

PRIMARY RESEARCH ARTICLE

Human activity shapes the wintering ecology of a migratory bird

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Abstract

Human behavior profoundly affects the natural world. Migratory birds are particularly susceptible to adverse effects of human activities because the global networks of ecosystems on which birds rely are undergoing rapid change. In spite of these challenges, the blackcap (*Sylvia atricapilla*) is a thriving migratory species. Its recent establishment of high-latitude wintering areas in Britain and Ireland has been linked to climate change and backyard bird feeding, exemplifying the interaction between human activity and migrant ecology. To understand how anthropogenic influences shape avian movements and ecology, we marked 623 wintering blackcaps at 59 sites across Britain and Ireland and compiled a dataset of 9929 encounters. We investigated visitation behavior at garden feeding sites, inter-annual site fidelity, and movements within and across seasons. We analyzed migration tracks from 25 geolocators fitted to a subset of individuals to understand how garden behavior may impact subsequent migration and breeding. We found that blackcaps wintering in Britain and Ireland showed high site fidelity and low transience among wintering sites, in contrast to the itinerant movements characteristic of blackcaps wintering in their traditional winter range. First-winter birds showed lower site fidelity and a greater likelihood of transience than adults. Adults that frequented gardens had better body condition, smaller fat stores, longer bills, and rounder wingtips. However, blackcaps did not exclusively feed in gardens; visits were linked to harsher weather. Individuals generally stayed at garden sites until immediately before spring departure. Our results suggest that supplementary feeding is modifying blackcap winter ecology and driving morphological evolution. Supplemental feeding may have multifaceted benefits on winter survival, and these positive effects may carry over to migration and subsequent breeding. Overall, the high individual variability in blackcap movement and foraging ecology, and the flexibility it imparts, may have allowed this species to flourish during rapid environmental change.

Miriam Liedvogel and Ben C. Sheldon should be considered joint senior author.

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KEYWORDS

animal movement ecology, annual cycle, anthropogenic effects, bird migration, carry-over, climatic effects, foraging, site fidelity, supplemental feeding

1 | INTRODUCTION

Humans are increasingly influencing the natural world. Organisms of all kinds are affected by a range of pressures, including effects of development and agriculture on natural habitats; changing temperature and precipitation regimes wrought by climate change; hunting and exploitation; and light and noise pollution (Benítez-López et al., 2017; Gaston et al., 2013; Kunc et al., 2016; Mantyka-pringle et al., 2012). Organisms differ in their abilities to adjust to environmental changes, and the extent to which ecological communities will be able to keep pace is unclear (Feeley & Rehm, 2012; Liang et al., 2018; Poloczanska et al., 2013; Urban et al., 2016). Migratory birds are key to ecosystem health (Bauer & Hoye, 2014), but they are particularly susceptible to environmental change because successful migration requires the integration of a number of different stages, each one sensitive to ongoing changes that may be poorly correlated. Migrants must time their journeys precisely; navigate accurately through a dynamic atmosphere; locate resources safely, reliably, and efficiently; and thrive in ecological contexts that differ across seasons and hemispheres. As climate change shifts optimal timing windows, wind regimes, and storm patterns, and as humans modify both the landscapes through which birds pass and the areas where they breed and winter, a migratory strategy may become increasingly untenable (Runge et al., 2015; Wilcove & Wikelski, 2008). These challenges are particularly acute for species that migrate long distances (Sanderson et al., 2006). Migrant birds are in decline across the world, raising concerns that many may lack the flexibility to rapidly respond and adapt (Both et al., 2010; Rosenberg et al., 2019; Sanderson et al., 2006).

Whether migratory species have the capacity to adjust to rapid change is a focal question of current research. Many migratory birds, especially long-distance travelers, are guided by innate timing and navigational programs thought to have limited flexibility (Åkesson et al., 2017; Gwinner, 1996). There is some evidence of microevolutionary change in these endogenous programs, but it is unclear whether this can match the pace of warming (Charmantier & Gienapp, 2014; Helm et al., 2019; Merilä & Hendry, 2014; Van Buskirk et al., 2012). Plasticity in response to climate change is also well documented, especially among short-distance migrants (Gienapp et al., 2007; Usui et al., 2017), and increasing evidence points to flexibility among long-distance migrants as well (Brown et al., 2021; Haest et al., 2020; Klinner & Schmaljohann, 2020). As changes continue, species will not only need to shift timing across multiple stages of the annual cycle, but also undergo large-scale distributional changes to track suitable conditions. Climate-induced range shifts have been documented in birds (La Sorte & Thompson III, 2007; Lehikoinen & Virkkala, 2016; Tingley et al., 2012), but we lack a full understanding of the ecological and behavioral processes that facilitate these shifts (Gill et al., 2019). This poses a challenge for predicting how species will respond in the future.

The Eurasian blackcap (*Sylvia atricapilla*) is a migratory songbird thriving in the face of environmental change (EBCC/BirdLife/RSPB/CSO, 2018). This widespread species shows a spectrum of migratory strategies from sedentary to fully migratory, including a range of migratory directions (Roselaar, 1992). In addition, it has shown substantial and continuing breeding population growth across Europe, increasing +155% since 1980 (EBCC/BirdLife/RSPB/CSO, 2018). Alongside these increases, the blackcap has expanded its European wintering range northward in the last half century, most notably in Britain and Ireland, where its status has changed from a rare winter visitor (before 1960) to an established component of the winter avifauna (Berthold & Terrill, 1988; Leach, 1981). In Britain and Ireland, its winter range increased by 77% between 1981–1984 and 2007–2011, and the species was present in 48% of 10-km squares in 2007–2011 (Balmer et al., 2013). This transformation may be linked to human activity in two ways (Berthold & Terrill, 1988; Plummer et al., 2015): first, climate change has resulted in milder winters, and second, abundant garden feeding stations now provide a reliable food source throughout the winter. Surprisingly, available evidence indicates that virtually all British overwinterers are *not* residents that originate from British breeding populations, but rather are visitors from continental Europe that undertake highly atypical north-westerly migrations in autumn (Berthold et al., 1992; Delmore et al., 2020; Wernham et al., 2002). These individuals differ from those that use traditional Mediterranean winter areas in a number of important ways: they use a novel migratory direction, winter at higher latitudes, utilize human-dominated habitats, and are closely associated with supplementary food provided by humans and fruit-bearing plantings. Blackcaps wintering in Britain and Ireland have adapted to many of the characteristic features of the Anthropocene, and understanding the processes linked to their success will reveal what it takes for a migratory bird to succeed in the face of global change.

Here, we study the ecology and behavior of blackcaps wintering in Britain and Ireland. We use ringing recoveries and a detailed dataset of individual captures and resightings to study how individually color-marked birds utilize garden habitats and food resources. We also examine how their behavior is influenced by local environmental conditions and mediated by body condition and morphology. We hypothesize that blackcaps are not wholly reliant on supplementary food throughout the winter, but that it may be a lifeline during challenging conditions. We also quantify the site fidelity of individuals between winters. Studies in Mediterranean and African wintering areas report winter blackcap recapture rates of only 0–5% in subsequent years (Cuadrado, 1992; Cuadrado et al., 1995; King & Hutchinson, 2001; Lövei et al., 1985); we investigate whether British overwinterers have adopted greater site fidelity to take advantage of more reliable garden feeding sites. We use ringing data to study movements within and across winters, and we combine ringing with

individual tracking to investigate the breeding origins of wintering blackcaps. Finally, we compare sighting records and geolocator tracks to examine the hypothesis that the high-quality food available in gardens plays an important role in migratory fueling.

2 | METHODS

2.1 | Individual marking and resighting

At 59 sites in Britain and Ireland (Figure 1a; Table S1), we color-ringed wintering blackcaps between November and April (Figure 1b). Capture sites were primarily suburban gardens and occasionally local parks. We gave each blackcap a unique combination of colored leg rings to enable individuals to be identifiable in the field. Most sites were active between the winters of 2016/17 and 2019/20, with the exception of the site run by GCMR and collaborators since 1992. The authors and volunteer observers made regular observations of individuals attending garden feeding stations throughout the winter. We provided observers with data sheets and asked them to record all sightings of marked blackcaps. Our analysis accounted for differences in effort and detectability among sites in two ways, described in detail below: (1) by omitting sites with less than 30 days of blackcap sightings in a given winter and (2) by specifying location random effects. We considered blackcaps to be confidently categorized as wintering individuals (as opposed to early or late migrants passing through) if they were encountered between 1 December and 1 March, defining these boundaries using ringing recovery data (Figure S1). We retained all records of these individuals, which spanned the period from 31 October to 22 April.

Our compiled records consisted of captures (mistnet or potter trap), visual resightings, and camera trap records. In total, we compiled a dataset of 9929 records of 623 color-ringed blackcaps, of which 357 were encountered one or more times after initial capture.

2.2 | Morphometrics

We measured blackcaps during ringing using wing and tail rules and analog calipers. We took the following measurements: maximum wing chord (figure 11.5 in Redfern & Clark, 2001); tail length (figure

11.12 in Redfern & Clark, 2001); minimum tarsus (figure 11.11a in Redfern & Clark, 2001); distance between tip of primaries and tip of outermost secondary (also known as “Kipp’s distance”; ΔS_1 in Lockwood et al., 1998); distance between tip of primaries and tip of the ninth (distal) primary (hereafter “P9 distance,” ΔQ_1 in Lockwood et al., 1998); bill-to-skull distance (figure 11.8 in Redfern & Clark, 2001); and bill width and depth at the distal end of nares (figure 11.10 in Redfern & Clark, 2001). In addition, we weighed birds and scored them visually for fat (ESF scale) and muscle (tables 11.13 and 11.14 in Redfern & Clark, 2001). Because birds tend to accumulate fat stores through the day, we adjusted scores by regressing fat score against time of day and using the model residuals. Similarly, we derived an overall body condition index by regressing body mass against both tarsus length (a proxy for body size) and time of day and using the model residuals. In both cases, we set time of day as a smooth term to allow for a possible nonlinear relationship with body condition.

For analysis, we used field measurements taken by authors BMVD, RJP, GCE, and GCMR. We excluded the first 15 birds measured by each person. As a precaution to eliminate any bias from differences among measurers, we centered measurements such that there were no average differences among measurers. When we occasionally caught the same bird multiple times in a season (23% of cases), we averaged measurements taken within the same season. To summarize morphological variation, we performed a principal component analysis of wing, tail, tarsus, and bill measurements and retained the first three components (Table S2). The first component showed positive loadings for all variables, particularly wing and tail measures. It showed strong differences by age, with first-winter birds having more negative values, likely corresponding to documented ontogenetic changes in wing length and shape (Figure S2; Pérez-Tris & Tellería, 2001). The second component showed positive loadings for bill width and depth and negative loadings for wing shape measures; this axis of wing and bill shape variation varied meaningfully by sex, with females of both age classes showing higher values, corresponding to thicker bills and somewhat smaller wing measurements (Figure S2; Rolshausen et al., 2009). The third component loaded primarily for bill-to-skull distance and P9 distance, both positively, thus capturing additional variation in bill and wing shape that did not show clear differences by age or sex.

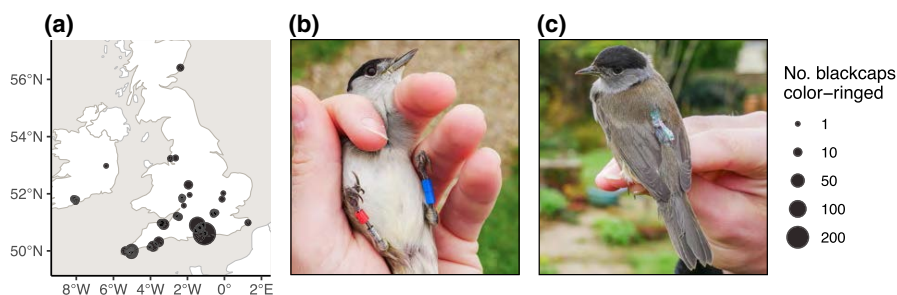


FIGURE 1 Blackcap capture sites. (a) Locations where wintering blackcaps were individually color-ringed in Britain and Ireland for this study, with the number of individuals marked. (b) A color-ringed male blackcap. (c) A male blackcap in a British garden carrying a light-level geolocator. Photos by Ben Porter

2.3 | Daily weather

We obtained local weather station data from the Met Office Integrated Data Archive System (MIDAS; Met Office, 2012; <http://catalogue.ceda.ac.uk/uuid/220a65615218d5c9cc9e4785a3234bd0>). We selected MIDAS weather stations as close as possible to blackcap observation sites (between 9 and 30 km). We extracted (1) daily minimum and maximum air temperature (across 24 h starting at 9 am), (2) total precipitation across the 12 h from 6 am to 6 pm, and (3) mean wind speed and direction across the 12 hours from 6 am to 6 pm. Our daily temperature measure was the average of minimum and maximum values.

2.4 | Daily counts

To understand the environmental factors influencing blackcap attendance at supplemental feeding stations, we counted the number of color-ringed individuals encountered daily at garden sites. We included only data from individuals categorized as wintering in Britain (see above). For analysis, we retained data from a given site in a given winter if there were blackcap observations from at least 30 days in that winter. Thus, we retained blackcap counts from 2615 days at eight sites across 21 years (Table S1). The majority of observation days came from the gardens of GCMR (63.5%) and GCE (16.3%).

We modeled daily counts of color-ringed blackcaps with a generalized linear mixed-effects model. We specified fixed effects of daily air temperature, precipitation, wind speed, and day of year (from 1 November). Because we expected that the effect of seasonal timing might not be linear, we specified date as a smoothed predictor and fit our model using the *gam* function in the R package *mgcv* (Wood, 2017) with Poisson distribution family. We hypothesized that blackcaps would be more likely to feed in gardens on cold and wet days with high winds because of increased energy demands and increased difficulty finding and using natural food sources. We specified interactions of temperature \times precipitation, temperature \times wind speed, and precipitation \times wind speed because we hypothesized that the effects of precipitation and winds could be exacerbated at low temperatures and that winds could influence the effect of precipitation. We specified random effects of year and location to account for differences in the average number of blackcaps detected across years and across sites. We standardized predictor variables so that we could directly compare effect sizes across predictors and interpret intercepts at the average value of predictors. We simplified the model by removing non-significant interactions ($p > 0.05$).

Our dataset comprised daily encounters compiled from dozens of observers, but we lacked observation effort data with which to infer zero counts for days with no marked birds reported. Therefore, our count dataset lacked zero counts, which are expected with a Poisson distribution family. To ensure that our Poisson model was not strongly affected by this lack of zero counts, we also fit a model with the R package *glmmTMB* (Brooks et al., 2017), which supports a truncated Poisson distribution family without zero counts. This

package does not support smoothed predictors, so we fit a quadratic term of date instead in this model. We compared it with the above *gam* model to verify that the choice of distribution family did not impact our conclusions.

2.5 | Individual visitation

Our observations at gardens suggested large individual variation in blackcap behavior. We leveraged our extensive dataset of individual observations to model the probability of individual blackcaps visiting garden feeding sites through the winter. We restricted our analysis to the eight well-covered sites in the previous “daily count” analysis. We used a binary response variable indicating whether each individual was observed on each day, restricting our analysis to the period during which the individual was observed at the site in a particular winter. We excluded individuals only encountered once in a winter and those with unknown ages. We used observations of 225 individuals (128 males and 97 females) encountered a median of 13 times (range: 2–225). In total, the dataset had 6104 positive observations and 10,982 inferred negative observations.

First, we used a generalized mixed-effects model with a binomial distribution and logit link function to model the probability of an individual being detected in a garden on a particular day. We fit the model with *bam* (a version of *gam* for large datasets). It included all fixed effects specified in the “daily counts” model, with the addition of sex and age. It included the smoothed term of date. We also included a continuous variable of the number of days since the bird was last physically captured, in case trapping a bird might subsequently reduce the likelihood of observation. We simplified the model by removing non-significant interactions ($p > 0.05$). We specified random effects of year, location, and individual to account for differences in the average probability of blackcap detection across years, sites, and individuals.

We next focused on testing for relationships between garden visitation and morphology and body condition, restricting the analysis to data from individuals that had been captured and measured at least once during the winter of observation. This reduced our dataset from 6104 positive observations of 225 individuals to 2777 positive observations of 90 individuals. We expanded the model above by adding fat score, body condition, and morphometric principal components 1–3 as additional fixed effects. Furthermore, due to ontogenetic changes in morphology (e.g., Pérez-Tris & Tellería, 2001) which could influence relationships, we tested interactions between fixed effects and age. As above, we then simplified the model by removing non-significant interactions ($p > 0.05$).

We calculated the proportion of variation in visitation explained by the random effects of location, year, and bird identity. We used the *rptR* package (Stoffel et al., 2017) to quantify these variance proportions on the original variable scale and used bootstrapping ($N = 100$) to generate 95% confidence intervals for these estimates. We included the fixed effects above with the exception of morphology, fat score, and body condition. Thus, we calculated the

proportion of variation in behavior explained after accounting for weather, sex, age, and day of year.

2.6 | Site fidelity

We examined the probability of a blackcap returning to the same garden in subsequent winters. For each individual, we determined whether or not it subsequently returned to the same site, considering data from up to three winters following initial ringing. We only retained data points for sites where we had visual observation data for subsequent winters ($N = 324$ individuals across 17 sites). We modeled site fidelity with a binary response variable for whether the bird returned to the ringing site at least once in the three winters after the winter of ringing. We included random effects of ringing year and location to account for variation in the average probability of return among years and locations, and a fixed effect of age to allow for different levels of philopatry among age classes. We also included a fixed effect describing the number of years of observation data available to account for differences in the number of resighting opportunities. In a second model, we added fixed effects of sex, the date of first encounter during the winter of ringing, the duration between first and last encounters during that first winter, and interactions between age and the latter two variables.

We fit the generalized linear mixed-effects model with the *glmer* function in R package lme4 (Bates et al., 2015) unless there was a singular fit, in which case we fit model with the *bgfmer* function in the R package blme (Chung et al., 2013), which extends *glmer*. This function fits mixed models in a Bayesian setting, with priors on model components that help prevent singular fits and aid convergence.

For individuals that returned to the same garden for multiple years, we examined the timing of their first and last sightings. For first sightings, we necessarily excluded the winter of initial capture because the bird likely arrived before capture but was unidentifiable until it was color-ringed. For departure, we used all years. As above, we used the rptR package.

2.7 | Transience

Our dataset included a large number of blackcaps that were encountered only briefly each year. Blackcaps are known to show transience during the winter, in which a proportion of the population stays in a given area while other individuals only pass through (Belda et al., 2007; Cuadrado, 1992). We modeled the likelihood of transience in our dataset with a binary variable of whether each individual bird was encountered for more than 1 week in a year. We considered observations from sites where we had at least 10 visual records of any individual blackcaps in a given winter to ensure sufficient sighting effort. We constructed a generalized linear mixed-effects model with a binomial distribution family and logit link (*glmer* function in R package lme4). To estimate overall transience rates by age class, we

first specified one fixed effect of age (excluding individuals with unknown ages) ($N = 350$ individuals). In a second model, we added sex, the date the bird was first encountered that winter, and the interaction between date and age. We included random intercepts of year, location, and bird ID to account for variation in the average probability of transience among years, locations, and among individuals encountered in multiple years.

2.8 | Movements

We examined blackcaps' movements within winters, among winters, and between winter and summer using ringing recoveries and individual tracking. We obtained ringing data from the British Trust for Ornithology (BTO) Ringing Scheme for Britain and Ireland. For resight data, we categorized blackcaps as British Isles winterers if they were encountered between 1 December and 1 March (Figure S1).

Given the evidence for transient individuals among wintering blackcaps visiting gardens, we used ringing data to study movements undertaken by individuals within the same winter. We filtered ringing data to individuals we were confident were wintering in Britain and Ireland (see above), but we considered all recoveries between 1 November and 1 April to understand how these individuals moved both early and late in the season. We also used ringing data to examine movements between winters, filtering the dataset to encounters that occurred between 1 December and 1 March.

We combined ringing data with tracks from light-level geolocators (Figure 1c) to identify where blackcaps wintering in Britain and Ireland spend the summer. We filtered ringing recoveries to those of wintering blackcaps between 15 May and 15 August. Geolocator data were from Delmore et al. (2020). In addition to identifying breeding locations, we compared the timing of migration determined by geolocators to observations in gardens. Specifically, we asked how soon after disappearing from gardens in spring do blackcaps leave Britain. A short interval would suggest that gardens are an important resource for migratory fueling.

3 | RESULTS

3.1 | Daily counts

Weather conditions and time of season strongly influenced garden blackcap counts (Table S3). More blackcaps were observed in colder temperatures, greater precipitation, and higher winds, although the combination of high winds and precipitation appeared to discourage feeding. Blackcap counts increased through the winter and began decreasing in mid-March (Figure 2a). The significance and directionality of these effects were consistent in a truncated Poisson model that included a quadratic instead of a smoothed term of date (not shown).

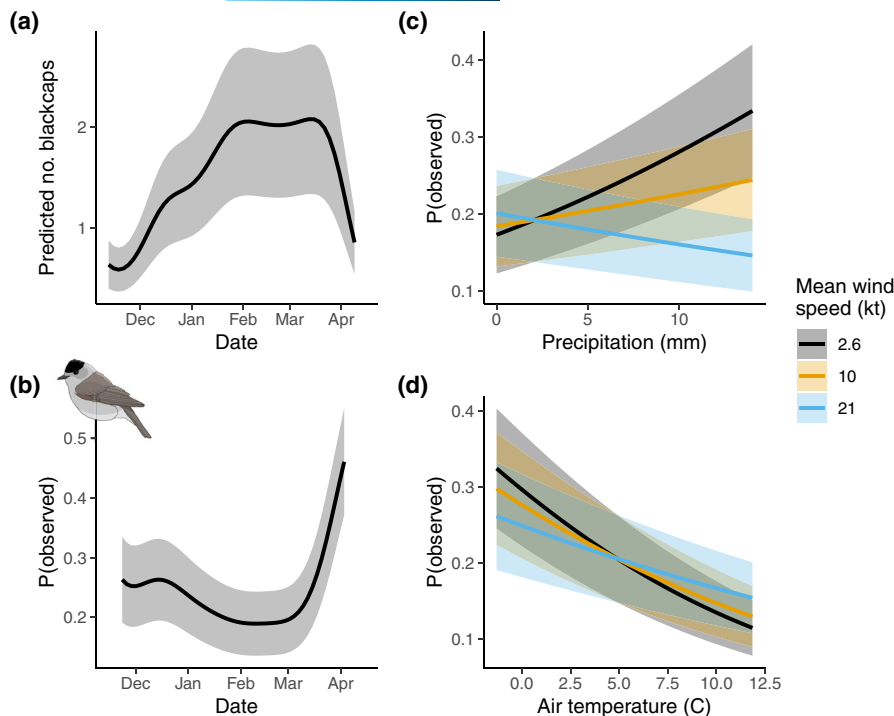


FIGURE 2 Blackcap occurrence in British and Irish gardens by seasonal timing and weather conditions. Shown are results from two models. The first model, shown in (a), predicts the number of color-coded blackcaps observed in gardens through the winter. The second model, shown in (b–d), predicts the probability of a given blackcap being sighted in a garden between its first and last sightings in a winter. (a) Seasonal variation in blackcap counts in British gardens, accounting for responses to weather. Blackcap numbers are highest in late winter. (b) Seasonal variation in garden presence for individual blackcaps. At the end of the winter, total numbers of individuals fall, but those remaining are likely to frequent gardens. (c) Association of precipitation (x-axis) with blackcap garden presence under different wind conditions (colors). (d) Association of temperature (x-axis) with blackcap garden presence under different wind conditions (colors)

3.2 | Individual visitation

There was a great deal of individual variation in behavior. Of 140 individuals observed over total spans of at least 50 days, 31 were observed on less than 15% of those days while 35 were observed on at least 50%. Unsurprisingly, individual identity explained more variation in the dataset (0.13, 95% CI [0.08, 0.16]) than location (0.05 [0, 0.12]) or year (0.04 [0.02, 0.07]).

We documented relationships between garden visitation rate and sex, body condition, morphology, and weather. Our first model, which incorporated all individuals but lacked body condition and morphology data, revealed strong relationships with air temperature, precipitation, and winds. Individuals were more likely to visit in colder and wetter weather; interactions indicated that associations with temperature and precipitation varied with winds (Table S4; Figure 2). There were no average differences among age classes, no effect of physical capture on subsequent visitation, and females were observed slightly less frequently than males.

Our model including morphology, body condition, and additional age interactions showed a strong relationship with morphometric PC3: adults with longer bills and rounder wingtips were significantly more likely to visit gardens (Table S5; Figure 3a). However, this relationship was absent in first-winter individuals. Fat score and body condition were strongly associated with garden behavior, with adults frequenting gardens likely to have smaller fat stores and better body condition than those visiting infrequently (Figure 3b,c). Among first-winter birds, the association was the opposite: those frequenting gardens were more likely to have larger fat stores and be in poorer condition. Finally, first-winter birds were more responsive to temperature than adults.

3.3 | Site fidelity

The overall probability of a blackcap returning to the same garden in subsequent years was 0.4 (95% CI [0.16, 0.7]) for adults and 0.24 (95% CI [0.086, 0.5]) for first-winter birds. There was no difference between males and females in return rate, but first-winter birds were half as likely to return in subsequent years. In addition, birds first encountered later in the winter and that stayed for longer durations were much more likely to return (Table S6). This may be due to early-winter movements (see below) as well as a tendency for individuals to return to sites they occupied at the end of the previous winter. Individuals showed low repeatability in the dates they were first and last observed in gardens each year. Repeatability of first-sighted dates was 0.1 (95% CI [0, 0.35]) and of last-sighted dates was 0.17 (95% CI [0.03, 0.32]).

3.4 | Transience

The overall probability of residence (i.e., being encountered for more than 1 week) for a first-winter ringed blackcap encountered for the first time was 0.5 (95% CI [0.3, 0.7]). Newly encountered adults and returning adults were more likely to be resident in a garden than first-winter birds (new adults: 0.67 (95% CI [0.44, 0.84]); returning adults: 0.75 (95% CI [0.52, 0.89])). There were distinctly different temporal patterns for different age classes (Table S7): returning adults first encountered early in the winter were most likely to be resident, but returning adults first encountered later in the winter were likely to appear only briefly (Figure S3). Newly encountered adults and first-winter individuals showed a significantly different pattern, with less change in the probability of residence through the season.

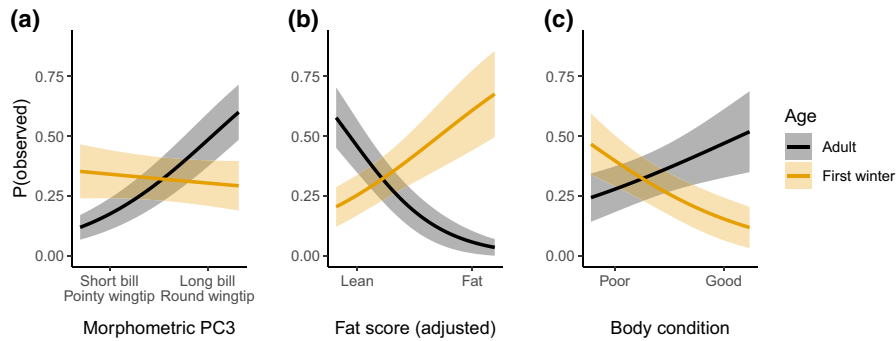
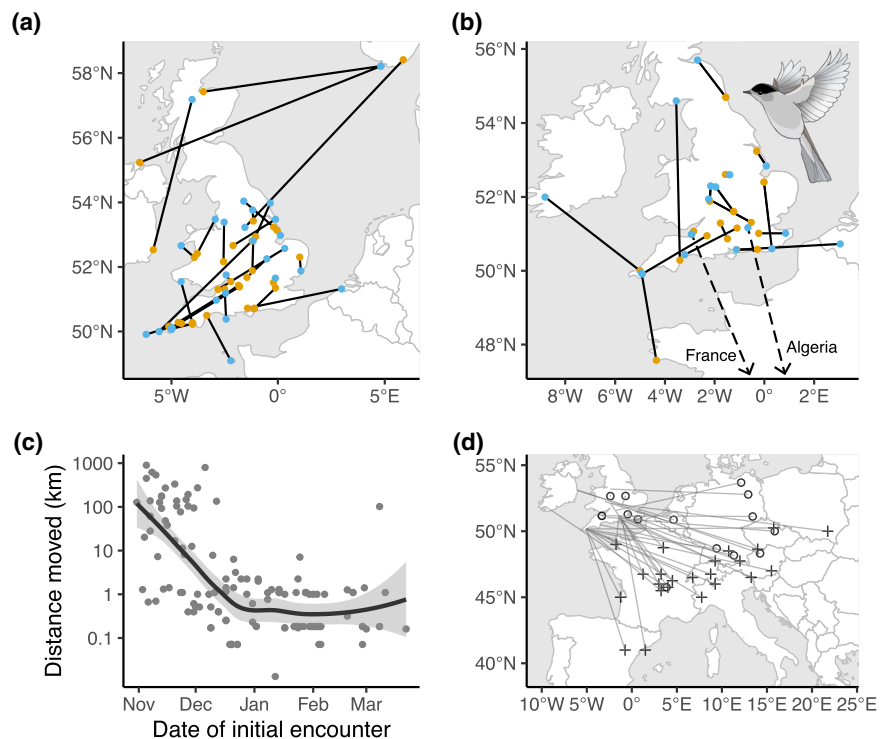


FIGURE 3 Blackcap occurrence in British and Irish gardens by morphology and body condition. (a) Association of morphometric PC3 (x-axis) with blackcap garden presence. Adults frequenting gardens were likely to have longer bills and rounder wingtips. (b) Association of fat load (x-axis) and garden presence. Adults frequenting gardens were likely to be lean, but the inverse was true for first-winter individuals. (c) Association of overall body condition (x-axis) with garden presence, accounting for fat load. Adults frequenting gardens were likely to be in better condition, but first-winter individuals frequenting gardens tended to be in poorer condition

FIGURE 4 Movements of blackcaps wintering in Britain and Ireland. (a) Ringing (blue) and recovery (gold) locations of within-winter movements. (b) Ringing (blue) and recovery (gold) locations of between-winter movements. Directions to recoveries in Algeria and central France are shown with dashed lines. (c) Distance of within-winter movements by ringing date. (d) Breeding (crosses and circles) and wintering (line endpoints) of blackcaps wintering in Britain and Ireland. Circles show ringing recoveries and crosses show geolocator data from Delmore et al. (2020)



3.5 | Movements

Ringing data revealed that blackcaps wintering in Britain and Ireland engage in within-winter movements, but movements of more than 10 km are largely restricted to November and December (Figure 4). Movements in November averaged $130 \text{ km} \pm 198 \text{ SD}$, in December averaged $37.6 \text{ km} \pm 146 \text{ SD}$, and in January and February averaged only $0.735 \text{ km} \pm 1.04 \text{ SD}$.

Above we show that many blackcaps return to the same garden in successive winters. Interestingly, individuals that do not show site fidelity may have moved substantial distances between winters. Ringing data showed that between-winter movements averaged $148 \text{ km} \pm 309 \text{ SD}$ (Figure 4b). Our detailed garden sighting data showed that even individuals established in a garden in

one winter may spend the following winter far from the initial site. One individual [N676642] was sighted by GCE on 63% of days between 16 December 2017 and 4 April 2018. The following winter, it did not return to this site, but was present (and photographed) at a garden 53 km away between 7 January and 12 February 2019.

3.6 | Breeding areas and migration

Combining ringing recoveries and geolocator data, we observe that blackcaps wintering in Britain and Ireland occupy a wide breeding area, spanning 2000 km across Europe (Figure 4d). Estimates from 25 geolocators (Delmore et al., 2020) suggest that the core source area for the

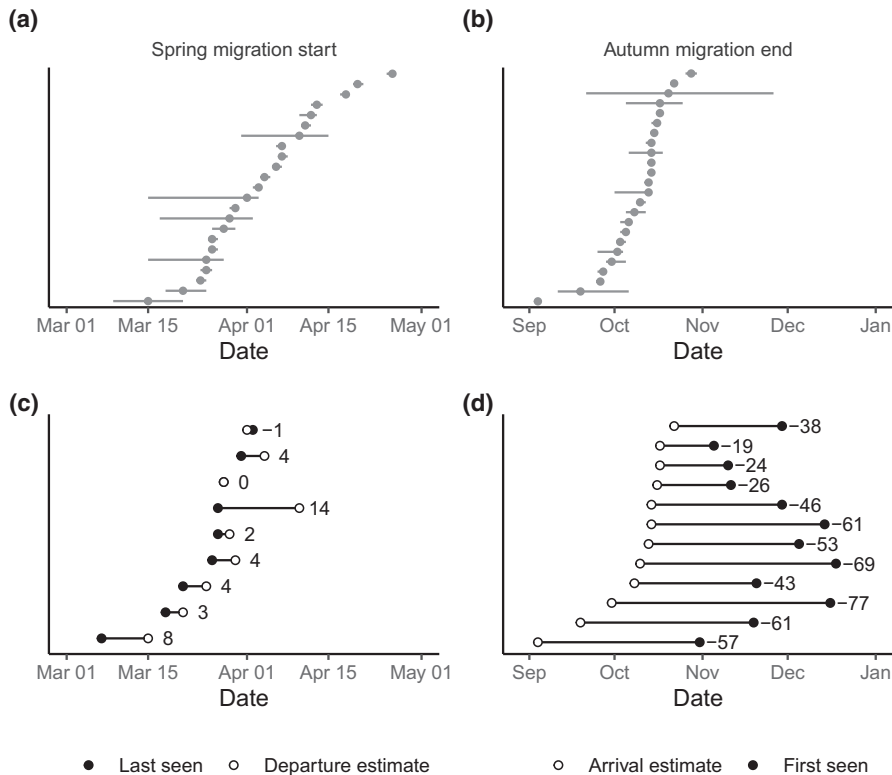


FIGURE 5 Migration timing of British wintering blackcaps. (a) and (b) show the distribution of departure and arrival dates; lines show uncertainty as the interquartile range of model estimates (Delmore et al., 2020). Spring and autumn timings are not matched horizontally to the same individual. (c) and (d) compare geolocator timing estimates (open circles) to the date the bird was first or last observed in the garden in which it wintered (closed circles), in spring and autumn, respectively. Numbers give differences in days. Individuals are *not* matched horizontally

wintering population is in western Europe (e.g., France), whereas almost all continental ringing recoveries ($N = 9$) come from further east. An additional six recoveries occurred within Britain and Ireland, suggesting some individuals may be year-round residents (though see Section 4).

Geolocator data indicated that British winterers departed on spring migration between 15 March and 26 April, with a median date of 2 April (Figure 5a). They returned in autumn between 4 September and 28 October, with a median date of 13 October (Figure 5b). We focused on observations of birds carrying geolocators at three sites with good observer coverage to determine how departure from gardens compared to migratory departure from Britain. After excluding individuals that left the garden shortly after being fitted with a geolocator ($N = 3$), we found that the remaining nine departures occurred on average 4.22 ± 4.49 SD days after the birds were last seen (Figure 5c). Due to short migration distances, these blackcaps typically arrived near breeding sites within a couple of days of departure; therefore, these birds arrived on or near the breeding grounds only 5.44 ± 5.48 SD days after last being seen in their winter garden. This close correspondence between departure from the garden and departure on migration stands in contrast to the situation in autumn. In autumn, blackcaps arrived in Britain on average 47.8 ± 18.5 SD days before being first detected by garden observers ($N = 12$; Figure 5d).

4 | DISCUSSION

Organisms are increasingly facing a need to adapt to a human-dominated world. The movements undertaken by migratory animals

may lend them increased abilities to explore and colonize new suitable areas, yet a migratory lifestyle also hinges on an intricately connected annual cycle where difficulties encountered at one stage may have reverberating consequences. We find that the ecology of blackcaps in a recently colonized high-latitude wintering area is shaped by human activity, including supplemental bird feeding, and mediated by environmental conditions.

4.1 | Human influence on blackcap behavior

Garden sites may be particularly important during periods of difficult weather, and our analysis shows increasing use of garden feeding stations in cold and wet conditions. In these conditions, foraging for berries and other fruit (Snow & Snow, 2010) may be energy intensive. Access to reliable and high-energy, fatty foods, which are frequently provided in gardens, may be particularly important when birds have increased thermoregulatory requirements. In gardens, blackcaps most commonly feed on fats, fruit, and seeds including sunflower hearts (Leach, 1981; Plummer et al., 2015). In addition, gardens are highly modified habitats which contain fruit-bearing plants and non-native flowering species that are important food sources for blackcaps (e.g., Beatty, 1994; Hardy, 1978; Harrup, 1998; Leach, 1981; Snow & Snow, 2010; Walton, 1983). Although some garden owners may provision food more frequently during harsher conditions, this is unlikely to have influenced the results of this study. Truly harsh weather events (e.g., with snow cover or prolonged freezing conditions) were rare in our dataset. In addition, 79.8% of our analyzed data come from the gardens of authors GCMR and GCE, who provided a constant food supply. Finally, increased demand

for supplementary food during harsher conditions generally results in greater competition among garden birds and rapid depletion of these resources.

A stationary and reliable food source is unusual for a species that is primarily frugivorous during winter. Blackcaps in traditional Mediterranean wintering areas track ephemeral fruit resources or are forced to move once they are depleted (Belda et al., 2007; Cuadrado, 1992; Rey, 1995; Tellería et al., 2008). Studies in Africa and Iberia report inter-annual recapture rates of 0%–5% for wintering blackcaps (Cuadrado, 1992; Cuadrado et al., 1995; King & Hutchinson, 2001; Lövei et al., 1985). A capture–recapture analysis in Spain estimated that 26% of individuals are likely to be resident at a given site during the winter, defining residency as presence for more than 1 week at that site (Belda et al., 2007). Our estimates of return rates and residency are substantially higher: we observed an average inter-annual re-encounter probability of 0.4 (95% CI [0.16, 0.7]) for adults and 0.24 (95% CI [0.086, 0.5]) for first-winter birds, and we estimated the probability of residency (>1 week) for young birds as 0.5 (95% CI [0.3, 0.7]) and 0.67 (95% CI [0.44, 0.84]) for newly encountered adults. We note that our estimates may not be directly comparable to those of Belda et al. (2007), as their data came from captures and ours primarily from visual resightings with variable effort; future work on blackcap garden behavior would benefit from more standardized observation effort and individual tracking data (e.g., via radio telemetry). Nonetheless, it appears highly likely that blackcaps wintering in Britain and Ireland show relatively low within-winter transience and relatively high between-winter site fidelity due to the higher reliability of supplemental garden food sources over fruiting plants. Although many important natural food sources are widespread in suburban environments, most are not available in mid-winter (e.g., ivy berries, *Hedera helix*, Snow & Snow, 2010), when blackcap counts in gardens are highest.

Wintering in Britain and Ireland might confer a number of advantages compared to traditional southwest migratory strategies (Berthold & Terrill, 1988). For example, a highly reliable winter food supply may improve survival by acting as a buffer against harsh weather. We found that adults frequenting gardens were able to carry smaller fat stores and were in better body condition than those visiting infrequently. On the other hand, first-winter birds frequenting gardens tended to be in poorer condition and have larger fat stores. This contrast may reflect adults' familiarity with reliable local food sources and social dominance over young individuals. Carrying less fat may also lower predation risk (Fransson & Weber, 1997; Kullberg et al., 1996). Our findings suggest that gardens are used both by successful adults adopting a sedentary strategy and by potentially struggling juveniles storing fat as a buffer against difficult conditions.

When preparing for migration, abundant supplemental food may allow blackcaps to attain better body condition and quickly amass the fat stores that will fuel their migratory flights. In turn, supplemental feeding may facilitate earlier and more successful breeding attempts. Blackcaps tracked with geolocators arrived at the breeding grounds on average only 5.4 days after last being seen in their gardens, suggesting that conditions at British

gardens will influence body condition on arrival. It is therefore plausible that the availability of reliable supplemental food puts British and Irish winterers at an advantage on the breeding grounds.

Adults with longer bills and rounder wingtips were more likely to visit gardens. This parallels differences in bill morphology between British and Iberian overwinterers; Rolshausen et al. (2009) posited that the narrower and longer bills of the British winterers in their sample reflected a more generalist diet, compared to the specialized, frugivorous diet and more robust food items (e.g., olives *Olea europaea*) of Mediterranean winterers (Jordano & Herrera, 1981; Tellería et al., 2008). Similarly, Great Tits (*Parus major*) in Britain have evolved longer bills in association with supplementary feeding (Bosse et al., 2017). Our results align with these findings and provide additional evidence that supplementary feeding is driving morphological evolution in bird populations. The presence of a strong relationship in adults but not in first-winter birds may reflect behavioral differences between naive and experienced individuals. It may also arise from age-related differences in selection pressures on morphology; for juveniles, selection for rounder, more maneuverable wings (Pérez-Tris & Tellería, 2001), especially during the critical post-fledging period, may dominate other pressures.

4.2 | Potential future changes in behavior

There is clear evidence that human activity has shaped the behavior of blackcaps wintering in Britain and Ireland, both directly and indirectly. Blackcaps are more likely to occur in warmer parts of Britain but use garden sites primarily in periods of cold and wet weather (Plummer et al., 2015). In the coming decades, Britain's climate is expected to continue to warm (Lowe et al., 2018). This may improve the suitability of the region for wintering blackcaps, but it may also affect their associations with gardens. In the future, milder weather may decrease blackcaps' use of gardens, even while the wintering population increases overall.

4.3 | How reliant are blackcaps on supplemental food?

Although supplemental bird food is likely important when winter conditions become difficult, our analysis indicates that blackcaps are far from reliant on garden feeders. Transient individuals, which did not frequent gardens, represented approximately half of all blackcaps captured. This high rate of transience is consistent with the possibility that garden feeding stations represent only a minor portion of the diet of most blackcaps wintering in Britain and Ireland. Indeed, we found that even the most site-faithful blackcaps do not appear in gardens until well after they arrive in the autumn—sometimes more than 2 months after arrival. Of course, we cannot rule out the possibility that transient individuals

simply move to other gardens; future radio-tracking would be a useful approach to better understand how wintering blackcaps interact with natural and artificial food sources through the winter. However, the most plausible explanation is that blackcaps do not need to use garden feeding stations until natural food sources dwindle after late autumn and early winter. Although supplemental food may make up a relatively small component of blackcap diet, our study shows that it may play an outsize role during harsher weather. Thus, garden feeding stations may have a disproportionate positive effect on survival.

4.4 | Individual variation and flexibility

Large individual variation was a defining feature of our dataset. In our model of individual behavior in gardens, individual identity explained the greatest proportion of variation. Blackcaps existed on a continuum from frequent visitors to single-visit transients. Young birds were more likely to be transient, especially early in the winter, which may indicate that these inexperienced individuals are more exploratory than established adults. Adults may also be dominant in garden sites, forcing naïve juveniles to be more mobile. Adults' higher site fidelity likely reflects higher adult survival but may also reveal age-related differences in movement strategies: adults established in a high-quality area may benefit from returning to that area, whereas first-winter individuals may focus on locating good sites. Regardless, our results show that blackcaps exhibit a great deal of variation and flexibility in their strategies, which may be a key to their success as environments rapidly change.

4.5 | Breeding origins of British winterers and evidence for residency

We combined ringing recoveries and individual tracking data to show that blackcaps wintering in Britain originate from a 2000 km wide swath of Europe (Delmore et al., 2020). Ringing recoveries alone supported central European origins of the wintering population, but tracking data show that the breeding range extends well into southwest Europe, even to the Iberian Peninsula, and farther east than suggested from ringing recoveries.

There were six recoveries of individuals encountered in Britain and Ireland during both summer and winter, suggesting limited year-round residency. (By comparison, a total of 5848 individuals were encountered during multiple summer seasons.) However, spatial biases in recovery effort make local recaptures far more likely than external recaptures, and our tracking results indicate that at least the vast majority of wintering individuals come from outside Britain and Ireland. None of the 25 geolocator tracks showed evidence for year-round residency in Britain, although one individual that wintered in Chilbolton, Hampshire, UK moved only a short distance to extreme northern France.

5 | CONCLUSION

Many migratory birds facing the pressures of environmental change are in decline, but the blackcap is thriving in a changing world. The recently established wintering population of blackcaps in Britain and Ireland provides an opportunity to understand how this species has managed to keep pace. Our results support the hypotheses that climate change combined with supplemental bird feeding has facilitated the rapid establishment of this wintering population and continues to shape its biology. Moreover, our individual-level data reveal the tremendous individual flexibility that blackcaps exhibit in their movement patterns and responses to conditions. Among migratory species, those with large variation and flexibility in movement and foraging behaviors will likely be best equipped to respond to the coming decades of environmental change.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

Benjamin M. Van Doren conceived of the study and organized data collection with Greg J. Conway, Miriam Liedvogel, and Ben C. Sheldon, who oversaw the project. Benjamin M. Van Doren, Greg J. Conway, Robbie J. Phillips, Glynne C. Evans, and Graham C. M.

Roberts collected the data for the study. Benjamin M. Van Doren analyzed the data and wrote the paper with input from all authors.

DATA AVAILABILITY STATEMENT

Blackcap encounter and measurement data and analysis scripts are openly available in figshare at <http://doi.org/10.6084/m9.figsh.14167259>. Geolocator data are openly available in Dryad at <https://doi.org/10.5061/dryad.2280gb5qc>. Weather data are available from the UK Met Office at <https://catalogue.ceda.ac.uk/uuid/220a65615218d5c9cc9e4785a3234bd0>. Ring recovery data may be requested from the British Trust for Ornithology (<https://www.bto.org>); restrictions apply to the availability of these data, which were used under license for this study.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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