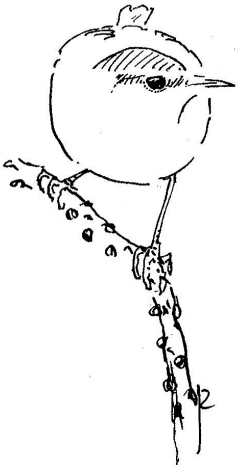
WITHIN AND BETWEEN-YEAR WINTER-SITE FIDELITY OF CHIFFCHAFFS *PHYLLOSCOPUS COLLYBITA*

PAULO CATRY[1,2*], INÊS CATRY[3], TERESA CATRY[3] & TERESA MARTINS[3]



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Current knowledge concerning between-year winter site fidelity in passerines suggests there might be important inter-specific and regional variations in recurrence rates (the proportion of birds recaptured in years subsequent to marking). However, there are virtually no studies reporting low recurrence rates that show this not to be simply the result of low recapture probabilities. This problem can be particularly acute for partly nomadic and mostly non-territorial species in their winter quarters. The present study shows that, in spite of the apparently nomadic behaviour of wintering Chiffchaffs *Phylloscopus collybita*, some individuals can become temporarily sedentary. Temporarily sedentary Chiffchaffs have very small linear home-ranges (ca. 200m) and their calculated recapture probability (by re-sighting of colour-ringed birds) is high. In spite of that, recurrence rate of temporarily sedentary birds is very low, suggesting that the majority of the surviving individuals are not site faithful. This is in contrast to what has been found in several detailed studies in other Sylviidae and also Parulidae involving mostly territorial birds. The type of approach developed here should be used in other studies before any comparisons and generalisations involving winter-site fidelity results are attempted.

Key words: *Phylloscopus collybita* – winter – site-fidelity

[1]Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Rua Jardim do Tabaco 44, 1149-041 Lisboa, Portugal; E-mail: paulo.catry@netc.pt; **Present Address*: British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK; [2] Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford. Oxford OX1 3PS, UK. [3]Departamento de Zoologia, Faculdade de Ciências de Lisboa. Bloco C2. Campo Grande. Lisboa, Portugal.

INTRODUCTION

Previous ownership and knowledge of a certain area is likely to confer advantages to philopatric individuals, by raising their ability to efficiently exploit and defend resources, and maybe to elude predators. These have been suggested as some of the main advantages of philopatry in migratory birds (Baker 1978). In the last few decades, it has become evident that many species of birds often show a relatively high between-year fidelity to wintering grounds (Evans & Townshend 1988; Holmes & Sherry 1992; Robertson & Cooke 1999). Amongst passerines, studies of (mostly territorial) insectivorous and frugivorous species (mainly Sylviidae and Parulidae) in the tropics have reported high winter recurrence rates, suggesting that most surviving (territorial) individuals come back to exactly the same area year after year (Nisbet & Medway 1972; Price 1981; Kelsey 1989, Holmes & Sherry 1992; Salewski *et al.* 2000; Wunderle & Latta 2000; Latta & Faarborg 2001). On the other hand, studies of wintering passerines (mostly Sylviidae and Turdidae) in the Mediterranean, although also showing that winter recurrence is a widespread phenomena, have generally reported lower return rates, indicating that many birds could be changing wintering locations from one year to another (e.g Herrera & Rodriguez 1979; Finlayson 1980; Ioalé

& Benvenutti 1983; Cuadrado 1992, 1993, 1995; Constant & Eybert 1995; Orsini & Bouillot 1995; Herrera 1998). In fact, we could not find a single study in the Mediterranean reporting recurrence rates approaching the high levels (ca. 50%) often found in the tropics. However, caution should be exercised in the interpretation of such reviews.

For example, the methods used and local conditions are often so different that results might simply not be comparable. Almost all the research reporting high return rates involved territorial species and individuals that were colour-marked and visually recaptured (but see Nisbet & Medway 1972). On the other hand, most authors reporting low recurrence rates used numbered rings (that could only be read with the bird in the hand) and probably many non-territorial individuals. Some studies using colour-ringed birds followed a mixture of territorial and non-territorial individuals (Constant & Eybert 1995; Cuadrado 1995). That these major variations in approach might be responsible for the apparent differences between the tropics and the Mediterranean is suggested by some tropical studies, involving mostly non-territorial and non-colour-marked individuals, that have also reported low recurrence rates (Sauvage *et al.* 1998; King & Hutchinson 2001).

Following itinerant or non-sedentary small passerines in the winter over large spatial or temporal scales will remain impossible until technology is developed allowing long-term remote tracking of individuals. However, it is possible to study site fidelity of individuals that show a limited degree of attachment to a reasonably small area, provided that one takes recapture probability into account and distinguishes itinerant from sedentary individuals. So far, virtually no studies of winter site fidelity of passerines have taken recapture probability into account. Some authors have used capture-recapture models, and have inferred high recurrence rates based on a very small proportion of recaptures in years subsequent to marking (Cuadrado *et al.* 1995). These studies implicitly suggest that low between-year recapture rates are simply the product of extremely low overall recapture rates (for example, due to a large home range). However, an alternative explanation is that one subset of the population behaves as site faithful, while another does not. It is not clear from the cited papers if the existence of such heterogeneity can be inferred, or not, from the available data. The fact the individuals within the same species show different degrees of site attachment might be the cause for apparently conflicting views. For example it is unclear whether Blackcaps *Sylvia atricapilla* are mostly nomadic, while tracking variable resources (Rey 1995; Herrera 1998), or faithful to a certain area both within and between winters (Cuadrado *et al.* 1995).

In this paper, we present the results from a study of Chiffchaffs *Phylloscopus collybita* wintering in Portugal that aimed to (1) identify and document the spatial behaviour of temporarily sedentary individuals and (2) study the between-winter site fidelity (or recurrence) of temporarily sedentary birds taking into account their recapture probability. We show that reported low recurrence rates for this species are not simply a product of low recapture probabilities.

METHODS

Chiffchaffs wintering in western Iberia originate mostly from Ireland, the United Kingdom, France and the Low Countries (Cantos 1992; Cramp 1992) and belong to the nominate subspecies (*P. c. collybita*). We have no evidence for the winter occurrence of the summer breeding Iberian Chiffchaff *Phylloscopus brehmii* at our study site (see also Svensson 2001). The study site (38º48'N, 8º55'W) is located in the Tagus (Tejo) Estuary Nature Reserve, some 15 km inland from Lisbon, in central southern Portugal. It consists of a discrete 1000m line of low tamarisk *Tamarix* sp. trees, growing on a dyke that separates a belt of reedbeds and the river from pastures that cover the Tagus alluvial plains. Chiffchaffs range on the tall vegetation over the dyke, on the reedbeds and along ditches and fences, but avoid the open pastures that cover most of the area. Chiffchaffs were trapped from dawn till early or mid afternoon with the aid of mist nets set to cross the tamarisk line. Capture sessions (one-day trapping) ranged from

11 Oct to 27 Dec in 1998 and from 5 to 26 Nov in 1999. A total of 16 capture sessions were organised (12 in 1998 and 4 in 1999) at approximately regular intervals and on no occasion were two successive trapping sessions less than five or more than 11 d apart. A total of 529 different individual Chiffchaffs were trapped (403 in 1998 and 126 in 1999). Every bird newly trapped was ringed. Maximum wing-chord was measured using a wing ruler and weight was taken using a Pesola spring-balance. The amount of sub-cutaneous fat reserves was assessed by visual inspection using a 9-point scale (Kaiser 1993). All captured Chiffchaffs were colour-marked. Birds captured in Oct and Nov 1998 were marked with a different "cohort" specific combination in each trapping session. If and when they were retrapped, these birds were individually colour-marked. Birds caught in Dec 1998 and in 1999 were individually colour-marked when first caught. All birds were released within the study site.

Regular (approximately weekly) visits for the observation of colour-marked individuals were carried out from Dec till Feb in 1998/99 and from Nov till Mar in 1999/2000. Observation effort was standardised, and constant in all visits. In the second winter, the study site was divided into forty 25m sections (marked with numbered flags) and the location of each colour-marked Chiffchaff seen was mapped to study local movements and home ranges.

Recapture probabilities in 1999/2000 were estimated using program MARK (White & Burnham 1999). The initial data matrix, which included all resightings but no recaptures in mist-nets, was simplified by dividing the study period into half-month (c.15 d) intervals. Cormack-Jolly Seber models (Lebreton *et al.* 1992) were applied with the full time dependent models fitted initially (F_t, p_t) and effects of age (juveniles vs adults) investigated separately. The initial capture was removed from each encounter history in order to minimise any biases related to differences between capture and recapture techniques (Schmutz & Ely 1999). We predicted that a number of unidentifiable individuals caught would be transients and thus should have lower local survival. We therefore tested several potential cohort models where overall survival rates in the first few encounters after capture were different to those later in the study. Subsequent model selection was based on Akaike's Information Criterion number of parameters and where models were nested likelihood ratio tests. Goodness of fit was tested using program RELEASE (GOF, Test 2 & Test 3). Although all biologically sensible models of survival were tested in order to ensure the most parsimonious model was selected, it was recapture probabilities that were of prime interest in this study and thus survival estimates will not be discussed. Age and previous duration of stay at the study site were found to have a weak effect in local survival estimates. We therefore pooled the data in relation to these variables in order to obtain one single and robust estimate of recapture probability based on a sample as large as possible. Means are presented with associated standard errors.

RESULTS

Evidence for itinerancy

The large majority (69.8%) of the birds individually colour-marked at first capture (n = 199) were never seen again, indicating that most of them were only transients at the study site. This proportion (69.9%, 51 / 73) is maintained when we restrict the analysis to birds first caught in Dec. The median duration of stay for the birds recaptured (visually or trapped) at least once was 20 d (n = 60). Again, a similar result (22.5 d, n = 22) is obtained when considering only Dec birds. Of birds ringed in Dec, only 9.6% (7/73) were recorded staying for over one month after capture. The fat reserves of transients were similar to the ones carried by birds that were recaptured at least once at the study site (both groups, median fat-score = 2.0, n = 435 transients and 90 non-transients, Mann-Whitney U = 18017, P = 0.22). Birds that stayed for a short period (< 15 d) did not significantly gain body mass during their stay (mean daily fattening rate = 0.020 ± 0.029 g d^{-1}, n = 16).

Local home range

We used all the birds observed on 3 or more different occasions (in different weeks) to study the local home range of Chiffchaffs. Thirteen birds were selected with a median number of 7 records each (range 3-15). Individual Chiffchaffs were highly constant in their location along the 1000m study line, which is shown by the high repeatability (r - the intra-class correlation coefficient) of their recorded positions ($r = 0.69$, ANOVA $F_{12, 79} = 16.6$, $P < 0.0001$). One bird appeared to change home range in the middle of the winter. If this bird is eliminated, or if its records are divided into two groups (before and after the change), repeatability increases to 0.86 (in both scenarios). The mean standard deviation of the mean individual position measured in 25 m units was 2.1 ± 0.3 (range 0 – 3.83, $n = 12$). If we assume that the normal linear home range is four times this value (see Jennrich & Turner 1969 and Piper & Wiley 1990 for this type of rationale), we conclude that the local home range at our study site is around 200 m (with a 50 m measurement error). Approximately 95% of all observations of the average individual Chiffchaff would fall in a home range of this size.

Probability of recapture of individually colour-ringed birds

To have an idea of the between-year site fidelity (or recurrence rates) it is important to know what the recapture probability of the birds being studied is. We estimated this by fitting a capture-recapture model to the 1999-2000 data. Although local survival showed some variation from month to month, the most parsimonious model was one with a constant recapture probability, estimated to be around 0.66 for each half-month (15 d) period (Table 1).

Between-year return rates

Of the 90 Chiffchaffs individually colour-marked in 1998, only 4 (4.4%) were seen in the autumn-winter 1999/2000. If we restrict the analyses to individually colour-ringed birds that settled at the study site in the first year and stayed at least 15 d, 4 (8.2%) of 49 birds returned in the second year. It seems unlikely that other birds might have been missed, since the recapture probability per 15 d was 0.66 and the birds that came back stayed at the site for long periods (between 2.0 and 3.5 months), and were seen on 2, 4, 9 and 11 different occasions, respectively. Considering the recapture probability of 0.66, even if some of the short-stay birds had come back and been missed, it is highly unlikely that the estimate of the recurrence rate would increase much. For example, if 4 recurring individuals came back for a short stay (15 d) and were all missed (an unlikely event, $P = 0.01$) the recurrence rate would still be only 16.4%. This means that the (large) majority of the resident birds (assuming a survival rate

Table 1. Estimation of local survival and recapture probability per half month for the autumn/winter 1999/2000 using capture-recapture models.

Period (half month)	F Estimate	SE	L. 95% C.L.	U. 95% C.L.
1	0.21	0.13	0.05	0.56
2	0.75	0.20	0.28	0.96
3	0.62	0.16	0.29	0.87
4	0.87	0.16	0.27	0.99
5	0.87	0.14	0.38	0.99
6	1.0	0.00	1.00	1.00
7	1.0	0.00	1.00	1.00
8	0.68	0.24	0.20	0.95
	Recapture Prob.			
Overall	0.66	0.07	0.51	0.78

of ca. 50%, Peach *et al*. 2001) do not display fidelity to this wintering site. If we consider all the birds marked (with either individual or 'cohort' specific colour-combinations) in 1998, only 6 (1.5%) out of 403 birds were either seen or caught in the following year. Two of these birds were not individually recognisable. One was retrapped in 1999, and colour-marked after that. The other one was seen on several occasions, always in the same area, and therefore we assume that only one individual of that "cohort" was involved.

DISCUSSION

Chiffchaffs have been suggested to be partly itinerant in their winter quarters, on the basis of observed within-winter abundance variations in different habitats and locations, low local recapture rates and observed movements of colour-ringed individuals (Cuadrado 1993; Finlayson 1998; Sauvage *et al*. 1998). Evidence from our study also supports this idea. The number of transients was consistently high in autumn and early winter, transients did not have larger fat reserves than residents (to be expected if they were typical migrants passing by), individuals did not fatten at the study site (to be expected if this was a typical stopover), and birds that settled locally rarely stayed for the entire winter.

In spite of this apparent itinerant behaviour, some Chiffchaffs did become temporarily resident with well-defined home ranges. Resident Chiffchaffs were never recorded displaying territorial behaviours, and often joined loose flocks of foraging conspecifics. Small home ranges of non-territorial wintering Old-World warblers have been described before (Nisbet & Medway 1972), showing that in this family, absence of winter territoriality does not necessarily mean that all individuals behave permanently as itinerants. The existence of fidelity to specific wintering sites by Chiffchaffs has been shown by several authors before (Herrera & Rodriguez 1979; Finlayson 1980; Sauvage *et al.* 1998). However, between-year recapture rates are typically low (1-10%) although this could result from suspected low recapture probabilities (King & Hutchinson 2001). In the absence of a more detailed analysis, Chiffchaffs wintering in Iberia have been inferred both to be extremely site faithful (Cantos 1992) and nomadic with little site fidelity (Cuadrado 1993). Our study, the first to carefully measure recapture probabilities at a winter study site, showed that temporarily resident individuals (those that stayed for at least 15 d at the study site) had a recurrence rate of approximately 8% (assuming that they would behave again as residents in their second winter at the study site). With an annual survival rate of around 50% (Peach *et al*. 2001) this low recurrence rate indicates that the (large) majority of the individuals are not site faithful. This is clearly different from what has been reported for other Old-World and New-World warblers that show territorial behaviour (Price 1981; Kelsey 1989; Holmes & Sherry 1992; Wunderle & Latta 2000). It also contrasts with evidence from Eastern Great Reed Warblers *Acrocephalus orientalis*, a non-territorial species (Nisbet & Medway 1972). In spite of this, a few birds can remain site-faithful in the long-term; for example, a Chiffchaff we caught in Dec 1998 was first ringed at this same site (by G. Elias) 6 years earlier.

Our analysis is based on one year only, and therefore a low between winter-site fidelity might be the result of unusual events, such as an exceptionally low survival between the two winters of study. However, there are other lines of evidence suggesting our results are not atypical. A large-scale study using ringing recoveries (considering reptraps in mist-nets only) in Iberia, has shown that only 51% of 138 Chifchaffs ringed and recovered during the winter period were recaptured (on a subsequent year) at the original ringing site (Cantos & Tellería 1994). Although not explicitly recognised by the authors (who were focusing on stopover site fidelity), this is also evidence of low winter site fidelity in Chiffchaffs. Only a tiny proportion of all the alternative wintering sites for Chiffchaffs would have been sampled (the species is a habitat generalist in winter). If, in spite of this, 49% of the Chiffchaffs recap-

tured were found away from the original ringing site, one must conclude that only a minority of the birds were site faithful. Our data does not allow an accurate assessment of recapture rates for transients or for individuals with short stopovers, but the extremely low recurrence rates suggest that site fidelity for those birds must also be low. Of course, the hypothesis that these birds have high recurrence rates to a large general area inside which they wander in a more or less unpredictable fashion (Cuadrado *et al.* 1995) cannot be excluded using these sorts of analytical techniques. This type of hypothetical area-fidelity would be, however, clearly different (from a biological point of view) from a site-fidelity to a small and localised winter home range. Descriptions of habitat preferences for this species elsewhere (Elias *et al.* 1998; Olioso 1991; Finlayson 1998), our personal experience and the large number of individuals trapped by us, suggest that our study site is a typical location for Chiffchaffs in winter. Therefore, we believe that conclusions from our study should be broadly applicable, although there could be differences between habitats still to be discovered.

In conclusion, our study demonstrates that reported low winter site recurrence rates for several species wintering in the Mediterranean region are not necessarily an artefact resulting from low recapture probabilities. At least in Chiffchaffs, but possibly in other species too, few birds return to the wintering locations used in the previous year. More studies using the field procedures and analytical techniques employed here are needed before generalisations on the patterns of winter site fidelity by passerine migrants can be attempted.

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SAMENVATTING

Is die Roodborst *Erithacus rubecula* in je tuin iedere winter dezelfde vogel of heb je ieder jaar weer een ander? Het is een algemene vraag naar plaatstrouw van wintergasten aan een bepaalde locatie. De tot nu toe verkregen resultaten over plaatstrouw van overwinterende trekvogels suggereren dat soorten hierin sterk kunnen verschillen en dat er tevens regionale verschillen bestaan in de kans dat een geringd individu in een later jaar weer op dezelfde plaats wordt teruggezien. Een probleem bij vrijwel alle studies is dat een geringe plaatstrouw die wordt waargenomen, ook veroorzaakt kan zijn door een lage kans om een vogel terug te zien of te vangen. Vooral bij soorten die gedeeltelijk nomadisch en niet-territoriaal zijn in de overwinteringsgebieden, speelt dit probleem in sterke mate. De onderhavige studie laat zien dat overwinterende Tjiftjaffen *Phylloscopus collybita* in Portugal gedurende de winter deels voor korte of langere tijd op dezelfde plek verblijven, ondanks hun schijnbaar nomadisch gedrag in de winter. Deze sedentaire individuen hadden een zeer klein, lineair leefgebied langs een rivier (*ca.* 200 m). De kans dat gekleurringde individuen hier werden weergezien, was daardoor hoog. Ondanks deze plaatstrouw binnen een winter was de kans dat zij in een daaropvolgend jaar werden teruggezien, erg laag. Dit wijst erop dat de meerderheid van de overlevende vogels geen plaatstrouw in latere winters vertoonde. Dit is in tegenstelling tot verschillende detailstudies aan zangers van het geslacht *Sylvia* en de Noord-Amerikaanse Parulidae, die vooral aan territoriale soorten zijn verricht. In de onderhavige studie is ook de vangkans meegenomen in de berekeningen over plaatstrouw. De auteurs adviseren dat andere studies voor een dergelijke aanpak zouden moeten kiezen, zodat een betere vergelijking van de resultaten met betrekking tot plaatstrouw aan overwinteringsgebieden tussen soorten gemaakt kan worden en generalisaties betreffende dit onderwerp mogelijk worden. (CB)

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