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Importance of sampling frequency to detect differential timing of migration: a case study with Blackcaps *Sylvia atricapilla*

Juan Arizaga[1,*] **& Emilio Barba**[2]



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Our aim was to assess to what extent detection of differential timing of passage in migrant birds depends on the sampling frequency (SF). We determined if Blackcaps *Sylvia atricapilla* performed differential migration by age and sex when passing over N Iberia. We mist netted and ringed migrating Blackcaps at a stopover site, both during the autumn (2005) and the spring (2006) migrations. During autumn, adult female Blackcaps passed later than juvenile birds and adult males. In spring, however, migration differed mainly by sex rather than by age. In particular, males passed over earlier than females, likely due to the pressure on males to earlier arrival at their breeding areas. A simulation based on daily captures at the Constant Effort Site showed that the ability to detect differential timing of passage was affected by SF, with P-values being higher with decreasing SF. However, the proportion of variance explained by differences in timing of passage between sex or age classes was not affected by SF. This implies that at Constant Effort Sites a low SF may be adequate to detect differential timing of passage if a higher sampling effort per day (e.g. by sampling with more mist nets, and/or for a longer period) is maintained.

Key words: Blackcap, *Sylvia atricapilla*, effect size, sampling frequency, age and sex classes, timing of passage

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INTRODUCTION

In bird migration, distances travelled, routes and timing can vary between age classes and sex, giving rise to a widespread phenomenon called *differential migration (DM)* (Gauthreaux 1982, Terrill & Able 1988). Patterns of migration have been reported to differ between age classes and sex in several species, both in autumn and spring. In autumn, the age of birds seems to be a major cause contributing to DM, with adult birds passing over earlier than juveniles (e.g. Cantos & Asensio 1989, Basciutti *et al.* 1997, Grandío 1997), although the opposite has been also documented (e.g. Grandío 1997). In spring, however, DM is mainly caused by the sex of birds with males in general passing over earlier than females (reviewed by Cristol *et al.* 1999; see also Rubolini *et al.* 2004, Kokko *et al.* 2006).

Differences in timing of passage between age classes or sex can vary from only a few days (e.g. 2 days in American Redstarts *Setophaga ruticilla*, Morris & Glasgow 2001) to more than a week (Rubolini *et al.* 2004). Migrants arriving early to their goal areas hold best territories, find a mate with a higher likelihood or rear more chicks (Newton 2008), so early arrival could be crucial, even when the difference is no more than few days. Thus, the frequency of catching (e.g. daily or once a week) is thought to play a very relevant role in the ability to detect DM (Leal *et al.* 2004). Small differences in timing of passage between age or sex might go undetected if *sampling frequency (SF)* is too low. To our knowledge, studies dealing with the effect of SF on the ability to detect differential timing of passage are lacking. This, however, can be of key importance from a methodological standpoint, since this could help to

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establish guidelines for the management of Constant Effort Sites where it is aimed to investigate DM.

A decreasing number of captures is invariably associated with a decreasing SF (if sampling effort per day does not vary), and in any statistical test *P* values depend on sample size. Therefore, decreasing SF should result in a decreasing ability to detect DM. However, effect size (i.e. difference between means divided by SD, or proportion of variance in timing of migration explained by age or sex) is independent of sample size, so this measure is the statistics to compare for different SF. The problem to solve is finding which SF gives similar results as daily trapping sessions at a Constant Effort Site.

The Blackcap *Sylvia atricapilla* is a common songbird in Europe (Cramp 1992), captured in large numbers at ringing sites. As its age and sex are easily determined, it is a good model species which with to test for the effect of SF on the ability to detect DM.

Our main aim was to explore to what extent sampling frequency affects the ability to detect differential timing of passage in passerines. Secondly, we tested if Blackcaps passing over through N Iberia showed DM by age and sex.

METHODS

The avian model

The Blackcap breeds within July isotherms 14–30°C (Cramp 1992), from W Europe to 85°E in Russia, and from N Africa to N Europe and Russia (63°N). Populations breeding westwards of longitude 11–12°E migrate towards SW directions, to overwinter in SW Europe, NW and W Africa, whilst those that breed eastwards of this divide move to SE directions. Iberia, therefore, receives many individuals from W Europe (Cantos 1995), either as winter visitors or as stopping-over migrants that overwinter in Africa (Cantos 1995, Shirihai *et al.* 2001).

The migratory behaviour of the Blackcap has been broadly studied, although the research was much focused on genetic studies (Helbig 1994, Berthold & Helbig 1992, Berthold & Pulido 1994) as well as on studies dealing with fuel management at stopover places (e.g. Hjort *et al.* 1996, Grandío 1997, Izhaki & Maitav 1998, Arizaga *et al.* 2008). Less abundant are analyses focusing on differential timing of passage between age classes and sex, and among these studies many have focused on DM by sex during the spring migration period of East-European populations (Table 1). Among those reporting DM in Iberia, Murillo & Sancho (1969) did not test statistically the differences in dates of passage, and the study by Grandío (1997) was the only one demonstrating that adults passed over before juveniles during the autumn migration period. This was also the only study performing daily trapping sessions. In other cases (e.g. Leal *et al.* 2004), it has been suggested that the lack of differences between age classes or sex was due to the relatively low SF. In conclusion, data on DM of West-European populations are scarce and contradictory.

Table 1. Published data on differential migration between age and sex classes of Blackcaps, during the autumn and spring migration period. Ad = adults, Juv = juveniles, M = males, F = females. Breeding zone is referred to the migratory divide around longitude 11–12°E; W = West, E = East.

Period	Age	Sex	Sampling frequency	Region	Breeding zone	Source
Autumn	Ad = Juv	No data	Recaptures	Europe	W–E	Fransson (1995)
	Ad = Juv	M = F	Recaptures	Iberia	W	Cantos (1995)
	Ad before Juv	No data	Daily	N Iberia	W	Grandío (1997)
	Ad before Juv	M = F	Unknown	SW Iberia	W	Murillo & Sancho (1969)
	Ad = Juv	M = F	Once a week	E Iberia	W	Leal *et al.* (2004)
Spring	Ad = Juv	No data	Recaptures	Europe	W–E	Fransson (1995)
	No data	M before F	Daily	N Europe	E	Rainio *et al.* (2007)
	No data	M before F	Daily	N Europe	E	Tøttrup & Thorup (2008)
	Ad = Juv	M = F	Recaptures	Iberia	W	Cantos (1995)
	Ad before Juv	M before F	Unknown	SW Iberia	W	Murillo & Sancho (1969)
	Ad = Juv	M = F	Once a week	E Iberia	W	Leal *et al.* (2004)

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Sampling area and ringing protocol

Data were obtained at a shrubby area at Loza (42°50'N 01°43'W, 415 m a.s.l.), 40 km S of the W Pyrenees (Navarra, N Spain), a 48 ha zone of prairies used by cattle. In these prairies there were also lines of hedgerows, composed mainly by some elms *Ulmus minor*, thorny shrubs and elders *Sambucus* spp. that supply abundant fleshy fruits during late-summer and autumn (Deán & Riezu 1987). This area is used by a small population of local breeding pairs and large numbers of foreign birds that use the area as a stopover site, both in autumn and spring. No wintering Blackcaps have been observed in this area (JA, unpubl. data). Blackcaps were mist netted daily (overall, 60 linear m of mist nets), from 12 September to 27 October, during the autumn migration period 2005, and from 13 March to 27 April during the spring migration period 2006. During the sampling period, mist nets were open during 4 h from dawn.

Once captured, each bird was ringed and its age and sex determined following Svensson (1998) and Shirihai *et al.* (2001). Blackcaps were classified as juvenile or adult birds. Overall, during the autumn migration period we ringed 1056 Blackcaps and registered 84 recaptures (some birds were recaptured more than once), whilst in spring 340 captures were obtained, of which two birds were recaptured (Table 2). We were not able to determine the age of 14 individuals and the sex of 4 individuals.

Statistics

Within each analysis, we only considered data on the first capture event for each bird, and of birds with their age and sex known. In both autumn and spring, daily captures did not follow a normal distribution (Kolmogorov test, $P < 0.05$), and were over-dispersed (SD/mean > 0.30). However, the distribution of captures in spring was symmetric and, during autumn, almost symmetric. Therefore, we used mean values to describe and parametric procedures to test for variations in timing of passage between age and sex classes.

First, we analysed how the SF affected the ability to detect DM (regarding sample size, *P*-values, effect size). Therefore, we reanalysed the same data set using daily trapping sessions, alternate days, 3 days a week and once a week. By decreasing the SF, the likelihood that a given age class or sex may be overrepresented in any particular day increases. Therefore, simulations of datasets with a SF lower than daily sessions were run twice, but changing the first day of the simulation (datasets A and B in Table 3). Statistics and parameters calculated were (1) *t*-values used to test for significant differences in timing of passage between age or sex classes, (2) difference (in days) in date of passage, (3) effect size (i.e. difference between means divided by SD, or proportion of variance due to the differential timing of passage between age or sex classes).

Most previous analyses of DM group birds into categories of either age or sex (for exceptions see Swanson *et al.* 1999, Stewart *et al.* 2002). This is an option when sample sizes are small, though it does not allow to study interactions between age and sex. Similarly, we grouped age and sex classes independently, so that sexes were lumped when testing for age effects, whilst ages were lumped when testing for sex effects. Secondly, we repeated the analyses with four age–sex categories (adult males, etc.). In these cases, we used an ANOVA with an *a posteriori* Tukey-B test (F_{Levene}, $P > 0.05$). Comparisons of proportions between age and sex classes were done using tests based on χ^2 values. We used programs SPSS 15.0 and G*Power 3.0.10.

RESULTS

Sample size, effect size

A decreasing number of sampling days per week affected the ability to detect DM, with *P*- values becoming higher with a decreasing number of trapping sessions in a week (Table 3).

Table 2. Captures (first capture event within each period) and recaptures of migrating Blackcaps at a stopover site in N Spain, during autumn (12 Sep – 27 Oct) and spring migration period (13 Mar – 27 Apr).

	Captures (first capture event)									Recaptures
Age	Juveniles			Adults			Unknown			
Sex	Unknown	Males	Females	Unknown	Males	Females	Unknown	Males	Females	
Autumn	4	483	397	0	100	68	0	1	3	84
Spring	0	117	122	0	56	35	0	1	9	2

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Table 3. Differential timing of passage between age and sex classes, given periods of passage (autumn/spring), number of trapping sessions in a week, and days selected for the analyses (datasets) from the general daily dataset. We show *t*-values and associated *P*, sample size and difference between means, in days. Significant *P*-values are in bold.

			Sex				Age			
Period	Frequency	Dataset	*t*	*P*	*n*	Δdays	*t*	*P*	*n*	Δdays
Autumn	Daily	-	1.438	0.151	1055	1	4.724	**< 0.001**	1055	5
	Alternate days	A	0.638	0.524	552	1	3.359	**0.001**	549	4
		B	1.249	0.212	551	2	3.448	**0.001**	552	4
	Three days per week	A	1.353	0.177	460	1	2.369	**0.018**	460	3
		B	0.341	0.734	486	0	4.725	**< 0.001**	484	6
	One day per week	A	1.386	0.168	176	3	2.486	**0.014**	340	8
		B	0.120	0.905	156	0	0.351	0.726	178	0
Spring	Daily	-	5.411	**< 0.001**	340	5	2.732	**0.007**	330	3
	Alternate days	A	3.691	**< 0.001**	178	5	1.924	0.056	171	3
		B	3.955	**< 0.001**	164	6	1.915	0.057	161	4
	Three days per week	A	3.040	**0.003**	139	4	1.455	0.148	134	3
		B	4.694	**< 0.001**	177	7	2.626	**0.009**	175	5
	One day per week	A	1.699	0.094	74	3	0.956	0.343	70	2
		B	1.039	0.308	29	4	1.114	0.275	28	4

Thus, in spring, differences between the sexes were still apparent when reducing SF to 3 days per week, but not any more when catching only one day per week. Similarly, catching in autumn on one day only was not sufficient to show the differences between age classes which arose with a higher SF. The rather small difference in timing of passage between age classes in spring was significant when catching daily but not at any of the lower frequencies. Obviously, this drop in significance when lowering the SF was associated with a decrease in sample size, as also confirmed by differences in significance between the two datasets. Thus, in autumn, dataset A ($n = 340$) showed a difference between age classes in contrast to dataset B ($n = 178$). That the ability to detect DM in our study was constrained by sample size, and not by SF per se, is supported by the fact that the effect size was more or less independent of SF (Table 4).

Table 4. Effect size in date of passage between age and sex classes, during autumn and spring migrations. Values for non-daily trapping sessions have been averaged after performing two runs (datasets A and B, Table 3). Effect sizes for non-daily trapping sessions ($n = 6$ for each age/sex class and period, considering two repetitions per type of sampling frequency) were compared with effect size obtained for the daily trapping sessions by means of a *t*-test (*P*-value is shown).

	Autumn		Spring	
Frequency	Sex	Age	Sex	Age
Daily	0.088	0.392	0.588	0.327
Alternate days	0.081	0.396	0.516	0.325
Three days per week	0.079	0.435	0.615	0.355
One day per week	0.114	0.370	0.394	0.342
t-test (*P*-value)	0.917	0.928	0.164	0.726

Timing of passage between age and sex classes

The proportion of age classes varied between autumn and spring, with a higher proportion of adults in spring (16.0% and 27.6%, respectively; $\chi^2_1 = 22.22$, *P*-exact < 0.001). The sex ratio was similar in autumn and spring ($\chi^2_1 = 1.95$, *P*-exact = 0.169), with a slight bias towards males (accounting for 54.5% of the captures, $\chi^2_1 = 11.05$, *P*-exact = 0.001).

In autumn, no significant differences in timing of passage between females and males were found (Table 5). By ages, however, adults passed over 5 days later than juveniles (Table 5). In a more detailed analysis with the four age–sex categories (Fig. 1), we also detected DM (ANOVA: $F_{3,1047} = 9.12$, $P < 0.001$). *A posteriori* analyses showed that adult females passed later than the other age–sex categories.

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Table 5. Mean date of autumn and spring passages of Blackcaps at a stopover site in N Spain. Ages were pooled when testing for sex effects, and sexes were pooled when testing for age effects. Data used are based on daily trapping sessions. Significant *P*-values are in bold.

	Sex				Age			
Period	Males	Females	*t*	*P*	Juveniles	Adults	*t*	*P*
Autumn	1 Oct (n = 584)	2 Oct (n = 471)	1.438	0.151	30 Sep (n = 886)	5 Oct (n = 169)	4.724	**< 0.001**
Spring	4 Apr (n = 174)	9 Apr (n = 166)	5.411	**< 0.001**	7 Apr (n = 239)	4 Apr (n = 91)	2.732	**0.007**

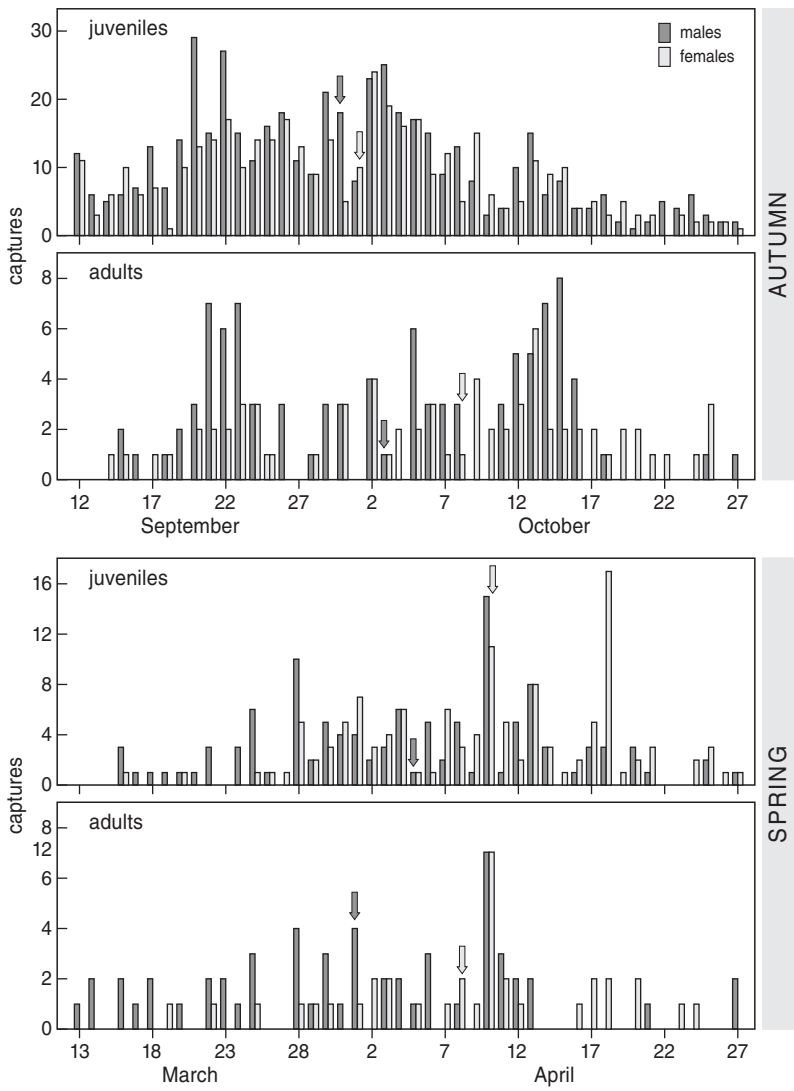


Figure 1. Captures of migrating Blackcaps in N Spain by age and sex. Only data on the first capture event for each bird have been considered. Arrows indicate mean passage date for each age–sex category.

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In spring, significant differences in the timing of passage were detected, both between sex and between age classes (Table 5). Within sexes, males passed 5 days earlier than females, whilst, in relation to age, adults passed 3 days earlier than juveniles. When the four age–sex categories were considered together (Fig. 1), significant differences were also detected (ANOVA: $F_{3,329} = 12.42$, $P < 0.001$). *A posteriori* analyses showed that adult males passed over significantly earlier than females. Juvenile males were also found to pass earlier than juvenile females. Within each sex adults and juveniles did not differ in their dates of passage (Fig. 1).

DISCUSSION

Effect of sampling frequency

The ability to detect differential timing of passage between age or sex classes in Blackcaps was strongly affected by SF. A major cause explaining this result was the decline in sample size when the number of catching days is restricted. Another cause that could affect the ability to detect DM was the time interval between mean passage dates. When the difference was small, a slight decrease in the SF was sufficient to obscure the ability to detect differential timing of passage, as observed during the spring migration period between age classes.

Interestingly, effect size did not vary with SF, suggesting that all SF were sufficient to detect differential timing of passage. Thus, a SF of once a week is sufficient to detect a difference of passage of just a couple of days. If DM was detected using daily trapping sessions but not at a lower SF, this was due to the low sample size, which, obviously, is positively associated with decreasing SF. Therefore, a solution to address this problem is to increase the catching effort per sampling day, e.g. by putting more mist nets and sampling for a longer period.

We should notice, however, that the accuracy of estimating the date of passage may decrease at a low SF due to random fluctuations among days in age or sex categories. Thus, our simulations showed several cases where – unexpectedly – a decrease in SF caused an increase in the difference in days of passage. Slight variations in timing of arrival at given destination areas (e.g. males to their breeding areas in spring; Rubolini *et al.* 2004) can have very relevant consequences in terms of survival or breeding success (reviewed by Newton 2008). Accordingly, if estimating DM accurately is relevant, then it is advisable to have daily trapping sessions.

Taking into account these results, previous analyses trying to detect differential timing of passage between age or sex classes of Blackcaps (e.g. Cantos 1995, Fransson 1995, Leal *et al.* 2004) should be cautiously considered. Sampling once a week (e.g. Leal *et al.* 2004) is inadequate to detect DM when sample sizes are small. Also, pooling data from several years probably reduces the ability to detect differential timing of passage, because inter-year variation could introduce additional noise and, therefore, larger sample sizes would be required (Leal *et al.* 2004). This may be one of the causes why analyses of recaptures, which are bound to combine data from many years, often fail to detect differential timing of passage between age or sex classes (Fransson 1995).

Blackcap migration

Overall, in autumn we caught more juvenile (84.0%) than adult birds. This is in agreement with several studies at other sites in Iberia (Murillo & Sancho 1969, Grandío 1997, Leal *et al.* 2004). In contrast, Cantos (1995) registered a higher proportion of adults for all Iberia. However, Cantos only used recaptures from abroad, which could be biased towards adults as adults often outnumber juveniles in a ringed population (Leal *et al.* 2004). Our results may simply reveal the age ratio of the populations of origin (i.e. productivity; Bermejo & De la Puente 2002), in which juveniles could be more abundant (Baillie *et al.* 2006). Also, it is possible that adults, owing to their experience, stop for shorter periods and in fewer stopover sites than juveniles (e.g. Ellegren 1991), which would be reflected in a higher proportion of juvenile Blackcaps at stopover. Unfortunately, we did not have enough data to estimate differences in stopover duration between age classes, and we are not aware of studies dealing with these data for the Blackcap.

The sex ratio was near 1:1, though significantly biased towards males (54.4%). If the sex ratio at breeding quarters is 1:1 or slightly male-biased (Herremans 1989, Holloway & Edwards 1989), these data would support that at least up to N Iberia, both sexes show the same migration distances. In S Iberia and in the Mediterranean façade, however, the proportion of wintering males seems to be higher than that of females (Murillo & Sancho 1969, Cantos 1995, Leal *et al.* 2004). In a recent work on segregation of sexes of Blackcaps at their wintering areas, Catry *et al.* (2006) found more males wintering in Europe than in Africa, suggesting that, though not as markedly as in other small birds such as Robins *Erithacus rubecula* (Catry *et al.* 2004) or Chiffchaffs *Phylloscopus collybita* (Catry *et al.* 2005),

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Blackcaps seem to show a weak geographical segregation by sexes in winter, with females overwintering further south than males.

A higher proportion of adults was caught during spring than in autumn. This might be caused by lower juvenile survival rates during winter, either since juvenile birds occupy less suitable habitats (Pérez-Tris & Tellería 2002), or/and because they are more likely to be predated. The proportion of the sexes did not vary between autumn and spring, suggesting that both sexes have a similar rate of survival. Indeed, Pérez-Tris & Tellería (2002) did not find significant differences in sex ratio among habitats, or in body condition between sexes.

In autumn, timing of passage was similar for both sexes when ages were pooled, but different for ages when sexes were pooled (adults passed over after juvenile birds). A more detailed analysis with the four age–sex categories showed that the difference was mainly caused by adult females passing later than the other age–sex categories (adult males also tended to pass later than juvenile males, but the difference was not significant). Overall, these results agree with the idea that in migrants that overwinter within the circum-Mediterranean region adults tend to pass later than juveniles (Newton 2008) since they leave their breeding areas later. A reason explaining this phenomenon is that in many medium-distance migrants, adults make a complete post-breeding moult, whereas juveniles only moult their plumage partially (Jenni & Winkler 1994; for the Blackcap in particular, see Shirihai *et al.* 2001). However, in some of the studies carried out in Iberia, adults were reported to be captured in a higher proportion during early autumn (Murillo & Sancho; Grandío 1997), suggesting that they passed over earlier. Fransson (1995) observed that adults maintained higher migratory speeds, so it is possible that even though departing from their breeding quarters later, adult Blackcaps are able to catch up juveniles before reaching their wintering areas.

In spring, males were found to pass over Loza earlier than females, both in adults and juveniles. At that time of the year, males are under a high pressure to arrive as early as possible to their breeding areas, which may enhance the chance to find a mate and establish a territory (Morbey & Ydenberg 2001, Rubolini *et al.* 2004). In Blackcaps, this has been established by Rainio *et al.* (2007) and Tøttrup & Thorup (2008).

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SAMENVATTING

Bij veel vogelsoorten verschilt het moment van trek tussen mannetjes en vrouwtjes en tussen oude en jonge vogels. Zo bleek uit een ringonderzoek aan Zwartkoppen *Sylvia atricapilla*, uitgevoerd in het najaar van 2005 en het voorjaar van 2006 in het noorden van Spanje, dat in de herfst oude vrouwtjes later doortrekken dan oude mannetjes en jonge vogels. Ook in het voorjaar lag er een scheidslijn tussen de geslachten, waarbij mannetjes eerder doortrokken dan vrouwtjes (jong en oud). Een belangrijke vraag bij dit onderzoek was of de verschillen in doortrek ook opgemerkt zouden zijn als minder vaak dan dagelijks zou zijn gevangen. Daartoe werden modelsimulaties uitgevoerd waarbij de frequentie van vangen in stapjes werd teruggebracht van zeven dagen naar één dag per week. De kans om verschillen in doortrek te zien liep snel terug naarmate minder frequent gevangen werd, maar de verklaarde variantie tussen oude en jonge vogels en tussen mannetjes en vrouwtjes bleef gelijk. Dit betekent dat zelfs met een lage vangfrequentie van eenmaal per week (voor veel ringers op Constant Effort Sites het best haalbare) doortrekverschillen aangetoond kunnen worden als er maar voldoende vogels per dag gevangen worden. Dat laatste kan bereikt worden door meer netten op te stellen of meer uren te maken. (JP)

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