No evidence for partial migration in two partial migrants Migratory strategies of Dutch sky- and woodlarks (*Alauda arvensis* and *Lullula arborea*)

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ABSTRACT: Partial migration can be found on the species level but also on a breeding population level. We know very little about the evolution of migration and since partial migration is often seen as an evolutionary precursor to full migration it gives us a great opportunity to look at the causes and consequences of migration. The aim of this pilot study is to find out where sky- and woodlark from our study population winter, using geolocators, and learn more about their migratory strategies. All bird migrated away and no evidence for partial migration was found. Skylarks seem to winter on the coast of France, the United Kingdom and the southern parts of Portugal and Spain, woodlarks seem to winter on the coast of France. Skylark females do migrate further south than males do. Spring migration is of shorter duration than autumn migrations. The duration of spring migration did show a significant difference between males and females skylark. Arrival at the breeding grounds did show a significant difference between male and female skylark. To get a more accurate wintering location and to get a better understanding of their migratory strategy over a longer time span it would be nice to start using GPS-tags.

Introduction

Birds often migrate away from breeding grounds to escape from harsh winter conditions and to ensure food availability. But there are also individuals that stay close to the breeding ground. This is called partial migration and can be found on the species level; northern population migrate south and southern population are residential (Spaepen & Van Cauteren, 1962; 1968; Zink, 1975; Glutz von Blotzheim, 1985; Spaepen, 1995), but also on a breeding population level; within a breeding population some birds are migratory and others are residential (Schwabl *et al.*, 1984; Smith & Nilsson, 1987; Adriaensen & Dhondt, 1990; Nilsson *et al.*, 2006; Partecke & Gwinner, 2007). We know very little about the evolution of migration. Since partial migration is often seen as an evolutionary precursor to full migration (Berthold, 1996), it gives us a great opportunity to look at the causes and consequences of migration.

Populations of Dutch sky- and woodlarks (*Alauda arvensis* and *Lullula arborea*) are thought to be partial migrants (Venema, 2001; SOVON, 2002; Hegemann *et al.*, 2010), and since northern population migrate south and southern population are residential (Spaepen & Van Cauteren, 1962; 1968; Zink, 1975; Glutz von Blotzheim, 1985; Spaepen, 1995), Dutch sky- and woodlark populations might be situated on the border of both strategies. For the population of sky- and woodlarks in our study area in Drenthe it has been shown with help of radio telemetry and stable isotopes analyses that these populations are indeed partial migrants (Hegemann *et al.*, 2010; 2015). Ring recoveries show that migratory Dutch skylarks are likely to winter in France and Spain (Hegemann *et al.*, 2010). For woodlarks this data is not available, but it is hypothesized that they winter in the same regions (SOVON, 2002).

An earlier study on the causes and consequences of partial migration did find some differences in individual immune parameters and survival rates for resident versus migratory individual skylarks, but those effects varied between years (Hegemann *et al.*, 2015). Since migratory individuals move away to a different environment it is expected that these birds adjust their physiology. This has been shown to be the case in studies on blue tits and dark-eyed juncos (Nilsson & Sandell, 2009; Holberton & Able, 2000). It is likely that the wintering strategy of an individual bird will shape its physiology, which might have effects carrying over to the next breeding season. Wintering strategy is therefore an important part of a birds life-history.

Geolocators are tiny devices that store light intensity and time periodically. With the help of astronomical algorithms a location can be calculated from these light intensities. Geolocators have proven to be good alternative for GPS-tags, which were not available for smaller passerines for a long time. Several studies have used geolocators to get more information on a birds wintering area and its migratory timing, for example in Wrynecks (*Jynx torquilla*) and Pied Flycatchers (*Ficedula hypoleuca*)(van Wijk *et al.*, 2013; Ouwehand *et al.*,2015).

Thanks to geolocators, it is also possible to look at migratory timing and duration of an individual and look for differences between classes of individuals. There are several hypotheses to why classes of individuals migrate differently. Differences between the sexes could be linked to differences in body weight, dominance, or benefits of early arrival. These factors could explain why males often winter closer to their breeding grounds than females (Catry *et al.*, 2005). It is also very interesting to look at differences between skylarks and woodlarks since both population show different population trends. Skylarks have declined with 95% since the 1970s (Teixeira, 1979; SOVON, 2002; van Dijk *et al.*, 2008), while woodlarks show a stable population trend (SOVON, 2002). More insight in the whereabouts of both species throughout the whole years is important for effective conservation (van Beusekom, 2006; Bos *et al.*, 2009), since different conditions during the wintering period might influence annual survival rates and breeding success.

The aim of this pilot study is to find out where sky- and woodlark from our study population winter, using geolocators, and learn more about their migratory timing. Also we want to look at differences in migratory timing and duration between skylark and woodlark, between males and females and between years. This will grant us the ability to study causes and consequences of partial migration in a later study. In this second study we want to look at the cost and benefits for residential and migratory birds by looking at reproductive success, physiology (immune system parameters), morphology (weight and tarsus length) and return rate. With the help of these data we can form hypotheses about the causes of partial migration; why do some birds leave and why do other birds stay. But also about the consequences of partial migration; what are the carry-over effects of a chosen wintering strategy. This will help unravel the evolution of migratory behaviour of larks and give insight into the effects of a certain migratory strategy choice on the life-history of an individual.

Methods

Study species and method

In the breeding seasons of 2013 and 2014 a total of 28 skylarks and 18 woodlarks have been equipped with geolocators. Only birds that had bred in the area before, and thus were site faithful, were used to increase the change of recovering the geolocators next year. This was done in our study population in Aekingerzand, Appelscha (52.93178, 6.30006). Geolocators were attached to the birds back using a harness with a weight of only about 1.0 gram (including harness) which is less than 5% of a birds total weight. To retrieve the data from these geolocators the birds should be caught back after the wintering period, approximately a year later. A total of 17 skylarks (8 males and 9 females) and 10 woodlarks (7 males and 3 females) could be retrieved. Based on sunset and sunrise the approximate wintering location can be calculated. Using the noon and midnight time from the geolocator relative to Coordinated Universal Time (UTC), longitudes can be estimated. Latitudes were derived via various calibration procedures that describe the relation between the measured day length and latitude by finding the right sun elevation angle (SEA). The distance to the wintering ground, migratory duration and migratory timing can also be determined from our geolocator data.

Data analyses

Data was processed with the program Transedit (BAS), using the threshold method (Hill & Braun, 2001; Ekström, 2004). In the threshold method a specific light intensity is set as a threshold. Every time the light intensity crosses this threshold a sunrise or sunset (depending on increase or decrease of light intensity) is saved for that specific time. Sunset and sunrises at the beginning and the end of the dataset are removed, because the geolocators were turned on at that time but were not yet or not anymore attached to the birds back. With the help of a minimal dark period filter (set on 4 hours) and visual inspection, all inexplicable sunsets and sunrises (due to car lights, street lights, etc.) were deleted from the dataset.

The data was analyzed using Excel (Microsoft), Locatoraid (BAS) and package Geolight (Lisovski *et al.,* 2012a) in R 3.1.0 (R Core Development). To calculate a location based on sunsets and sunrises, a sun elevation angle (SEA) is needed. Four different SEA were used to determine the wintering location. The first SEA was calculated using Locatoraid and is based on sunsets and sunrises from the first breeding period. Since the breeding location is known the SEA can easily be calculated for each day. The median of all these SEA is used as the first SEA. The same can be done for the second breeding period, which gives the second SEA. The third SEA can be calculated based on the sunsets and sunrises from the wintering period using the Geolight package in R which holds the Hill-Ekstrom (HE) - calibration. This calibration can also be done visually in MS Excel by plotting the latitude against the date for a range of different SEA and choosing the SEA that minimizes the variation around the equinoxes (Ekström, 2004). The median wintering location Q2 with its 25-75% quartiles (Q1-Q3) are plotted for the four SEA's that were calculated.

For further analyses of the data the SEA that was determined visually in Excel was chosen. Since the SEA is influenced by factors like the weather conditions, amount of feathers grown over the geolocator, vegetation type and the condition of the geolocator, it is unlikely that the SEA will be equal for the breeding seasons and the wintering season. The visual SEA was chosen over the HE-calibration in R, because the HE-calibration in R is rather sensitive to outliers in the data. The visual determination of the SEA is not influenced by these outliers and is more robust and will therefore give a more accurate SEA which results in a more accurate wintering location.

For each bird the distance between breeding location and wintering location has been calculated. Also the duration of spring and autumn migration and the timing of departure and arrival on the breeding and wintering grounds could be determined. This was done based on plotting the longitude over time. Stationary periods can easily be determined and shifts in longitude can be seen as periods in which the bird is migrating.

Statistics

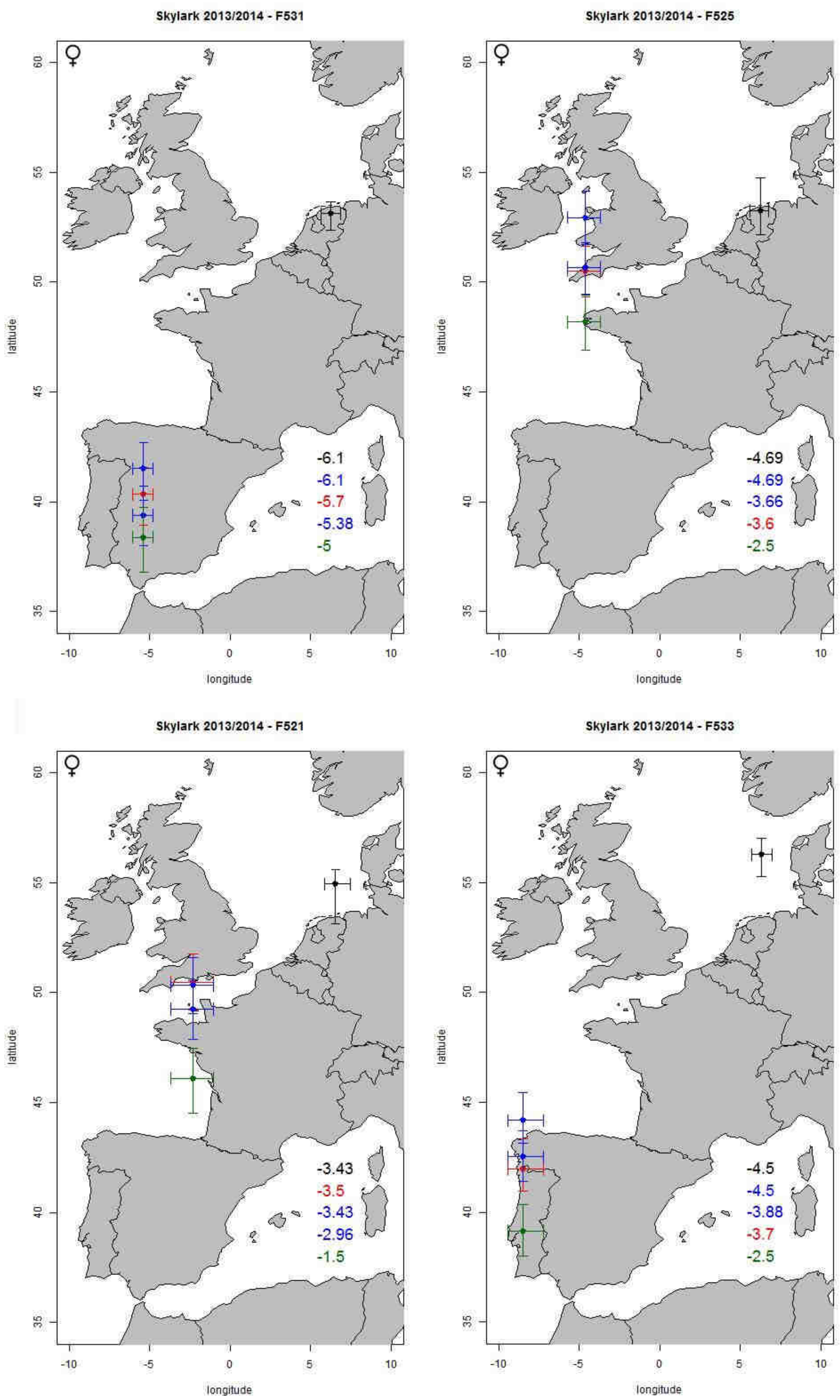
Distance, duration and migratory timing have also been tested for significant differences between: skylark and woodlark, skylark female and skylark male, woodlark 2013-2014 and woodlark 2014-2015. It was not possible to test for differences between other groups due to low samples sizes. All the data were not normally distributed and was therefore log-transformed. After transformation all data were normally distributed, expect for the arrival time for the two years of woodlark data, and therefore a Wilcox-test was used.

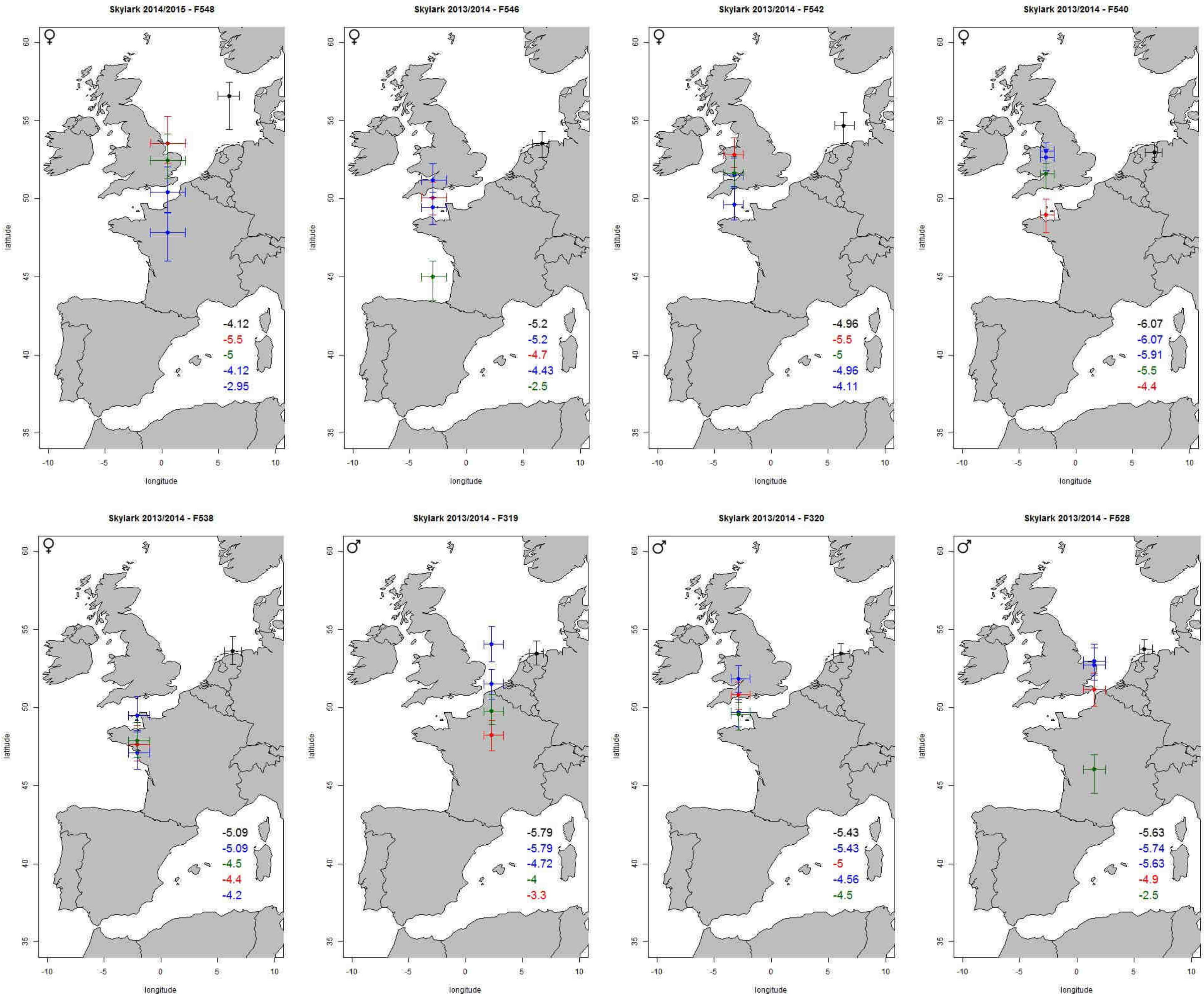
Variances were not equal for the arrival time in the two species and a Welsh test was used. For all the other variables a normal t-test was used. Except for testing for differences in duration between autumn and spring, here a paired t-test was used.

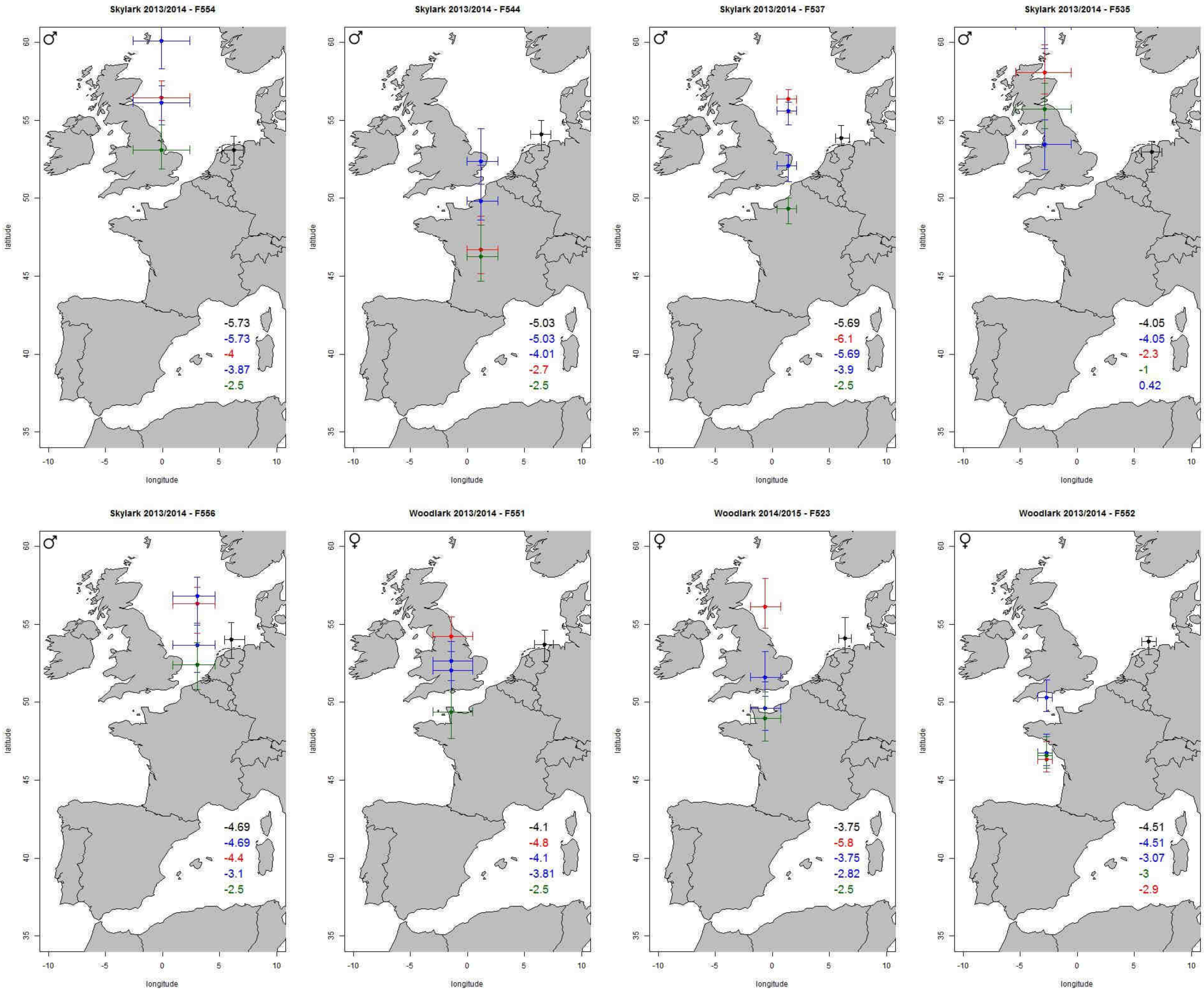
Results

No partial migration

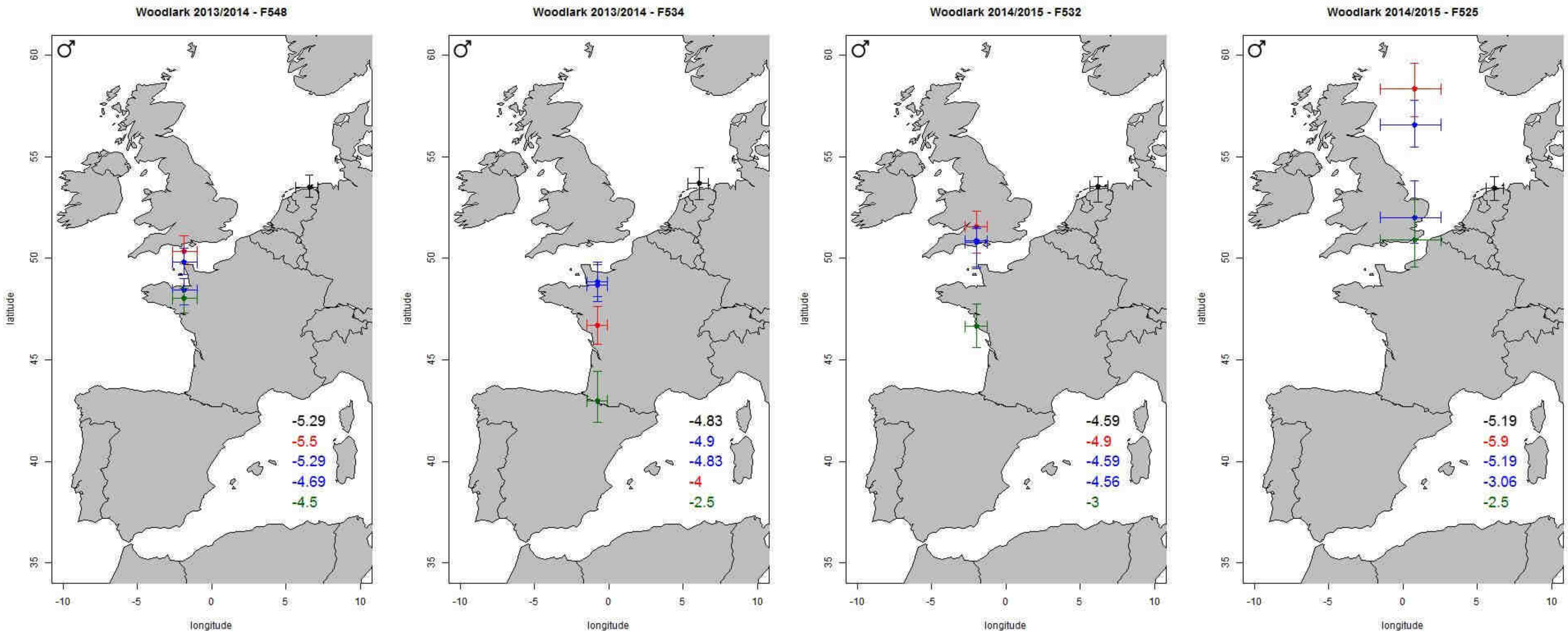
Most interesting is that all birds have migrated away from the breeding grounds, as can be seen in figure 1.

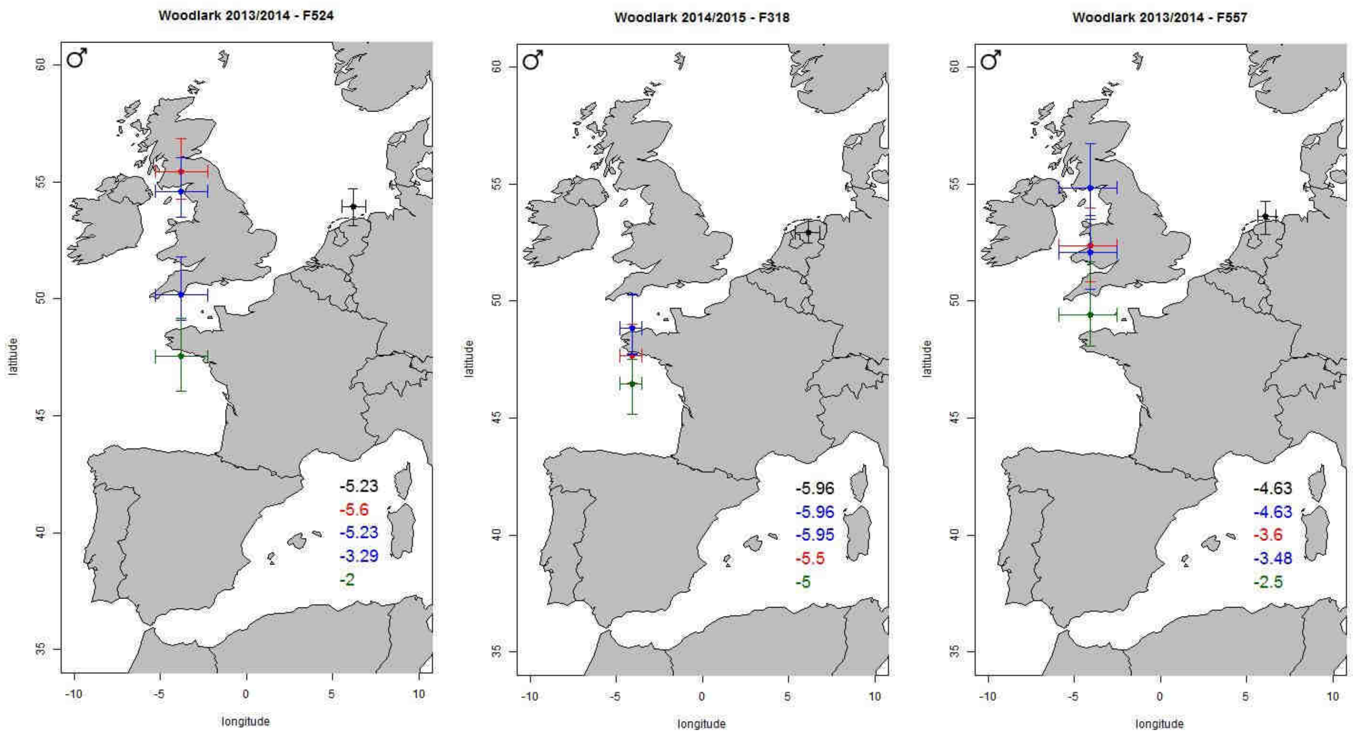



Skylark 2014/2015 - F548
♀
-4.12
-5.5
-5
-4.12
-2.95
Skylark 2013/2014 - F546
♀
-5.2
-5.2
-4.7
-4.43
-2.5
Skylark 2013/2014 - F542
♀
-4.96
-5.5
-5
-4.96
-4.11
Skylark 2013/2014 - F540
♀
-6.07
-6.07
-5.91
-5.5
-4.4
Skylark 2013/2014 - F538
♀
-5.09
-5.09
-4.5
-4.4
-4.2
Skylark 2013/2014 - F319
♂
-5.79
-5.79
-4.72
-4
-3.3
Skylark 2013/2014 - F320
♂
-5.43
-5.43
-5
-4.56
-4.5
Skylark 2013/2014 - F528
♂
-5.63
-5.74
-5.63
-4.9
-2.5
latitude
longitude



Skylark 2013/2014 - F554
♂
-5.73
-5.73
-4
-3.87
-2.5
Skylark 2013/2014 - F544
♂
-5.03
-5.03
-4.01
-2.7
-2.5
Skylark 2013/2014 - F537
♂
-5.69
-6.1
-5.69
-3.9
-2.5
Skylark 2013/2014 - F535
♂
-4.05
-4.05
-2.3
-1
0.42
Skylark 2013/2014 - F556
♂
-4.69
-4.69
-4.4
-3.1
-2.5
Woodlark 2013/2014 - F551
♀
-4.1
-4.8
-4.1
-3.81
-2.5
Woodlark 2014/2015 - F523
♀
-3.75
-5.8
-3.75
-2.82
-2.5
Woodlark 2013/2014 - F552
♀
-4.51
-4.51
-3.07
-3
-2.9
latitude
longitude





- Figure 1: Breeding and wintering location of each individual bird. Medians with 25-75% quartiles are plotted for each location. Locations are calculated based on the different SEAs that were found during analysis. Breeding location is based on the SEA of breeding season 1 and shown in black. Blue shows the wintering locations based on the SEAs of both breeding seasons. Red shows the wintering location based on the SEA that was found using Geolight, and green shows the wintering location based on the SEA that was determined visually in Excel. In the upper left corner the sex of the bird is shown.

So our population does not show partial migration in the wintering periods 2013-2014 and 2014-2015. In figure 1, the mean wintering locations are plotted for every geolocator based on the four calculated SEAs. From these maps, it becomes clear that the SEA that is chosen has a major effect on the latitude that is calculated, because latitude estimates are based on the time of sunset and sunrise, which are influenced by the chosen SEA. SEA does not have an effect on the longitude since longitude estimations are based on the time of solar noon. For each geolocator the variance in the median latitude was calculated (table 1). The mean variance in latitude over all geolocators was 5.83, with a minimum of 1.06 and a maximum of 13.94.

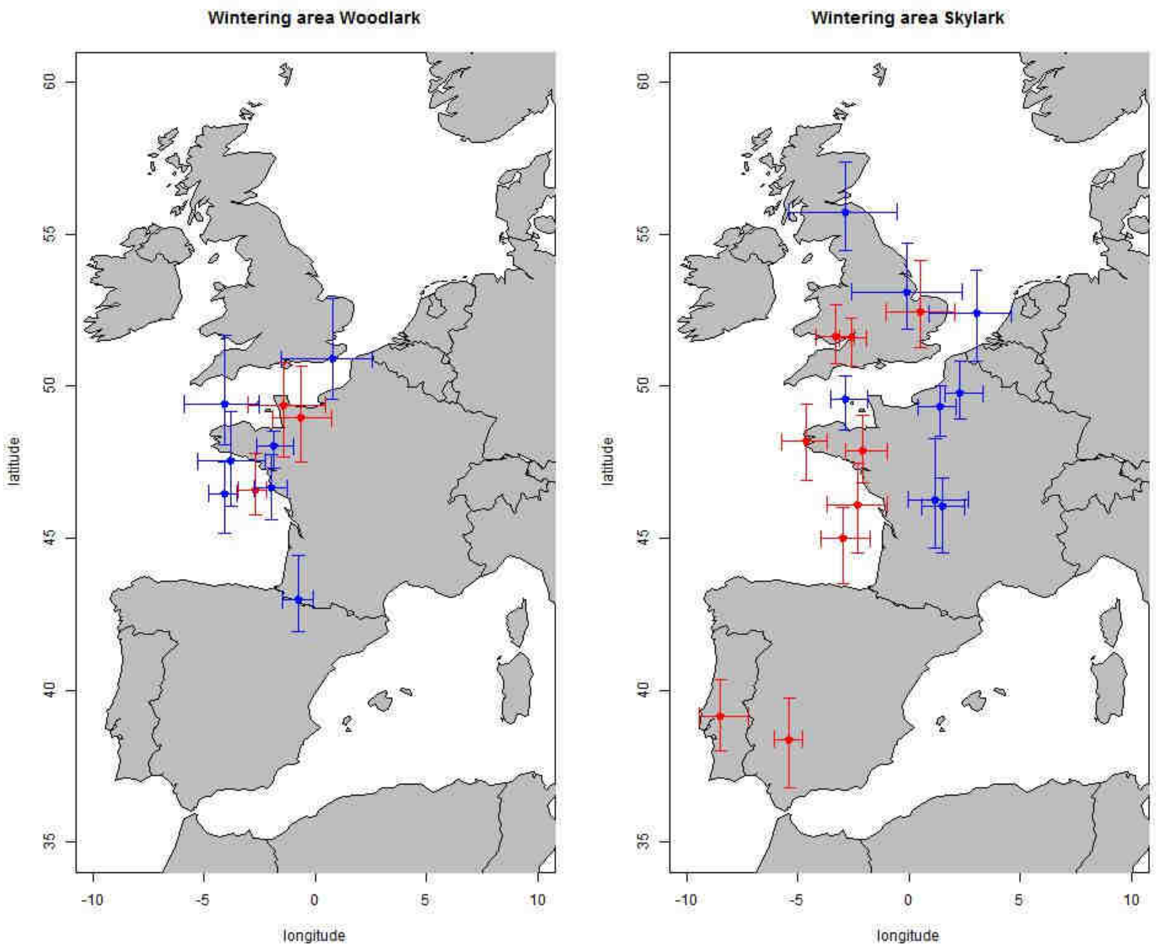
- Table 1: Variance in median wintering latitudes, calculated for every geolocator. Mean variance is calculated over all geolocators.

Skylark			**Woodlark**		
Geolocator	**Year**	**Variance**	**Geolocator**	**Year**	**Variance**
F319	2013/2014	6.24	F524	2013/2014	13.94
F320	2013/2014	1.14	F534	2013/2014	7.39
F521	2013/2014	4.13	F548	2013/2014	1.20
F525	2013/2014	3.79	F551	2013/2014	4.08
F528	2013/2014	10.39	F552	2013/2014	3.56
F531	2013/2014	1.79	F557	2013/2014	4.94
F533	2013/2014	4.40	F318	2014/2015	1.29
F535	2013/2014	10.57	F523	2014/2015	10.54
F537	2013/2014	10.65	F525	2014/2015	12.72
F538	2013/2014	1.06	F532	2014/2015	5.00
F540	2013/2014	3.34			
F542	2013/2014	1.75			
F544	2013/2014	7.17			
F546	2013/2014	7.39			
F554	2013/2014	8.19			
F556	2013/2014	4.51			
F548	2014/2015	6.31		**Total mean:**	5.83

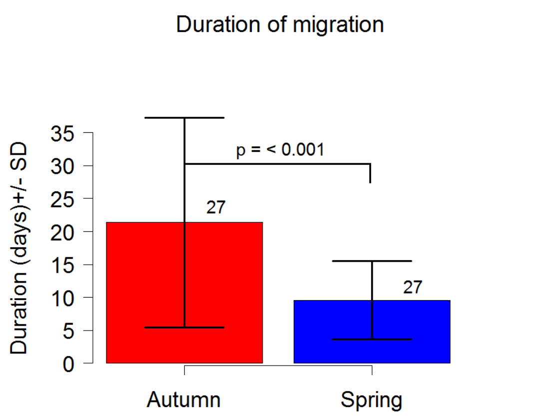
In figure 2 the wintering locations of the birds are plotted based on the SEA that is visually determined. The maps show that skylarks seem to winter on the coast of France, the United Kingdom and the southern parts of Portugal and Spain. Female skylarks seem to go further south than males do. Woodlarks seem to winter on the coast of France and are more clustered than the skylarks, which show much more spread in their wintering location.

Migratory duration and timing

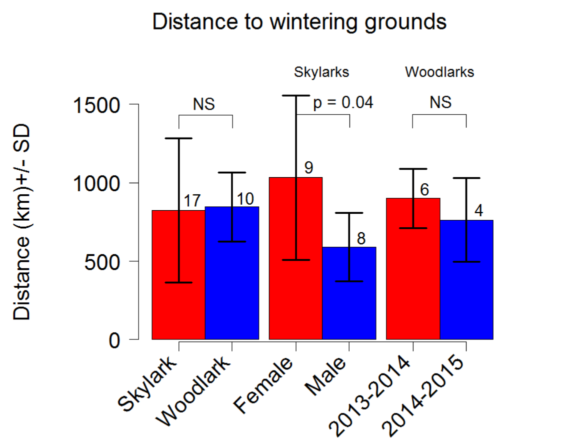
Skylarks do not winter significantly further away than woodlarks and the distance to the wintering grounds did not differ in Woodlarks between the two years. Skylark females do migrate further south than males do ($t = -2.27$, $df = 15$, $p = 0.04$), figure 3. Spring migration is of shorter duration than autumn migrations ($t = -4.00$, $df = 26$, $p < 0.001$), figure 4.



- Figure 2: Wintering location (medians with 25-75% quartiles). Woodlarks and skylarks are plotted separately. Males are shown in blue, females in red.



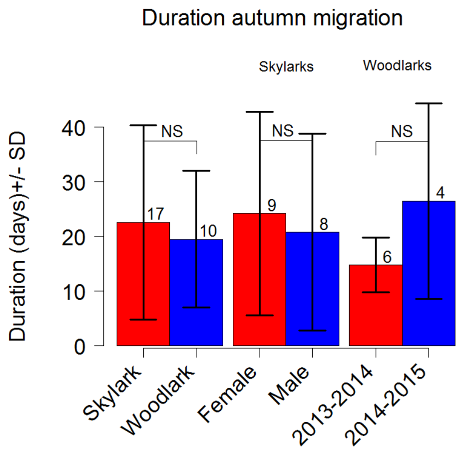
- Figure 3: Migratory duration in days. Top of the bar shows the mean, error bars show standard deviation. P-value and sample sizes are plotted in the graph.



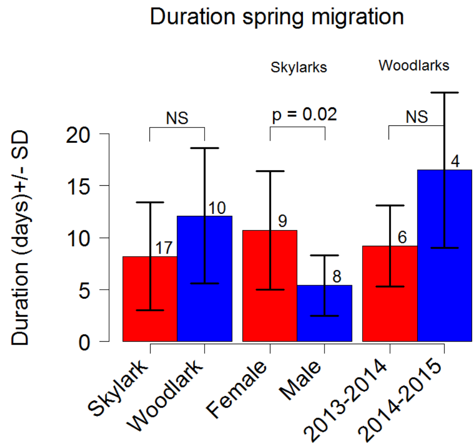
- Figure 4: Distance to wintering grounds in kilometers. Top of the bar shows the mean, error bars show standard deviation. Sample sizes are plotted for every subgroup. When significant differences were found, the p-value is shown.

There was no difference in the duration of autumn migration between sky- and woodlark, between females and males skylark and between the two years of woodlark data (figure 5). The duration of spring migration did only show a significant difference between males and females skylark ($t = -2.72$, $df = 15$, $p = 0.02$), see figure 6. The timing of leaving the breeding grounds did not differ between any of the tested groups.

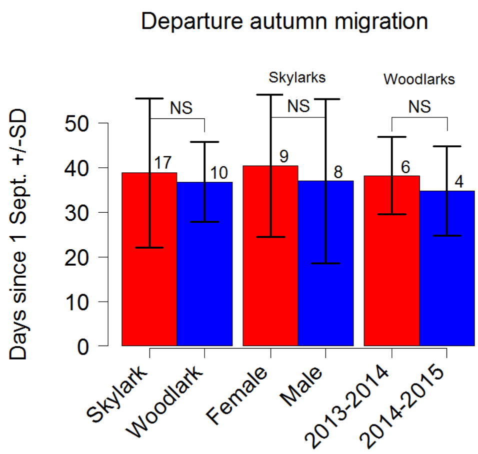
Arrival at the breeding grounds did show a significant difference between male and female skylark ($t = -3.88$, $df = 15$, $p = 0.001$) and between the two years of woodlark data ($w = 2$, $p = 0.04$) (figure 7 and 8). Means, standard deviations and samples sizes for each group tested can be found in table 2.



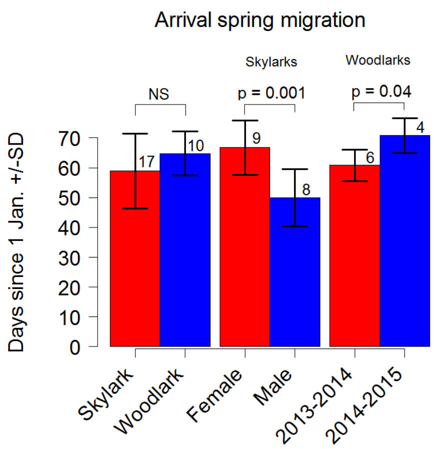
- Figure 5: Duration of autumn migration in days. Top of the bar shows the mean, error bars show standard deviation. Sample sizes are plotted for every subgroup. When significant differences were found, the p-value is shown.



- Figure 6: Duration of spring migration in days. Top of the bar shows the mean, error bars show standard deviation. Sample sizes are plotted for every subgroup. When significant differences were found, the p-value is shown.



- Figure 7: Departure day (since 1. September) from breeding grounds in autumn. Top of the bar shows the mean, error bars show standard deviation. Sample sizes are plotted for every subgroup. When significant differences were found, the p-value is shown.



- Figure 8: Arrival day (since 1. January) at breeding grounds in spring. Top of the bar shows the mean, error bars show standard deviation. Sample sizes are plotted for every subgroup. When significant differences were found, the p-value is shown.

- Table 2: Means, standard deviations and sample sizes for each subgroup of geolocators that was used in statistical analyses.

	Mean	**SD**	**N**
Migratory distance (km)			
Skylarks	824	458.5	17
Woodlarks	845.3	220.3	10
Skylark female	1032.6	524.7	9
Skylark male	589.3	216.8	8
Woodlark ‘13/’14	900.2	189.7	6
Woodlark ‘14/’15	762.9	265.7	4
Duration migration (days)			
Spring	21.4	15.9	27
Autumn	9.6	5.9	27
Duration autumn migration (days)			
Skylarks	22.6	17.8	17
Woodlarks	19.5	12.5	10
Skylark female	24.2	18.6	9
Skylark male	20.8	18	8
Woodlark ‘13/’14	14.8	5	6
Woodlark ‘14/’15	26.5	17.9	4
Duration spring migration (days)			
Skylarks	8.2	5.2	17
Woodlarks	12.1	6.5	10
Skylark female	10.7	5.7	9
Skylark male	5.4	2.9	8
Woodlark ‘13/’14	9.2	3.9	6
Woodlark ‘14/’15	16.5	7.5	4
Departure day autumn since 1. Sept. (day)			
Skylarks	38.8	16.7	17
Woodlarks	36.8	9	10
Skylark female	40.4	16	9
Skylark male	37	18.4	8
Woodlark ‘13/’14	38.2	8.7	6
Woodlark ‘14/’15	34.8	10	4
Arrival day spring since 1. Jan. (day)			
Skylarks	58.9	12.5	17
Woodlarks	64.8	7.3	10
Skylark female	66.8	9.1	9
Skylark male	50	9.6	8
Woodlark ‘13/’14	60.8	5.2	6
Woodlark ‘14/’15	70.8	5.9	4

Return rates

In 2013 a total of 23 skylarks and 8 woodlarks were equipped with a geolocator. In 2014, 5 skylarks and 10 woodlarks were equipped. In 2014, 16 skylarks and 6 woodlarks could be retrieved and in 2015 1 skylark (but 2 others were observed) and 4 woodlarks were retrieved. Return rates are calculated and can be found in table 3. While other studies often found low return rates for passerines that carry geolocators (Arlt & Paert, 2013; Gomez *et al.*, 2014), these return rates are quite high and comparable with the return rates Hegemann *et al.* found in 2010 when equipping larks with radio tags. We can therefore conclude that there was little negative effect of geolocators on survival.

- **Table 3:** Return rates (in percentages) for both species.

Year	Skylark	Woodlark
2014	70%	60%
2015	20% / 60% (with observed)	40%

Discussion

Migratory strategy

The maps show that these past two winters, none of the birds did stay close to the breeding grounds. In other words there was no sign of partial migration. Earlier studies of this population did show partial migration (Hegemann *et al.*, 2010; 2015). We know for sure that the birds did move away from the breeding grounds. In our data there is a major spread of wintering location when looking at the latitude, but longitude is very accurate since these are estimated on local noon and not influence by the SEA that is worked with.

In the Netherlands the Skylark population has dramatically declined the last years, about 95% since the 1970s (Teixeira, 1979; SOVON, 2002; van Dijk *et al.*, 2008). As with a more farmlands birds, these declines are linked to intensification of agriculture which results in deterioration of the breeding habitat (Newton, 2004; Donald *et al.*, 2006). But also in winter these results in problems for the birds. It has been shown that food supply is reduced in winter and survival rates are dropping (Donald *et al.*, 2001, Newton, 2004, Siriwardena *et al.*, 2007; 2008). It could be that normally residential birds could not find enough food close to the breeding ground and therefore decided to migrate away.

Another possibility is that, as hypothesized by Hegemann *et al.* in 2015, birds that are infected are forced to show a residential strategy, because of a bad condition. When equipping these birds, that are already in a poor condition, with a geolocator, one provides these birds an extra workload, which could result in these birds dying during winter. This is likely since it was shown previously that the reaction of the immune system to an experimentally increased workload can take weeks to months (Hegemann *et al.*, 2013). This could mean that all residential birds died during winter.

Return rates

The return rates that were found in this study (table 3) are quite high, indicating that there was little negative effect of geolocators on survival. However these return rates cannot be calculated for residents and migrants separately, which makes it possible that the residential birds did show high mortality during winter. It is however impossible to give estimates of survival rates for residential birds, even when combining different tracking methods. Only when tracking devices are so far developed that live data can be transferred back, this will become possible. This is of course already possible for large species, but for the larks these devices are still too heavy.

Migratory timing and duration

Skylark males do winter further away than females do and arrive earlier back in their breeding grounds. Also the duration of spring migration is shorter in males than in females. Of course these three parameters are linked with each other; if the wintering area is closer, you have to fly fewer days and can return earlier in the breeding grounds. This findings are in line with the 'arrival time hypothesis" (Ketterson & Nolan, 1976). This hypotheses states that if one sex experience more competition for breeding resources than the other, then individuals of that sex benefit by early return to the breeding grounds to ensure a good breeding territory. In both sky- and woodlarks males do indeed defend a territory throughout the breeding season. It is likely that males stay closer to the breeding grounds and return earlier than females to make sure they can find and defend a suitable breeding territory. The migratory period is shorter in spring than in autumn, which could be explained by the approaching breeding season, because of strong competition for spring arrival order among individuals to get the best breeding territories (Kokko, 1999), or to increase reproductive success (van Noordwijk *et al.*, 1995). The fact that no differences were found between skylark and woodlark indicates that the difference in population trends of these two species is most likely linked with factors acting during the breeding season and not during the wintering season.

Geolocator versus GPS-tags

The geolocator analyses was based on the threshold method (Hill & Braun, 2001; Ekström, 2004). A more sophisticated and accurate way of analyzing the data may be achieved by using a template fitting method (Rakhimberdiev *et al.*, 2015), in which the slope of change in light intensity is used to calculate a location. However, the data should be suitable for this analyses, meaning that it should be of good quality, with proper light levels during the wintering period. A few geolocators have been analyzed using the latter method, but this analyses did show that the light levels measured are too low during winter to be able to do this.

Geolocator data is not very accurate. Within a chosen SEA the accuracy is about 100 km. Because of low-light level data from the winter it is also hard to get an accurate estimate of the SEA using the HE-calibration, which results in a range of latitudes on which the bird could have been. Light levels can be influenced by weather, topography and vegetation, which can influence the calibration significantly (Lisovsky, 2012b). The SEA used in this study is the most suitable, but does not give the guarantee that it is the correct SEA. This means that indeed most birds are likely to winter in France and a few in the United Kingdom, but to be completely sure GPS-tags should be attached to the bird. These GPS-tags can save several GPS-location on pre-programmed times and give a accurate wintering position of the birds. To get a more accurate wintering location and to get a better understanding of their migratory strategy it would be nice to start using the GPS-tags, which are now so light they can be used on sky- and woodlarks. With the help of this new data we will be able to link multiple years of wintering area data to the birds reproductive success, physiology (immune system parameters), morphology (weight and tarsus length) and return rate. Giving us an insight in the causes and consequences of partial migration and get a full understanding of the larks life-history.

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