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ORIGINAL ARTICLE

Cold weather increases winter site fidelity in a group-living passerine

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Abstract Site fidelity during the non-breeding season is beneficial if habitat quality and environmental predictability are high. In group-living species, the costs and benefits of site fidelity may be linked to the non-social (weather) and social (dominance hierarchy) environments, but little is known about factors influencing movements during the non-breeding season. We studied both within- and between-winter site fidelity of the great tit (*Parus major*), a partial migrant in northern Finland. We collected mark-resight data on wintering great tits across two winters at multiple sites, and tested for the effects of age, sex, season, temperature and day length on site fidelity. Within-winter movement was lower during mid-winter and decreased during cold periods. This pattern is probably linked to energy saving and predator escaping strategies during these demanding periods when energy expenditure is high and birds have limited daylight hours to forage. Site fidelity was lower for juveniles than adults within a winter, but it was unaffected by sex. These results agree with an age related dominance structure and site-specific dominance found in great tits, but they can also be related to prior experience as young individuals still collect information during their first winter. In contrast, between-winter site fidelity was not affected by age or sex, suggesting equal benefits from site fidelity. Juveniles probably gather information on resource abundance and distribution in their first winter, and thereby gain the same benefits as adults from returning the next winter.

Keywords Between-winter site fidelity · Dispersal · Great tit · Non-breeding season · Temperature dependent movement

Zusammenfassung

Kaltes wetter im winter erhöht die standorttreue sozial lebender sperlingsvögel

Standorttreue außerhalb der Brutperiode ist dann von Nutzen, wenn die Habitatqualität hoch und die Umgebungsbedingungen stabil sind. Bei in Gruppen lebenden Arten hängen Kosten und Nutzen von Standorttreue möglicherweise auch mit nicht-sozialen Faktoren (Wetter) und mit sozialen Umgebungsbedingungen (Dominanz-Hierarchien) zusammen. Man weiß aber nur wenig über Faktoren, die die Ortsveränderungen der Vögel außerhalb der Brutsaison beeinflussen. Wir untersuchten die Standorttreue der Kohlmeise (*Parus major*), einem Teilzieher in Nord-Finnland, sowohl während des Winters als auch zwischen Wintern. Hierfür sammelten wir an unterschiedlichen Standorten Wiederfang-Daten von Kohlmeisen und untersuchten diese auf mögliche Auswirkungen von Geschlecht, Alter, Saison, Temperatur und Tageslänge auf die Standorttreue. Die Ortsveränderungen waren während des Mittwinters geringer und nahmen während Kälteperioden ab. Dieses Verhaltensmuster steht wahrscheinlich in Zusammenhang mit Strategien zum Sparen von Energie und Vermeiden

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von Räubern während dieser schwierigen Jahreszeit, wenn der Energieverbrauch hoch ist und den Vögeln nur wenig Tageslicht zum Futtersammeln bleibt. Während des Winters zeigten Jungtiere weniger Standorttreue als ältere Tiere, ein Zusammenhang mit dem Geschlecht konnte jedoch nicht nachgewiesen werden. Diese Ergebnisse passen gut zu einer von Kohlmeisen bekannten altersabhängigen Dominanz-Struktur sowie Standort-spezifischen Dominanz. Sie können aber auch zu früheren Erfahrungen der Vögel in Beziehung gesetzt werden, da Jungtiere während ihres ersten Winters noch Informationen sammeln. Im Gegensatz dazu gab es in der Zeit zwischen Wintern keinerlei Einfluss vom Alter und Geschlecht der Vögel auf die Standorttreue. Jungtiere sammeln wahrscheinlich in ihrem ersten Winter Informationen zum Vorhandensein und der Verbreitung von Nahrungsquellen, was ihnen vermutlich die gleichen Vorteile schafft wie älteren Tieren, die im nächsten Winter wiederkehren.

Introduction

Site fidelity is beneficial for fitness due to familiarity and knowledge of resources and of predators if the environment is stable (Bowler and Benton 2005; Piper 2011). The majority of site fidelity and dispersal studies have focused on sites of reproduction (e.g. Doligez et al. 1999; Andreu and Barba 2006; Pakanen et al. 2015, 2017), but site fidelity during the non-reproductive season has received less attention, especially in terms of causes of individual variation (e.g. Belda et al. 2007; Catry et al. 2012; Cresswell 2014, Grist et al. 2014; van Overveld et al. 2014). However, for many species the non-breeding season constitutes the largest part of the annual cycle. The ability to find food and shelter during this period can have survival consequences and hence affect lifetime reproductive success (Lahti et al. 1998). Therefore, non-breeding site fidelity should be a good option in high quality and predictable environments (Switzer 1993).

Site fidelity to wintering sites is typical in obligate seasonal migrants that move annually from their breeding grounds to predictable environments (Robertson and Cooke 1999; Newton 2012; Blackburn and Cresswell 2016; Lourenço et al. 2016). In contrast, facultative migrants move only when the prevailing conditions make survival unlikely, and site fidelity is typically low both within and between non-breeding seasons (Newton 2008, 2012). Site fidelity during the non-breeding season may be linked to the variable costs and benefits associated with food availability or other environmental factors (Newton 2008, 2012). There may, for example, be temporal variation in the costs and benefits of movement during the winter.

We studied the effects of different environmental factors on wintering site fidelity of a partial migrant, the great tit (*Parus major*). This small passerine shows facultative migratory behaviour in the temperate parts of its range where conditions allow survival year round. Adults leave their territories and congregate in flocks only when forced by poor environmental conditions (van Balen 1980). In the colder conditions of northern Europe, some individuals migrate south while others winter closer to their breeding grounds (Nowakowski and Vähätalo 2003). Here, most of the birds move from natural habitats close to human habitation. Therefore, among the wintering birds there might be true migrants and birds that have moved only a short distance from their summer home range. By supplying unlimited (i.e. predictable) food sources, we were able to examine other non-social environmental factors (effects of ambient temperature, day length) and factors linked to the social environment (age and sex) affecting site fidelity in a northern range margin population of the great tit (Orell 1989; Karvonen et al. 2012). Because cold weather increases energy requirements (Tatner and Bryant 1986) and because great tits need to attain sufficient fat levels for surviving the long nights (Krams et al. 2013), we hypothesise that during cold weather great tits invest more time and energy in foraging, and consequently allocate less to movement. Consequently, movement of great tits should decline with decreasing temperatures. In addition, because the photoperiod affects daily routines (Krams 2000), movement should be at a minimum during the period of shortest day length (about 3 h at winter solstice at our study area).

Great tits winter in large non-territorial flocks that do not have a stable structure (de Laet 1985, Ekman 1989; Hogstad 1989; Sandell and Smith 1991). In group-living species, the social environment (e.g. dominance hierarchy) may have an important influence on the predictability of resource access for the individuals (Lange and Leimar 2004). We hypothesise that dominant individuals benefit more from site fidelity than subordinates because dominants have better access to food resources and predator-safe feeding (Ekman 1989). Furthermore, because dominance is often site related (de Laet 1984; Krams 1998), dominant individuals have more to lose and may benefit less from moving. Great tit males are dominant over females and adults are dominant over juveniles (Ekman 1989; Hogstad 1989; Sandell and Smith 1991). Old individuals are also likely to attempt wintering close to their breeding area (van Balen 1980) and therefore benefit from prior residency in terms of knowledge of resources (Koivula et al. 1993; Sandell and Smith 1991). We therefore predict that wintering site fidelity is lowest among juveniles and females.

We tested the above predictions by marking great tits at multiple feeding sites during the autumn months, and by collecting mark-resight data by following these marked individuals through two consecutive winters in two-week intervals. Because the feeding sites were distributed across a large area, we were able to examine within-winter and between-winter site fidelity.

Materials and methods

Data collection

We conducted this study during two non-breeding seasons in 2008–2010 on the islands of Mustasaari and Hietasaari, which are located in the city of Oulu (65º01′N, 25º27′E; Online Resource (1) in northern Finland. The area is characterised by a mixture of woodland, old parks, housing, cultivation areas, and areas maintained for leisure activities. We annually maintained five feeding sites, each including 2–3 large feeders filled with sunflower seeds and peanuts from late-September onwards until late April (Online Resource 1). We positioned the feeders on average 1382 meters (min 676, max 2633 meters) from each other. The feeding sites covered a large part of the suitable wintering habitats on the islands (Online Resource 1). Because the majority of the study area was not inhabited, there were only a few small private feeding sites kept in addition to our larger feeding sites (Online resource 1). The islands are neighboured by the Bothnian Bay in the west and an industrial harbour in the south, both unsuitable for great tits. Northern and eastern boundaries are surrounded by the Oulu river delta and the city center.

We began catching great tits with mistnets at the feeders in late September. We ringed them with individual combinations of a numbered aluminium ring and one to three plastic colour rings. We ringed the majority of the birds by early November but we continued ringing until January (Fig. 1). We sexed and aged (juvenile vs. adult) the birds based on plumage characteristics (Svensson 1992). Starting from the 6th of November in both 2008 and 2009, we resighted great tits at the feeders in two-week intervals based on their individual colour ring combinations (Online Resource 1). The encounter occasions (when birds were resighted) lasted 4 days (Thursday–Sunday) in 2008–2009 and 3 days (Friday–Sunday) in 2009–2010, and sampling continued until the 29th of March in 2009 (11 encounter occasions) and the 11th of April in 2010 (12 encounter occasions; Fig. 1), ending 4–5 weeks before breeding started (Orell and Ojanen 1983). Resighting effort at each feeder was roughly equal during each encounter occasion. Each feeder had an observer on 3–4 days of the encounter occasion. Observers were distributed to feeders so that time spent per feeder each feeder was at about 3–5 h per day. Because the great tits were foraging mostly at our feeders, we had good chances of sighting all birds that were present. Trapping of birds was not done during the encounter occasions.

We ringed 454 great tits in the autumn 2008 and resighted 329 (72.4%) of them during in at least one encounter occasion in winter 2008–2009. These resulted in 3619 resightings (only one resighting listed per individual per encounter occasion per location). In autumn 2009, we ringed an additional 204 individuals. From these and birds surviving from the previous winter, the resighting data for the second winter included 335 individuals and 1433 resightings.

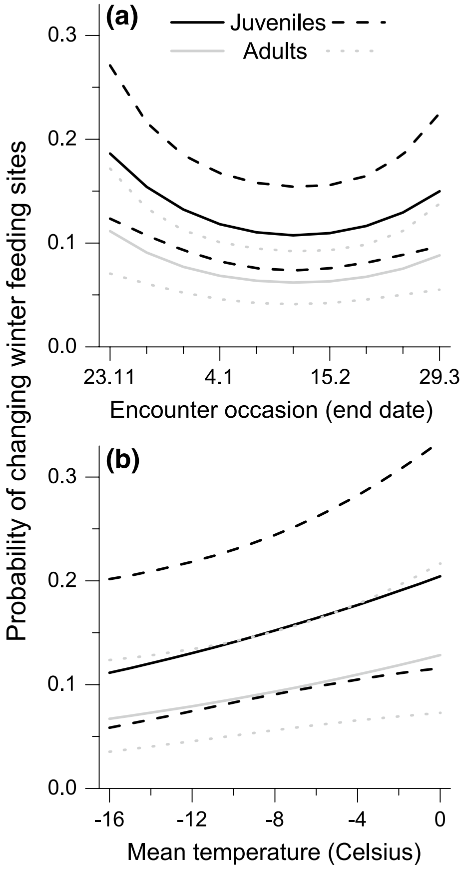

Fig. 1 Probability of within-winter movement in juvenile and adult great tits (**a**) during different encounter occasions across the winter 2008–2009, and (**b**) in relation to mean temperature between the encounter occasions in 2009–2010. Estimates were derived from the most parameterized models (Table S1, models A2 and B3, respectively) among models with ΔAICc ≤ 2. Dashed/dotted lines indicate 95% confidence intervals

Data analysis

Within-winter site fidelity

We analysed within-winter site fidelity in two ways. Firstly, we investigated the probability of changing sites between encounter occasions using generalized linear mixed models (GLMM, binomial errors, logit link). If an individual was seen at the same site in two consecutive resightings that were done in different encounter occasions, the observation was scored as zero. If an individual was at a different site when next resighted, the score was one. In addition to the effects of sex and age, we considered calendar effect, because movement patterns may change due to changing weather and day length. We tested for both linear and quadratic temporal trends and in separate models for the effects of mean temperature and day length during the two-week periods. Individual identity was included as a block random factor in all tested models (Online Resource 2, Table S1).

Secondly, we calculated an individual-specific site fidelity index (SFI) introduced by Catry et al. (2012),

$$\mathrm{SFI} = 1 - \left[\left(\frac{n_i - 1}{n - 1}\right) \times \left(\frac{p_i}{o_i - 1}\right)\right]$$

It considers the number of sites used by an individual (n_i), the number of observed changes between sites performed by an individual (p_i), the total number of sightings made of an individual (o_i) and the total number of sites surveyed (n). The index describes site fidelity from zero (no site fidelity) to one (complete site fidelity). We included individuals that were seen at least three times during the winter. The effects of sex and age on the site fidelity index were analysed with the Wilcoxon rank sum test.

Because the two winters differed markedly in weather (mean temperature, 2008–2009: − 5.2 °C; 2009–2010: − 9.4 °C, $t = -1.97$, $df = 14.68$, $p = 0.034$) and because the encounter occasions were of different length (3 and 4 days), we analyzed data from both years separately. The lowest temperatures observed were −26.9 °C in 2008–2009 and − 33.3 °C in 2009–2010.

Between-winter site fidelity

We analysed the effects of sex and age on between-winter site fidelity in two ways. First, we examined between-winter site fidelity [did an individual change its feeding site(s) (1) or did it return back to the same feeding site(s) (0)] with generalized linear models (GLM, binomial errors, logit link). We included sex and age as factors. In addition, we added the number of resightings during winter 2008–2009 because the number of observations of an individual in the first winter affects the ability to accurately define its wintering site. Some individuals may have only visited the area for a short period. As we were forced to move two feeding sites between the winters due to construction projects (sites Mustasaari and Toppila were replaced with sites Seilitie and Masto; Online Resource 1), this analysis concerns only individuals that were observed wintering only at sites Johteenhovi, Jähtikuja and Hyry during the first winter.

Second, we used GLMs (binomial errors, logit link) to analyse the probability of return to the study area in the winter 2009–2010 for birds marked and seen in the winter 2008–2009. We included sex and age as fixed effects. Return rates are the function of site fidelity and survival (Sandercock 2006). Therefore, to control for mortality that occurred during the first winter, we included a linear effect of the last encounter occasion when an individual was resighted. Return rates should be the highest for individuals seen in the last encounter of the first winter. To control for the possibility that some birds were transient (not wintering in the study area), we included the number of encounter occasions when an individual was observed in the analysis. Some individuals could have wintered outside the study area, and been seen, for example, only during the spring when moving back to their breeding territories.

Models were run in R 3.0.3 (R Development Core Team 2014). GLMMs were run with function ‘glmer’ in package ‘lme4’ (Bates et al. 2015), and GLMs with function ‘glm’ in package ‘stats’. We ranked models with the Akaike information criterion corrected for small sample size (AICc). We considered models with ΔAICc ≤ 2 as the best models with equal contribution, and considered model selection uncertainty by averaging the coefficients (full averages) over these best models with function ‘model.avg’ in the package ‘MuMIn’ (Bartón 2016).

Results

Within-winter site fidelity

Probability to change sites

During the winter 2008–2009, juveniles moved between feeding sites more frequently than adults. Sex had no effect (Table 1a, Fig. 1a). Site change was most likely during the autumn and spring periods, while individuals were more site faithful during the mid-winter period in January/February (Table 1a, Fig. 1a). Site change was more probable during warm weather, while the probability of changing sites dropped during the cold periods. However, this pattern emerged only in the second colder winter (Table 1b, Fig. 1b).

Site fidelity index

Most of the birds used only one site: among both sexes and age classes, SFI was close to one. Still, it was lower for juveniles than for adults in the winter 2008–2009 (males: $W = 2066.5$, $p = 0.002$, $n = 150$; females: $W = 1317$, $p = 0.043$, $n = 115$), but not in the winter 2009–2010 (males: $W = 1316$, $p = 0.198$, $n = 110$; females: $W = 568$, $p = 0.087$, $n = 74$; Fig. 2). Site fidelity did not differ by sex among juveniles (2008–2009: $W = 2132.5$, $p = 0.253$,

Table 1 Factors affecting within-winter probability of changing sites in great tits during winters (a) 2008–2009 (n = 1820) and (b) 2009–2010 (n = 746), analysed with generalized linear mixed models (GLMM, binomial distribution, logit link)

	Coefficient	SE	*z*	*p*
(a) Parameter				
INTERCEPT	− 1.5328	0.4257	3.5980	0.0003
AGE (juvenile)	**0.5927**	**0.2205**	**2.6870**	**0.0072**
TIME	**− 0.3521**	**0.1356**	**2.5950**	**0.0095**
TIME2	**0.0249**	**0.0103**	**2.4210**	**0.0155**
SEX (male)	0.0316	0.1292	0.2450	0.8068
(b) Parameter				
INTERCEPT	− 1.8657	0.4317	4.3160	< 0.0001
AGE (juvenile)	0.5381	0.3053	1.7600	0.0785
DAY LENGHT	− 0.0310	0.0415	0.7450	0.4561
MEANTEMP	**0.0462**	**0.0227**	**2.0350**	**0.0419**
SEX (male)	0.1047	0.2330	0.4490	0.6534

Individual ID was included as a random term, (2008–2009: 293 individuals, variance 1.366; 2009–2010: 222 individuals, variance 1.568)

The table shows model averaged parameter coefficients and their significance derived from most supported models (ΔAICc ≤ 2). Variables with $p < 0.05$ are in bold

AGE age of the individual, *SEX* sex of the individual, *TIME* linear temporal effect, *TIME2* quadratic temporal trend, *MEANTEMP* mean temperature (C°) between the ends of two encounter occasions, *DAY LENGTH* length of the average day between the encounter occasions

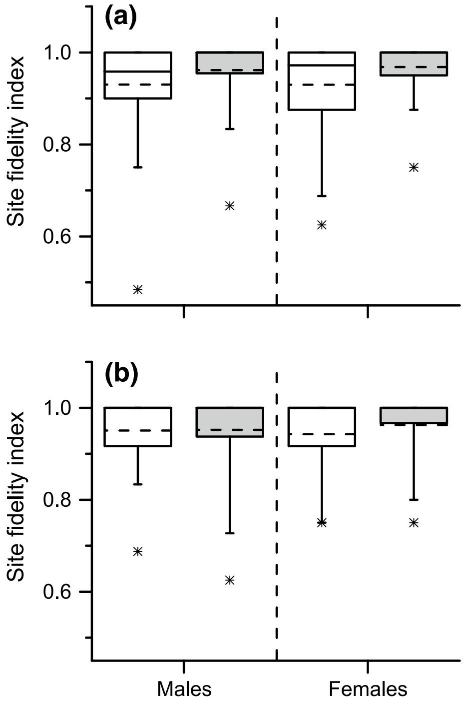

Fig. 2 Site fidelity indices of wintering great tits in (**a**) the first winter (2008–2009) and (**b**) the second winter (2009–2010) separately for juveniles (open) and adults (filled) in both males and females. Median = solid line, mean = dashed line, whiskers denote 95% of observations and asterisk denotes the smallest observed value

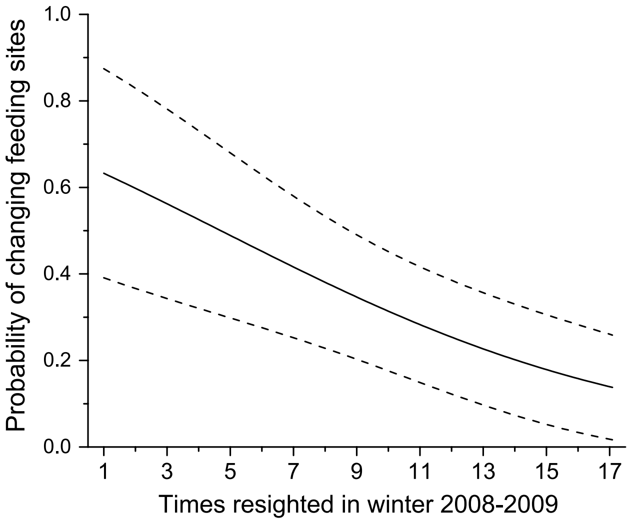

Fig. 3 Probability of between-winter movement in juvenile male great tits in relation to the number of resightings made in the first winter (2008–2009). Dashed lines indicate 95% confidence intervals

Table 2 Factors affecting (a) between-winter fidelity of great tits analysed with generalized linear models (binomial distribution, logit link, n = 133) and (b) return rates of great tits back to the study area in the following winter analysed with generalized linear models (GLM, binomial distribution, logit link, n = 329)

	Coefficient	SE	*z*	*p*
(a) Parameter				
Intercept	0.1096	0.5329	0.2040	0.8384
AGE (juvenile)	0.5461	0.4828	1.1260	0.2604
RESIGHTINGS	**− 0.1486**	**0.0517**	**2.8490**	**0.0044**
SEX (male)	0.0420	0.2056	0.2030	0.8394
(b) Parameter				
Intercept	− 2.5786	0.4475	5.7420	< 0.0001
ENCOUNTERS	**0.1301**	**0.0493**	**2.6270**	**0.0086**
LAST ENCOUNTER	**0.1796**	**0.0576**	**3.1060**	**0.0019**
SEX (male)	0.0967	0.1964	0.4910	0.6233
AGE (juvenile)	0.0217	0.1151	0.1880	0.8508

Table shows model averaged parameter coefficients and their significance derived from most supported models (ΔAICc ≤ 2). Variables with $p < 0.05$ are in bold

AGE age of the individual, *SEX* sex of the individual, *RESIGHTINGS* number of resightings in winter 2008–2009, *LAST ENCOUNTER* the encounter occasion when an individual was last resighted, *ENCOUNTERS* the number of encounter occasions when an individual was resighted

$n = 135$; 2009–2010: $W = 717$, $p = 0.536$, $n = 76$) or adults (2008–2009: $W = 1978$, $p = 0.561$, $n = 130$; 2009–2010: $W = 1257$, $p = 0.389$, $n = 108$; Fig. 3).

Between-winter site fidelity

The probability of changing sites between winters was, on average, 28.6%. Although birds ringed as juveniles had a slightly higher probability of changing sites, the effect of age was not statistically significant (Table 2a, Fig. 3). The probability of changing sites was highest if the individual was resighted only few times, but decreased when it was resighted multiple times during the first winter (Table 2a, Fig. 3). For the mean number of observations (9.5) the probability of changing sites was 35.8% for juvenile males and 20.8% for adult males.

Average return rates in 2009–2010 were high and were not influenced by sex or age for individuals resighted on at least one encounter occasion during the winter of 2008–2009 (Fig. 4, Table 2b). Instead, return rates were higher when the last resighting of an individual occurred late in the season (Table 2b, Fig. 5). For example, birds seen only on the first encounter occasion of year 2008–2009 had a very low (9%) probability of returning. Return rates also increased strongly with the number of occasions resighted during the first winter (Table 2b), such that return rates were lower for individuals seen only on the last occasion (about 41%) but very high for individuals seen on all occasions (72%; Fig. 5).

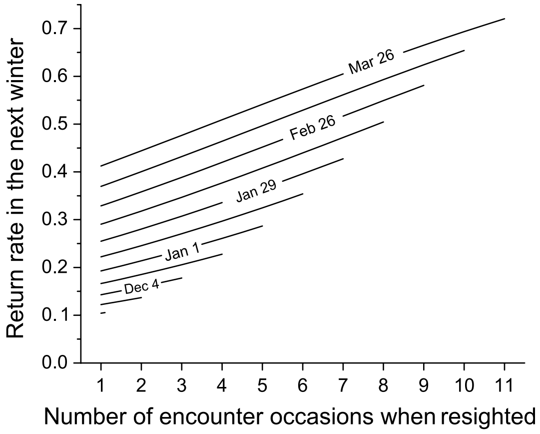

Fig. 5 Return rates in winter 2009–2010 for wintering great tits in relation to the encounter occasion when they were resighted for the last time (lines; first day of encounter occasion indicated on every other line) and in relation to the number of encounter occasions when an individual was resighted (*x*-axis; 1 = seen on only one encounter occasion, 11 = seen on all encounter occasions) during the previous winter 2008–2009. The predicted return rate is indicated for each encounter occasion when an individual was seen or resighted for the last time. For example, return rates for individuals seen on the 11th encounter occasion (first day of encounter occasion March 26th) are indicated by the line at the top and for individuals seen on the 3rd encounter occasion (first day of encounter occasion December 4th) is the third line from the bottom

Discussion

We studied effects of temperature, day length, age and sex on winter site fidelity in a group-living passerine, the great tit. We used supplemental feeding to remove variation caused by differences in food availability in order to concentrate on other factors acting on site fidelity, and assumed that the effect of food availability on site fidelity was equal across all groups. While we found that wintering great tits were site faithful to feedings sites, there were both temporal and individual variations in within-winter site fidelity, indicating that benefits from site fidelity are not the same for all individuals in all environmental conditions. There was a clear reduction in movement in mid-winter during the warmer winter. Furthermore, during the cold winter, movement decreased with declining mean temperature. Juveniles moved more than adults but there were no sex differences. These results suggest temporal variation in great tit home ranges during the winter.

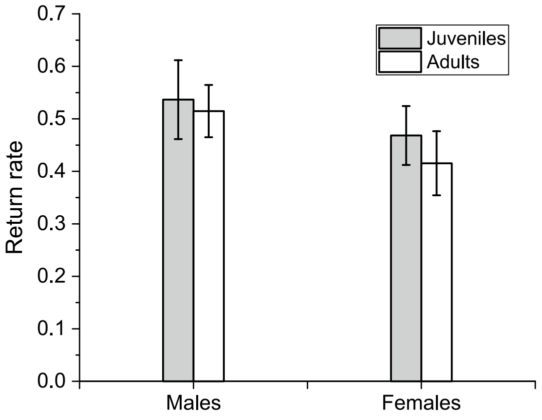

Fig. 4 Return rates of juveniles and adults of both sexes (± SE) that returned to the study area in the winter of 2009–2010 after being resighted at least once during the winter of 2008–2009

The relatively strong site fidelity both within and between winters suggest that great tits benefit from wintering in familiar areas or close to the former or forthcoming breeding site. While previous studies on between-winter site fidelity are lacking, the high within-winter fidelity is consistent with previous feeding site studies from more southern latitudes (de Laet 1984; Krištín and Kaňuch 2016). The high predictability of food availability probably enhanced site fidelity in these studies.

Great tit movement was most common in autumn and spring but markedly reduced in mid-winter (January to February) in the first, milder winter. A similar temporal pattern was described for the occurrence of floaters (transient birds) during the non-breeding season in a Hungarian population of great tits (Báldi and Csörgő 1991), so this pattern may be partly linked to movement to and from breeding sites. While mid-winter is the coldest period of the year at our study site, movement was reduced by decreasing mean temperature only during the second winter, which was colder than the first winter. Foraging rates have been shown to be temperature dependent (Grubb 1978; Hogstad 2015a) and cold weather may induce obligate within-winter movement of some species (e.g. Sauter et al. 2010). However, previous studies have not shown cold weather to reduce within-winter movement of birds. Our results thus contrast with studies on great tits wintering in areas of milder weather (Mérő and Žuljević 2014). Clearly, winter conditions are more challenging for great tits in the northern latitudes (Orell and Ojanen 1983; Broggi et al. 2004, 2007). Daily routines of wintering tits are dictated by the need to safely attain sufficient fat deposits in order to survive the long, cold nights (e.g. Koivula et al. 2002; Krams 2000; Krams et al. 2010). Because movement significantly increases energy expenditure (Tatner and Bryant 1986; Masman and Klaassen 1987), reduced movement is probably a strategy for saving energy during energetically demanding cold periods (Broggi et al. 2004, 2007). At the same time, short day length (3–5 h in winter in Oulu) allows less time for foraging. While this obviously means that individuals may have less time to invest in movement, day length itself was not found to affect movement. Despite the fact that constant movement and flocking are strategies to escape predation (de Laet 1985, Ekman 1989, Cresswell 1994), individuals may be more willing to take risks during these demanding periods, as predator vigilance becomes costly and difficult (Elgar 1989). Finally, aggression may be suppressed during cold periods due to increased costs of energetic stress, which would reduce the need to change sites (Hogstad 1989, 2015b).

We found juvenile great tits to have lower within-winter site fidelity than adults, which was predicted based on the dominance of adults over juveniles (Ekman 1989; Hogstad 1989; Sandell and Smith 1991). As juveniles are subordinates and consequently in a poorer position in terms of safe foraging (Ekman 1989), they may benefit more from moving between sites to escape predation or to find sites with better access to safe foraging. Juveniles may also be collecting information about the relative quality of different wintering areas and finding their position in the flocks during their first winter. While males dominate females (Ekman 1989; Hogstad 1989; Sandell and Smith 1991), we found no sex differences in site fidelity. This may reflect the fact that great tit pairs affect each other's foraging decisions (Firth et al. 2015). Males often protect their mates and therefore females paired with alpha males receive less aggression from other flock members (Ekman 1990; Hogstad 2015b).

Overall, we did not find support for age or sex differences in between-winter site fidelity. We found that 64% of wintering Great tits that survived until spring (late March), returned to the same area the following winter. Furthermore, birds that were most site faithful during the first winter (were seen on each occasion) had a very high probability of returning the following winter (72%). Because this estimate includes mortality from late March to the second winter, site fidelity to the study area was apparently very high. Furthermore, great tits showed high fidelity to the same sites between years. This is consistent with national ring recovery data, which shows that 95% of great tits ringed during the winter are found within one kilometre from their ringing site in subsequent winters (Valkama et al. 2014). Clearly, the cost–benefit association between juveniles and adults is different for within- and between-winter fidelity. Juveniles probably gather information on resources and build relationships with flock mates in their first winter, and therefore, gain the same benefits as adults from returning the next winter.

The proportion of birds that returned the next winter was over 50% for birds that were present in the autumn time (November–December; i.e. about 1 year in between). This value is much higher than the average annual adult survival estimated from a breeding population in the same region (0.38; Karvonen et al. 2012), and closer to that estimated from the southern parts of the species distribution (Payevsky 2006). This means that either survival was very high during that year (autumn 2008–autumn 2009) and/or great tits are more site faithful to their wintering areas than breeding areas in the north. The proportion of individuals (74%) that were observed during the first two encounters and were still alive on the last two encounters, plus high annual apparent survival (54%) estimated from capture-recapture data from the breeding population (Pakanen et al. unpublished data), suggest that survival was also high during that winter.

Some variation in site fidelity is probably not related to sex and age. This is suggested by the large range in the return rates (resighted in the second winter) of individuals seen in the last encounter occasion of the first winter (41–72%). In addition, individuals that were seen only few times in the first year had a higher probability of changing sites between years. There may be a portion of floaters that only visited the area (Hogstad 2014). Some of the observed variation in return rates may have been caused by the fact that some of the individuals that were resighted in the last occasion had wintered elsewhere, which would fit the higher movement rates during the autumn and spring. However, as the individual variation (captured by the block random term) was high, it is possible that individuals have consistently different movement strategies, some being transient while others are resident (Belda et al. 2007), that could be related to personalities and behavioural syndromes (Cote et al. 2010; Dingemanse et al. 2012; Aplin et al. 2013).

As in other partial migrants, great tit individuals follow several different strategies in non-breeding season movement (Newton 2012). At high latitudes, the great tit is essentially a facultative migrant, i.e. when conditions are poor, they move to an area where they can survive the winter but also often remain in their breeding territories (van Balen 1980). This means that individuals breeding or born in an area where birds are fed can be resident throughout the year, i.e. highly site faithful between winters. However, in northern conditions, great tits are forced to move from their breeding areas if they breed outside the reach of winter feeding (Orell 1989). Therefore, many of them act like obligate migrants that are known to have high site fidelity (Newton 2012). The origin of the wintering birds in our study is unknown. While some may be local breeders, the study area cannot carry the sampled number of birds as territorial breeding pairs. Interestingly, one bird was subsequently resighted about 170 km northeast in Posio during the breeding season, which suggests that the city of Oulu and the study area draw wintering great tits from a large area.

Our results have implications to our understanding of the effects of cold weather on movement behaviour in birds. Cold weather may reduce the ability to use available resources. This may be a mechanism by which winter weather limits the behaviour and distribution of birds, ultimately resulting in lower survival at the northern range margin (e.g. Karvonen et al. 2012; Tolvanen et al. 2017).

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Compliance with ethical standards

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Conflict of interest The authors declare that they have no conflict of interest.

Data availability The datasets during and/or analysed during the current study are available from the corresponding author on reasonable request.

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