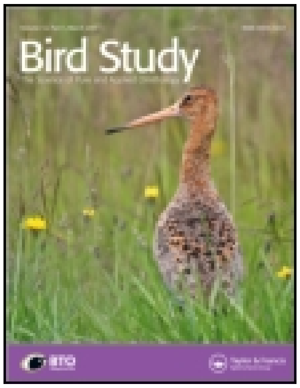

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Wintering survival of insect-eating passerines in southern Europe

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Wintering survival of insect-eating passerines in southern Europe

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Capsule Intra-year survival during the winter is high for some insect-eating passerines in northern Iberia.
Aims To estimate intra-year survival of insect-eating passerines wintering in northern Iberia.
Methods Capture–recapture data from four passerines (European Robins *Erithacus rubecula*; Common Chiffchaffs *Phylloscopus collybita*; Firecrests *Regulus ignicapillus*; and Dunnocks *Prunella modularis*) captured during four consecutive winters were analyzed using Cormack–Jolly–Seber models.
Results Intra-year survival during the winter differed between species, possibly revealing different survival or wintering strategies. Thus, Dunnocks and Firecrests showed survival rates close to 1, whereas Chiffchaffs and Robins had lower survival rates (0.4 and 0.3–0.6, respectively). Transients were detected only in Dunnocks (60%). This strategy in which some birds are resident and others are vagrant is already known for other species, particularly those that feed on plants or change to a more vegetarian diet during the winter.
Conclusions Northern Iberia, and particularly its coast, is a good wintering area for several insect-eating species.

The winter period is critical for survival of many bird species, especially those living at high or temperate latitudes (Newton 1998). Most analyses where survival rates have been estimated are based on data obtained during the breeding period (Dobson 1990, Peach *et al.* 1991, 2001, Siriwardena *et al.* 1998) and, therefore, the impact of the winter period on survival is typically assessed indirectly. Such analyses commonly assume that mortality is generated mainly during the non-breeding period which, in migrant species, includes both migration and wintering. Thus, wintering mortality is usually unknown for many species.

Winter survival can be analyzed from either an intra- or inter-year perspective. Intra-year survival analyses allow estimates of the impact of winter on survival and, therefore, of the importance of this period on bird population dynamics (Newton 1998). Although of such importance, this is an approach rarely considered (Greenberg 1986, Holmes *et al.* 1989), and in general studies have focused on year-to-year analyses (Belda *et al.* 2007, Cuadrado 1992, Mezquida & Villaran 2006, Salewski *et al.* 2000). Intra-year survival studies also provide a good tool with which to estimate the presence of transients (i.e. birds which do not remain in the same site during the entire wintering period) (Belda *et al.* 2007, Pradel *et al.* 1997). Such transient habits are of high interest in the study of life strategies during the winter period (Senar & Borras 2004).

Mortality during the winter period is one of the main causes regulating population size in many bird species, especially if the birds over-winter in regions with adverse meteorological conditions that impose food shortage (Newton 1998). In contrast, studies carried out in tropical areas have shown high over-winter survival (Holmes *et al.* 1989), suggesting that when good conditions are set, wintering mortality can be as low as during summer months. Southern Europe, and particularly the circum-Mediterranean region (Santos & Tellería 1985, Tellería 1988), is a goal wintering area for many European bird species (Cramp 1988, 1992). Climatic conditions within the circum-Mediterranean area are mild, so survival prospect in this region could be high, but survival may decrease towards the north. Although within the circum-Mediterranean region,

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cold or snow spells can generate important mortality episodes (Galarza & Tellería 1985, Senar & Copete 1995), over-winter survival is predicted to be low.

Birds can adopt two main movement-associated strategies during the winter: residence versus transience (Belda *et al.* 2007, Catry *et al.* 2003, Cuadrado 1992, Senar *et al.* 1992). The circumstances that determine which of these strategies is adopted depends on the type and availability of food used by a species (reviewed by Senar & Borras [2004]). Thus, insect-eaters are more likely to adopt a resident strategy as compared with seed- or fruit-eating birds, since the seed and fruit resources may become locally diminished (but see Catry et al. [2003]). Although it is well documented that the same individual can change its territorial behaviour depending on food availability and distribution (Davies 1976, Zahavi 1971), transience should be unexpected, or less common, among insect-eating birds.

Population dynamics and survival of European passerines at their wintering areas have rarely been analyzed, and those studies which have investigated this have chiefly focused on the circum-Mediterranean region (Catry et al. 2003, Cuadrado 1992). In contrast, much less research has been carried out in transition regions between northern and southern Europe. The Cantabrian region in northern Iberia is a transition area between northern Europe and the circum-Mediterranean region, and provides refuge to several passerine species during the winter (Tellería *et al.* 2009, Tellería & Santos 1986), particularly insect-eating birds (Senar & Borras 2004, Tellería & Santos 1986). Our aim in the present study was to estimate intra-annual survival of insect-eating passerines wintering in northern Iberia (southern Europe). With this goal, we used data from the most common small-sized insect-eating passerines that were captured at a constant effort ringing station in northern Iberia, during a period of four consecutive winters.

MATERIAL AND METHODS

Sampling site

Data were collected between April 2006 and March 2010 at the ringing station located at Plaiaundi Ecological Park, Txingudi marshlands, northern Iberia (43° 21′ N, 01° 48′ W, municipality of Irún). The vegetation in this area is a mosaic of flooded meadows, grasslands, small woods of alders *Alnus* spp., willows *Salix* spp. and mixed deciduous trees and some beds of reed *Phragmites* (Arizaga *et al.* 2007).

Birds were captured with mist-nets (96 linear metres) at sampling sessions that were performed four times a month. Mist-nets remained open during a period of 4 hours starting at dawn per sampling day (for further details see Arizaga *et al.* 2007). Once captured, birds were ringed with metal ring (or the ring was read if recaptured) and released.

The most common passerines with a sufficient number of captures/recaptures to estimate wintering survival were: European Robin *Erithacus rubecula* (hereafter, Robin), Common Chiffchaff *Phylloscopus collybita* (hereafter, Chiffchaff), Dunnock *Prunella modularis*, and Firecrest *Regulus ignicapillus* (Table 1; Fig. 1). The winter period was defined as November to February. October and March were excluded owing to the presence of probably migrating, non-wintering individuals (Arizaga *et al.* unpubl. data, Arizaga *et al.* 2010).

Survival analyses

To estimate survival we used Cormack–Jolly–Seber (CJS) models, which allow separate estimation of survival (ϕ, probability that a bird captured in t is still alive in $t+1$) and recapture probability (p, probability that a bird captured in t and still alive in $t+1$ is recaptured in $t+1$). Months were used as a time unit, so that survival rate was the survival from a given month to the next one within a winter.

To estimate intra-year survival we considered month as a unit time (small sample sizes prevented us considering a smaller unit time; Table 1), so therefore we obtained matrices of n rows (individuals) × 4 columns (months). We pooled years because of sample size constraints (i.e., we did not test for variations of within-winter survival among years) (Belda *et al.* 2007).

Before starting to select models, we explored the fit of data to CJS assumptions. To do this, we used a goodness-of-fit (GOF) test. A GOF test on a CJS model where

Table 1. Number of captures/recaptures of four common passerines at Txingudi, Northern Iberia, during the winter period (November–February). Each individual was considered only once per month and year (winter).

	Winter			
Species	2006/07	2007/08	2008/09	2009/10
Robin	52/19	27/6	28/11	32/6
Chiffchaff	38/6	26/3	19/1	59/3
Dunnock	10/4	15/5	11/3	7/4
Firecrest	8/2	8/4	20/5	13/6

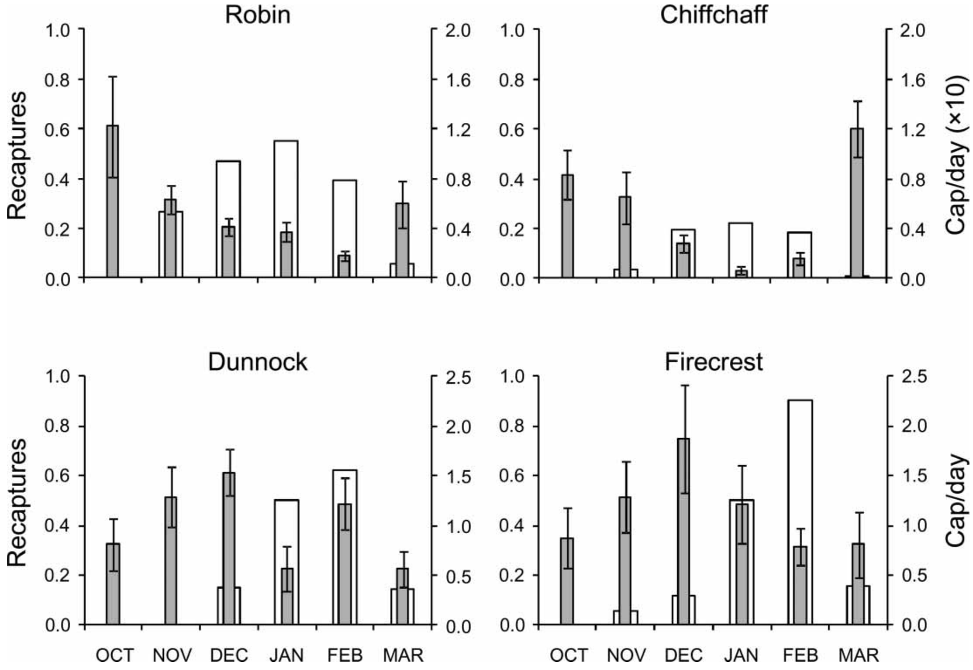

Figure 1. Phenological patterns of four common passerines at Txingudi, Northern Iberia during the winter period (November–February) showing proportion of recaptures (white bars) and mean number of captures per day ± se. The proportion of recaptures in October is zero because each bird was considered only once a month.

both ϕ and p varied with time [$\phi(t)$, $p(t)$] was done with the U-CARE software (Choquet *et al.* 2001), allowing us to identify a basic starting model that fit the data used to start model selection. $\phi(t)$ $p(t)$ was the most complex model from which to start the model selection. All other fitted models were nested within our starting one. Additionally, we conducted a second analysis in order to test possible survival differences between species. For that analysis, species was introduced as a factor (category variable) into CJS models.

In data sets in which transient birds were detected, we calculated the proportion of transients as: $1 - (\phi_1/\phi_2)$, where ϕ_1 is survival of previously unmarked birds, and ϕ_2 is survival of previously marked birds (Pradel *et al.* 1997).

Corrected Akaike values (AICc) were used to rank the fit of models to data (Burnham & Anderson 1998). Models with an AICc difference less than 2 were considered to fit well to data, and those for which the difference was higher than 2 were considered to differ significantly. Models with an AICc difference $<$ 2 from the first model in the ranking were averaged based on their AICc weight. We used the software MARK 4.3 (White & Burnham 1999) for all these analyses.

RESULTS

Global GOF test for the data was non-significant for all cases (Table 2), but the specific Test 3SR to detect transients was significant for the data set for Dunnocks (Table 2). Therefore, except in the case of Dunnocks, our data did not break the CJS assumptions (Pradel *et al.* 1997, Belda *et al.* 2007). When 'species' was introduced as a factor into a single matrix with all data the global GOF test was not significant, nor was the specific Test 3SR to detect transients (global test: $\chi^2_{14} = 10.316$, $P = 0.739$; Test 3SR: $\chi^2_{14} = 1.268$, $P = 0.205$).

In Robins, Models 1 [$\phi(t)$, p] and 2 [ϕ, $p(t)$] were observed to fit the data equally (Table 3). Thus, averaged ϕ values were 0.43 ± 0.09 (survival from November to December), 0.60 ± 0.13 (December to January), and 0.27 ± 0.08 (January to February). Regarding p values, they ranged from 0.44 ± 0.12 (January to February) to 0.57 ± 0.14 (December to January), but the high se suggests non-significant monthly differences of recapture rate (p).

In Chiffchaffs, the model that best fitted the data was that with constant ϕ and p values, although models including monthly variation of p (Model 2) or ϕ (Model 3) were also significant (Table 3). Averaged ϕ

Table 2. Goodness-of-fit tests used to determine whether data violated the Cormack–Jolly–Seber (CJS) assumptions.

Species	Global test	Test 3SR (transience)
Robin	$\chi^2 = 0.009$ $P = 0.999$	$\chi^2 = 0.069$ $P = 0.945$
Chiffchaff	$\chi^2 = 0.000$ $P = 1.000$	$\chi^2 = 0.000$ $P = 1.000$
Dunnock	$\chi^2 = 8.394$ $P = 0.078$	$\chi^2 = 2.468$ $P =$ **0.014**
Firecrest	$\chi^2 = 1.913$ $P = 0.591$	$\chi^2 = 0.000$ $P = 1.000$

The Test 3SR is a specific test used to check whether there are transients; significant values are in bold; df = 3 for all cases; data sets were insufficient to test for the CJS assumptions in Chiffchaff and the Test 3SR in Firecrest

Table 3. Cormack–Jolly–Seber models used to estimate intra-year survival of four common passerines at Txingudi, Northern Iberia, during the winter period (November–February).

Models	AICC	ΔAICC	AICC weight	*N*p	Deviance
Robin					
$\phi(t)$, p	195.651	0.00	0.592	4	4.507
ϕ, $p(t)$	197.225	1.57	0.269	4	6.081
$\phi(t)$, $p(t)$	199.557	3.91	0.084	6	4.088
ϕ, p	200.408	4.76	0.055	2	13.467
Chiffchaff					
ϕ, p	100.360	0.00	0.443	2	7.908
ϕ, $p(t)$	101.147	0.79	0.299	4	4.466
$\phi(t)$, p	101.941	1.58	0.201	4	5.259
$\phi(t)$, $p(t)$	104.437	4.08	0.058	6	3.386
Dunnock					
ϕ(transients), p	70.735	0.00	0.656	3	14.215
ϕ(transients, t), p	73.258	2.52	0.186	4	14.215
ϕ, p	74.390	3.66	0.105	2	20.245
ϕ, $p(t)$	76.437	5.70	0.038	4	17.395
$\phi(t)$, p	78.594	7.86	0.013	4	19.551
$\phi(t)$, $p(t)$	81.724	10.99	0.003	6	17.132
Firecrest					
ϕ, p	75.226	0.00	0.728	2	8.397
$\phi(t)$, p	78.652	3.43	0.131	4	7.159
ϕ, $p(t)$	78.700	3.47	0.128	4	7.207
$\phi(t)$, $p(t)$	83.402	8.18	0.012	6	6.791

ϕ, survival; p, recapture rate; AICC, corrected Akaike's values; ΔAICC, difference in AICC values of each model and the first model; *N*p, number of parameters; ϕ or p can be either constant or time-dependent (t); for Dunnocks, ϕ was also shown to be affected by the presence of transients, as shown in Table 2.

values were 0.36 ± 0.15 (November to December), 0.34 ± 0.14 (December to January), 0.48 ± 0.24 (January to February), so survival did not differ among months. p values ranged from 0.16 ± 0.11 (December to January) to 0.31 ± 0.26 (January to February). In both cases such a high standard error precluded us considering such ϕ and p monthly-related differences as significant.

The population of Dunnocks was observed to be composed of both transients and non-transients, without differences between months (Table 3). The proportion of transients was 60%, and survival of non-transients was nearly 1 (0.99). The p was 0.43 ± 0.14.

In Firecrests, both ϕ (0.98 ± 0.31) and p (0.14 ± 0.08) were constant (Table 3).

When taking all the species into account in the same matrix (i.e., when 'species' was introduced as a category variable), four models equally fitted to the data. From these, two models (accounting for 46.4% of weight; Table 4) supported the existence of significant survival differences between species (Models 1 and 4). The rest of the models considered ϕ to differ across the winter (Model 2) or to be constant (Model 3; Table 4). We averaged ϕ values as obtained in each model and found that ϕ tended to increase during mid-winter in all species but much more markedly in Robins. In addition, Dunnocks and Firecrests tended to have higher survival rates than Robins and Chiffchaffs (Fig. 2).

DISCUSSION

Data obtained during several consecutive winters in northern Iberia allowed us to estimate intra-year survival in four insect-eating passerines. However, sample sizes were small and, therefore, our results should be considered with caution. Monthly survival rates differed between species and this may indicate different survival prospects or wintering strategies of these species. Thus, Dunnocks and Firecrests showed higher survival rates than those for Robins and Chiffchaffs. The high rate observed for Dunnocks and Firecrests (>0.8 during mid-winter) supports the idea that northern Iberia, and particularly its coast, is a good wintering area for several insect-eating species (Tellería & Santos 1986). In contrast, Chiffchaffs had much lower survival rates (about 0.40), as did Robins, although in this latter species monthly survival varied from about 0.30 to 0.60. Since no transients were detected in these two species, such lower survival rates must be linked with higher mortality rates through the winter period.

Only in one of the species (Robins) was survival found to differ between months. In this case, the decreasing survival rate observed from January to February was linked with a decrease in the abundance and proportion of recaptures (Fig. 1). Therefore, although a higher mortality in January cannot be excluded because of adverse

Table 4. Cormack–Jolly–Seber models used to estimate intra-year survival of four common passerines at Txingudi, Northern Iberia, during the winter period (November–February). Here, the species was introduced as a category variable.

Models	AICc	ΔAICc	AICc weight	*N*p	Deviance
1. $\phi(s), p(s)$	449.998	0.00	0.251	8	50.017
2. $\phi(t), p(s \times t)$	450.066	0.07	0.242	15	35.091
3. $\phi, p(s \times t)$	450.725	0.73	0.174	13	40.096
4. $\phi(s), p$	451.644	1.65	0.110	5	57.905
5. $\phi(s), p(s \times t)$	452.316	2.32	0.079	16	35.148
6. $\phi(s \times t), p(s)$	453.658	3.66	0.040	16	36.491
7. $\phi(s \times t), p$	454.345	4.35	0.029	13	43.716
8. $\phi, p(s)$	454.525	4.53	0.026	5	60.787
9. $\phi(s \times t), p(t)$	454.537	4.54	0.026	15	39.562
10. $\phi(s), p(t)$	455.556	5.56	0.016	7	57.668

ϕ, survival; p, recapture rate; AICc, corrected Akaike's values; ΔAICc, difference in AICc values of each model and the first model; *N*p, number of parameters; ϕ or p can be constant, time-dependent (t), or species-dependent (s); only the best 10 models are shown out of 16 models tested overall.

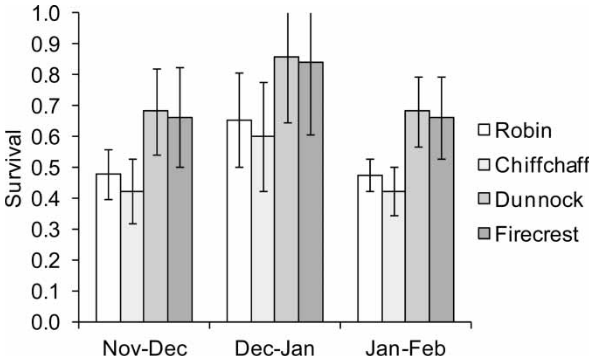

Figure 2. Intra-year survival rate (± se) of four insect-eating passerines during the winter period (November–February) at Txingudi, Northern Iberia.

weather in mid-winter, these results would indicate that some of the Robins may abandon the area in January, probably because they started to move to their breeding areas (Cramp 1988). The hypothesis that Robins from northern Europe who have been forced to move southwards by cold/snow spells (Cramp 1988, Elkins 1983) could reach Txingudi in mid-winter and then displace already settled birds is less likely and has less support. This is for two reasons: (1) prior occupancy ('owners always win' hypothesis) appears to determine dominance in wintering Robins (Tobias 1997), so that newly arrived birds are unlikely to expel already settled Robins; and (2) Robin abundance was observed to decrease over this period. Thus, the observed survival variations across the winter were more likely to be because of the fact that some birds left the area rather than that these birds experienced high mortality during January. Therefore, our results are in line with the idea that survival rate did not differ across the winter within each species.

Interestingly, transients were detected only in Dunnocks, a species feeding on seeds more often than the rest of the species studied (Cramp 1988). Such transience is likely to be because of the fact that some Dunnocks (about 60%) emigrated from the area soon after arrival, while others overwintered in Txingudi. Such a dual strategy with one fraction of residents and another one of vagrants is already known for other species, particularly those that feed on plants or change to a more vegetarian diet during the winter (Belda *et al.* 2007, Senar *et al.* 1992, Skórka *et al.* 2006).

The lack of transient Chiffchaffs is in contradiction to other studies where the species was reported to show some degree of vagrancy (Catry *et al.* 2003). Such a difference could be because of either a methodological constraint (our sample was relatively low) or geographical-associated variations. Concerning methodological problems, we observed that the Chiffchaffs' sample size was not sufficiently high for the Test 3SR, which checks for the presence of transients (Table 2). Therefore, we cannot totally reject this possibility. However, geographical variations are also possible because food availability in northern Iberia is much more restricted as compared with milder areas further south (Tellería 1988), and this may change the proportion of transients (Tellería *et al.* 2008). Thus, it is possible that our study site close to the coast may offer sufficient food to maintain a population of resident Chiffchaffs. Such a strategy is also applicable to Firecrests, which indeed show a similar foraging pattern to Chiffchaffs during the winter (Cramp 1992).

The lack of transients in Robins is in agreement with previous studies (Catry 2005), in which the species was shown to defend territories during the winter (Adriaensen & Dhondt 1990, Cuadrado 1997, Johnstone 1998, Tobias 1997). Thus, our results support the idea of a resident population of territorial wintering Robins (for further details see also Arizaga *et al.* [2010]).

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