ± 256 SD (range 3–1587 m) from their natal tree. There was a significant positive correlation between the mean and maximum observed ranging distances (Fig. A1) and neither the mean nor the maximum ranging distances differed between birds that dispersed ($N = 37$) and birds that were philopatric ($N = 30$) in their first year postfledging (mean: $Z = -1.437$, $N = 67$, $P = 0.151$; maximum: $t_{65} = 0.912$, $P = 0.365$; Fig. 1).

We observed more males ($N = 45$) away from the nest than females ($N = 22$), but the number of sightings per bird (mean ± SD = 7.6 ± 6.1; $N = 67$) did not differ significantly between males (mean ± SD = 8.4 ± 6.2) and females (mean ± SD = 5.9 ± 5.6; Wilcoxon rank sum test: $Z = -1.869$, $N = 67$, $P = 0.062$). Neither the sex (Fig. A2) nor the number of sightings of an individual was significantly related to either the mean or maximum observed ranging distance (Table 1).

We investigated whether postfledging ranging behaviour was related to subsequent dispersal behaviour using data from 34 individuals with both dispersal and ranging distances. Dispersal distance was not significantly related to either the mean (linear regression: $F_{1,32} = 0.992$, $N = 34$, $R^2 = 0.030$, $P = 0.327$) or the maximum ranging distance ($F_{1,32} = 1.408$, $N = 34$, $R^2 = 0.042$, $P = 0.244$), indicating that birds that were recorded ranging further from the nest in the first few months postfledging did not disperse greater distances subsequently. Indeed, for 20/34 birds (59%), the maximum observed ranging distance exceeded their eventual dispersal distance, indicating that birds readily ventured further than they dispersed and that our use of mean dispersal distance (386 m) to define sampled habitat for nesting tree selection was appropriate.

Nesting Tree Selection Following Natal Dispersal

Birds fledging from palm trees were more likely to disperse than birds fledging from pine trees (GLM: $\chi^2 = 5.5$, $P = 0.019$; Fig. 2). For the birds that dispersed, we found a significant preference for the natal tree type (intercept $P < 0.05$; Table 2) and this effect was

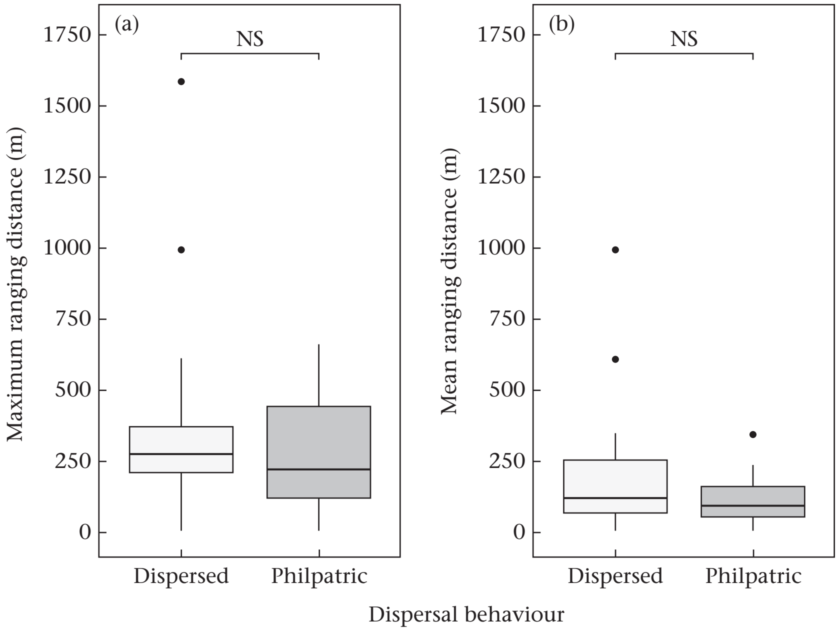

Figure 1. (a) Maximum and (b) mean ranging distances of juvenile birds that dispersed for their first breeding season ($N = 37$) compared to birds that were philopatric in their first season ($N = 30$). All data were recorded in the months postfledging (June–September). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Table 1
GLM examining factors affecting mean and maximum observed ranging distances of juvenile monk parakeets

Model	Parameter	Estimate±SE	*t*	*P*
Mean ranging distance[a]	(Intercept)	1.951±0.113	17.240	<0.001
	Sex	0.088±0.123	0.718	0.476
	No. of sightings	−0.004±0.010	−0.380	0.705
Maximum ranging distance[b]	(Intercept)	13.056±1.696	7.698	<0.001
	Sex	1.988±1.838	1.081	0.284
	No. of sightings	0.213±0.142	1.494	0.140

$N = 67$ birds: 22 female, 45 male.
[a] Mean ranging distance was log-transformed.
[b] Maximum ranging distance was square-root transformed.

stronger for birds fledging from palm trees compared to pine trees ($P < 0.05$; Table 2). The probability of changing tree type was not significantly affected by the proportion of the natal tree type available, the interaction between the proportion of the natal tree type available and the natal tree type itself, the interaction between log(dispersal distance) and the natal tree type, or log(dispersal distance; all $P > 0.05$; Table 2).

Nesting Tree Selection Following Breeding Dispersal

We observed 25 breeding dispersal events by 24 adults, all involving birds that dispersed from pine trees (Dawson Pell et al., 2021). Most breeding dispersal events involved birds moving from one pine tree to another pine tree (23/25 birds, 92%), and just two birds (8%) moved from a pine tree to a palm tree. Birds were significantly more likely to select the same tree type as the one they were dispersing from, despite the availability of the alternative tree type; this was the case when using the most abundant tree type to generate expected choices (pine: $\chi^2 = 239.7$, $P < 0.001$; Fig. 3a) and when using the overall proportions of trees to generate expected numbers of birds nesting in each tree type ($\chi^2 = 63.4$, $P < 0.001$; Fig. 3b). Eight (33%) of these breeding dispersal events were by individuals marked as nestlings in 2017: five used the same tree type in their first breeding season as their natal tree type and the other three changed tree type for their first breeding season. When these eight individuals undertook breeding dispersal, seven used the same tree type following dispersal and the remaining bird changed tree type, reverting to its natal tree type.

Breeding Success

We monitored breeding success in 23 palm trees containing 23 nests and 40 separate breeding chambers and 10 pine trees containing 41 nests and 49 breeding chambers. There was no significant difference between palm and pine trees in either clutch size ($Z = -0.996$, $N = 89$, $P = 0.32$; Fig. 4a) or the number of fledglings ($Z = -0.564$, $N = 89$, $P = 0.57$; Fig. 4b).

DISCUSSION

Monk parakeets were significantly more likely to select their natal tree type in their first breeding season, rather than change tree type. This preference was expressed regardless of the availability of the nesting substrates because the proportion of the natal tree type available within the search radius did not significantly influence the probability of changing tree type between natal nest and first breeding attempt. This result provides evidence for NHPI, a phenomenon rarely demonstrated outside a laboratory environment.

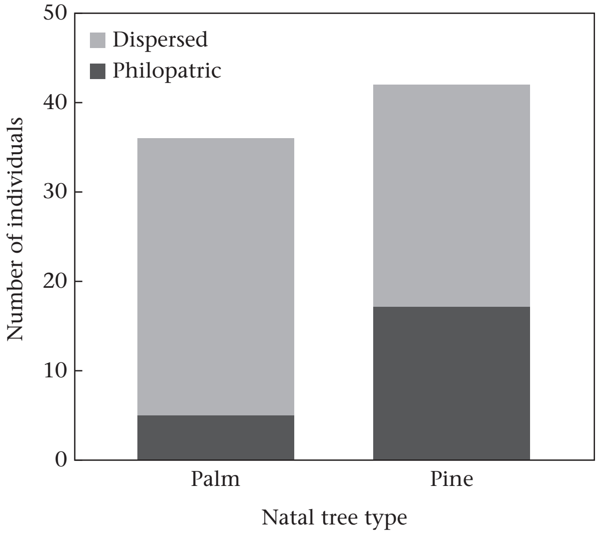

Figure 2. The number of individuals fledging from pine and palm trees that were philopatric to their natal tree or dispersed for their first breeding season ($N = 78$).

Table 2

Correlates of the probability of monk parakeets changing tree type, showing parameter estimates (β), SE, Z and P values for binary logistic regression models

Parameter[a]	β[b]	SE	Z	P[c]
Intercept	4.011	± 1.685	2.381	0.017**
Natal tree type	−1.524	± 0.659	−2.313	0.015**
Log(dispersal distance)	−1.129	± 0.638	−1.771	0.064*
Proportion natal tree				_0.564_
Proportion natal tree*Natal tree type				_0.828_
Log(dispersal distance)*Natal tree type				_0.246_

$N = 56$ birds: 24 male, 18 female, 14 unknown sex.

[a] Information given for terms in the final models and those removed through stepwise backwards elimination. Terms were retained at $P < 0.1$ ($^{*}P < 0.1$, $^{**}P < 0.05$). Dropped terms are indicated in italics.

[b] Effect sizes (± SE) were obtained from the minimal model in each case.

[c] Dropped terms removed during model selection were individually returned to the minimal model to assess significance using likelihood ratio tests, where appropriate also including individual terms from the interaction in this assessment.

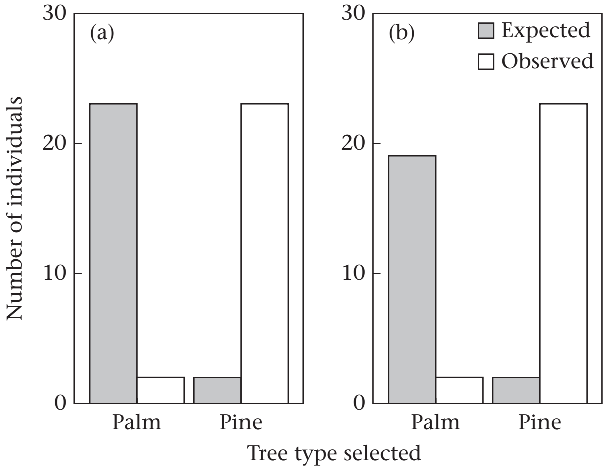

Figure 3. Breeding dispersal tree type selection by adult monk parakeets ($N = 25$ breeding dispersal events). Observed and expected values for tree type selection are shown for (a) expected values calculated by assigning the expected tree type per individual based on abundance within an individual's 386 m search radius ($P < 0.001$) and (b) expected values calculated using the mean proportions of available vegetation ($P < 0.001$).

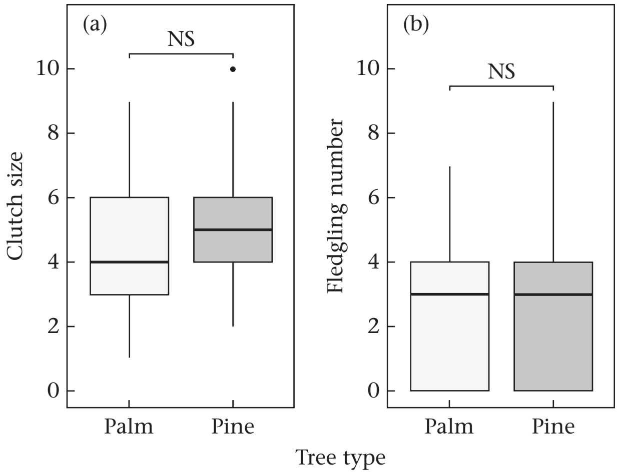

Figure 4. Breeding success in palm and pine trees: (a) clutch size and (b) fledgling number (more than ca. 21 days old assumed to have fledged). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

These results add to a growing body of evidence suggesting NHPI may be a common mechanism for habitat selection (e.g. Merrick & Koprowski, 2016; Piper et al., 2013; Selonen et al., 2007).

Where NHPI has been demonstrated in nature, the availability of alternative habitat types has not always been taken into account (e.g. Tordoff et al., 1998). Palm and pine trees are widely distributed across Barcelona and both tree types were available to all but three individuals in our study within the assigned search area. In addition, we demonstrated extensive ranging movements by recently fledged monk parakeets and adult birds have been shown to routinely travel hundreds of metres and even several kilometres to forage (Carrillo-Ortiz, 2009; Senar et al., 2016), so our results cannot be attributed to limited habitat availability or insufficient sampling.

There are a number of hypotheses explaining why NHPI as a mechanism for habitat selection may be adaptive (Davis & Stamps, 2004). NHPI may be selected for if it enables individuals to effectively and quickly discern high-quality habitat (Davis, 2019; Davis & Stamps, 2004). As habitat enabling the rearing of offspring to independence is likely to be of sufficient quality (Stamps et al., 2009), settling in habitats that exhibit similar stimuli to natal habitats may reduce the costs associated with habitat assessment and hence reduce dispersal risks, a process termed ‘habitat cuing’ (Davis & Stamps, 2004; Stamps, 2001; Wauters et al., 2010). Alternatively, experience accrued in the natal habitat may improve an individual's performance in similar habitats after dispersal. This is termed ‘habitat training’ and can refer to any morphological, physiological or behavioural change (Stamps, 2001; Stamps & Davis, 2006). Juvenile monk parakeets frequently delay dispersal, often for many months (Emlen, 1990; Martín & Bucher, 1993) providing ample opportunity to learn nest-building techniques appropriate for their natal tree type. Building techniques are likely to differ between trees; pine tree nests are often constructed around thin, densely packed branches, whereas palm tree nests are built with much more structural support from the bases of palm fronds. Therefore, birds may be more efficient when building their own nest in the same tree type as their natal nest. However, this hypothesis remains untested.

NHPI is usually considered to be a learned preference for cues from the natal habitat, but preferences could be heritable (Jaenike & Holt, 1991). Without addressing the possibility for an inherited genetic preference driving habitat selection in the monk parakeet, we have not demonstrated NHPI sensu stricto, but a cross-fostering experiment could be employed to address this, as suggested for previous study systems in which NHPI has been demonstrated without directly addressing the issue of heritable preferences (e.g. Piper et al., 2013).

Monk parakeets showed a marked preference for building new nests in pine trees in breeding dispersal events from pine trees, indicating that a preference for this nesting substrate is maintained through the process of breeding dispersal. Although we cannot disentangle whether this is a maintained natal preference or perhaps the result of preference driven by personal breeding experience, the majority of these breeding dispersal events (84%) occurred following nest destruction as part of an invasive species control programme (Dawson Pell et al., 2021). Nest destruction and any consequential loss of reproductive success could influence dispersal decisions. For instance, northern flickers, *Colaptes auratus*, disperse further after nest predation than after a successful nesting attempt (Fisher & Wiebe, 2006) and breeding failure in black kites, *Milvus migrans*, leads to breeding dispersal in both sexes (Forero et al., 1999). However, despite nest destruction, monk parakeets were still highly faithful to the nest site (Dawson Pell et al., 2021) and the vast majority (90%) that did disperse moved to the same tree type, indicating that reproductive failure or significant disturbance of nesting sites did not influence preferences for nesting in pine trees. Note that nest destruction in this instance occurred after the first brood and at the start of the second brood, so birds may have fledged a successful first brood before nest destruction. Our results may point to long-term preferences for the natal tree type, potentially with significant consequences. For example, NHPI could lead to assortative mating for a specific preference if partners select common habitat features. Also note that we did not follow the majority of birds from fledging so we had no data on whether they had previously changed tree type and now demonstrated an alternative preference. A maintenance of natal preference could be confirmed by longer term investigations over multiple breeding seasons.

Despite female monk parakeets demonstrating a greater propensity to disperse and dispersing further (Dawson Pell et al., 2021), this pattern was not reflected in the ranging distances of individuals in the first 4 months postfledging. North American red squirrels, *Tamiasciurus hudsonicus*, also exhibit no sex difference in exploration distance (Haughland & Larsen, 2004), but our results contrast with the exploratory forays of Florida scrub-jays, in which sex differences in exploratory distances are reflected in subsequent patterns of sex-biased dispersal (Sherer, 2019; Fitzpatrick et al., 1999; Woolfenden & Fitzpatrick, 1984). In addition, the movements we observed in the monk parakeet were not related to whether an individual dispersed or was philopatric in its first year. This result is similar to that observed in the flying squirrel, *Pteromys volans* (Selonen & Hanski, 2006), but differs from the pattern of exploratory forays in roe deer, *Capreolus capreolus*, in which individuals that dispersed explored more than those that remained philopatric (Debeffe et al., 2013). It is possible that the distances moved by juvenile monk parakeets increase or change over time, so the movements we recorded in the first 4 months postfledging may not have captured exploratory behaviours most relevant to dispersal that may occur prior to the onset of the first breeding season. Using remote means of assessing ranging behaviour would allow for further investigations across longer time periods into the relationship between ranging behaviour postfledging, exploratory forays and subsequent dispersal behaviour. In addition, our estimates of ranging distances included all movements away from the nesting tree, including foraging trips as well as potential exploratory forays. Indeed, there may be no clear distinction between the two kinds of movement in a nonterritorial species where home ranges may be very large and overlap extensively with those of conspecifics. However, the important point is that, whether movements were made for habitat exploration or for foraging, we have shown that monk parakeets routinely travel distances that exceed dispersal distances, and therefore that birds have ample opportunity to sample habitat beyond that selected as a nest site.

We also tested whether public information regarding relative breeding success in pine and palm trees may be useful during the process of nesting tree selection. The prolonged breeding season of monk parakeets in Spain, often including two broods over 6–7 months (Senar et al., 2019), would likely allow for assessment of conspecific breeding success because fledged birds roost in their natal nest postfledging and are regularly fed by adults at the nest and are therefore visible to prospecting individuals. Moreover, colonial behaviour facilitates the use of public information (Brown et al., 2000; Danchin et al., 1998) which may be particularly useful for naïve individuals with no personal experience of breeding (Nordell & Valone, 1998). However, productivity did not differ between pine and palm trees, at least for first broods, so if public information is used, it would indicate that these substrates are equally suitable for nesting. To further address the possibility that public information influences nest site choice in the monk parakeet, experimental manipulation of breeding success and subsequent monitoring of habitat selection, and assessments of offspring quality and recruitment, could shed more light on the salient cues used during habitat selection in this species.

Our results are consistent with patterns of nesting substrate use by monk parakeets across their native and invasive range. Nesting substrates vary between locations, but within each location certain substrates are used consistently despite the availability of alternatives. For example, cedars, *Cedrus* spp., are preferred in both Rome (Di Santo et al., 2017) and Madrid (Roviralta & Garc, 2001), while artificial structures, such as electricity substations, are often used in North America, causing power outages and safety risks (Newman et al., 2008, pp. 355–363). If individuals fledging from nests on artificial structures exhibit NHPI, and adults retain nesting substrate preferences even after significant nest disturbance or destruction, the problems that such nests cause could be perpetuated. If NHPI is indeed a phenomenon common to all monk parakeet populations, this could lead to predictable expansion patterns, particularly at small spatial scales and in urban environments where vegetation types are well known. On the other hand, a degree of flexibility in substrate choice may also contribute to their success as an invasive species (Duncan et al., 2003; Wright et al., 2010); such behavioural flexibility has been suggested to be particularly relevant to species capable of both individual and social learning (Wright et al., 2010). For example, for monk parakeets in Argentina, there has been a recent shift to eucalyptus trees *Eucalyptus* spp. (Bucher & Aramburú, 2014) from previously preferred tree species (Volpe & Aramburú, 2011), a shift that has been credited with facilitating large-scale range expansion in the species (Bucher & Aramburú, 2014). Likewise, during the invasion of Barcelona, monk parakeets preferred palm trees initially (95%; Sol et al., 1997), but have since shifted to exploiting pines and other substrates. Such flexibility may be indicative of innovation in this species and could influence dispersal capability and resulting dispersal patterns. Our results, combined with the patterns observed around the world, indicate conservatism in nest tree choice within populations, perhaps driven by NHPI, but they also demonstrate a degree of plasticity, which may facilitate invasion success in novel environments.

In conclusion, our results demonstrate that the mobility of juvenile monk parakeets allows for extensive habitat sampling prior to dispersal. Our results support the NHPI hypothesis in the monk parakeet, that a preference for nesting tree type is the result of natal experience, as opposed to being driven by tree availability or being influenced by public information regarding the suitability of nesting substrates. Taking NHPI and breeding dispersal habitat preferences into account could lead to a better understanding of dispersal patterns and improved predictions of range expansion, which is important for the design of effective management strategies for this invasive species.

Author Contributions

J.C.S., F.S.E.D.P. and B.J.H. designed the study. A.O.S., J.C.O. and F.S.E.D.P. collected field data and F.U. extracted vegetation data. F.S.E.D.P. conducted laboratory work and analysed the data. F.S.E.D.P. wrote the paper with input from the co-authors. All authors read and approved the final manuscript.

Data Availability

Data are provided in the Supplementary Material.

Declaration of Interest

None.

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Supplementary material

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Appendix

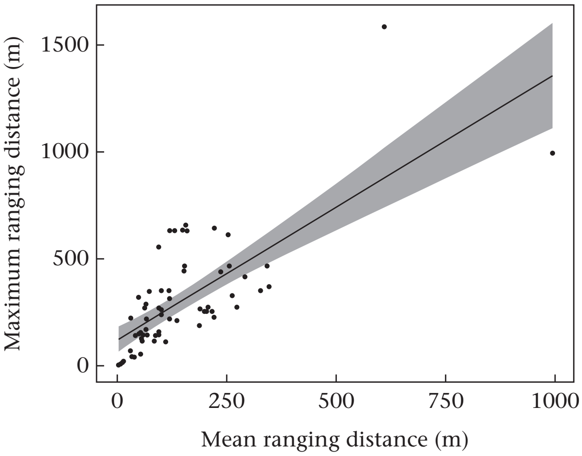

Figure A1. Correlation between mean and maximum ranging distances of juvenile monk parakeets (Spearman correlation: $r_S = 0.756$, $N = 67$, $P < 0.001$). Grey shading represents 95% CI.

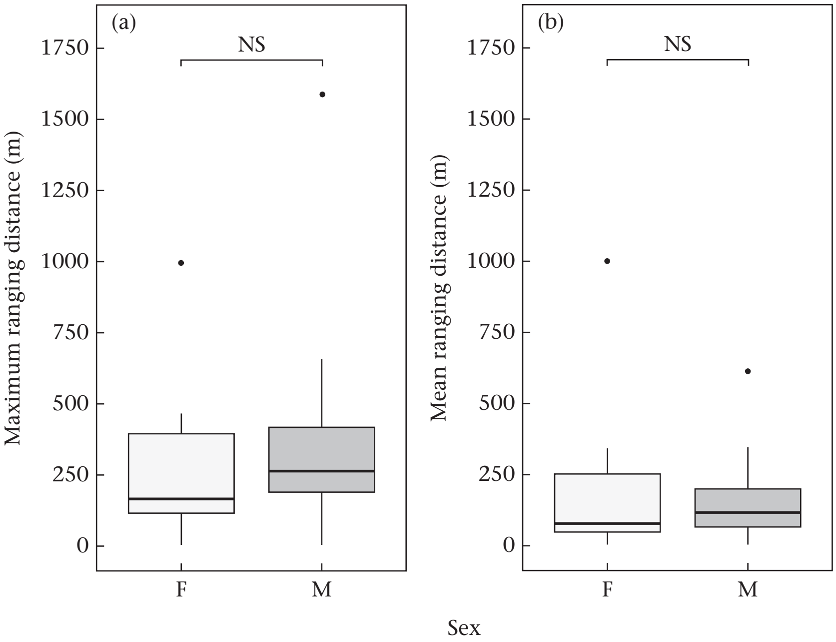

Figure A2. (a) Maximum and (b) mean ranging distances of male (*M*; $N = 45$) and female (*F*; $N = 22$) juvenile monk parakeets recorded in the months postfledging (June–September). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.