Are Dutch Skylarks Partial Migrants? Ring Recovery Data and Radio-Telemetry Suggest Local Coexistence of Contrasting Migration Strategies

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Are Dutch Skylarks partial migrants? Ring recovery data and radio-telemetry suggest local coexistence of contrasting migration strategies

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In recent years, Skylarks *Alauda arvensis* have undergone dramatic population declines in many European countries. Evidence exists for deteriorating conditions during the breeding season, but little is known about the situation during the rest of the annual cycle. Here we use two approaches to test if the Dutch breeding population of Skylarks consists of resident and/or migratory individuals. First, we present an analysis of ring recoveries from the Dutch Ringing Centre "Vogeltrekstation". Out of 25 recoveries, 12 Skylarks were resident in winter, 10 migrated and three were classified as probable migrants. Resident birds were accompanied during winter by birds from northern and eastern Europe. Very limited natal and breeding dispersal recorded in the same dataset suggests that our results were not influenced by long dispersal distances. Next, we compared these results to a local radio-telemetry study in the northern Netherlands. During two different years we equipped a total of 27 Skylarks from a breeding population with radio-transmitters and followed them during the subsequent winter. Four birds were found to winter locally. Out of 23 individuals that we did not find in winter, 14 returned in the following breeding season to the study area, all with a working transmitter, suggesting that they wintered outside our study area. Two ring recoveries of birds from the same study population indeed showed migration to south-west Europe. Based on these two lines of evidence, we conclude local coexistence of a resident and a migrant strategy in Dutch Skylarks. The findings of our study are important for the planning of conservation efforts, as we can only protect this rapidly declining species when we know their behaviour and whereabouts throughout the entire annual cycle.

Key words: wintering, partial migration, ringing, The Netherlands, conservation, dispersal, radio-telemetry

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In western Europe, farmland birds have declined in recent decades by almost 50% (BirdLife International 2004, EBCC 2009, PECBMS 2009). While declines are frequently associated with changed or changing conditions during the breeding season and deterioration of the breeding habitat (Newton 2004, Donald *et al.* 2006), the importance of factors operating outside the breeding season is less clear. However, the general change in agricultural practise from summer to winter cereal and the subsequent loss of overwintering stubble fields is thought to reduce food supply in winter and could reduce survival rates (Donald *et al.* 2001, Newton 2004, Siriwardena *et al.* 2007, 2008).

In The Netherlands, the Skylark *Alauda arvensis* is one of the farmland species with the steepest decline: numbers dropped by almost 95% from around 700,000

breeding pairs in the 1970s to only about 38,000 in 2005 (Teixeira 1979, SOVON 2002, van Dijk *et al.* 2008). In The Netherlands, Skylarks are also common during migration (LWVT/SOVON 2002), and in winter (e.g. Vergeer & van Zuylen 1994, Poelmans & van Diemen 1997, Venema 2001, Bijlsma *et al.* 2001, Hustings *et al.* 2006). From the patterns of passage and from ringing recoveries it is well established that Skylarks from northern breeding populations migrate through The Netherlands on their way to the wintering grounds in south-west Europe (Speek & Speek 1984, Spaepen 1995, LWVT/SOVON 2002). However, it is unclear whether Skylarks that breed in The Netherlands are resident or migratory. It has been hypothesized that part of the population of Dutch breeding birds winter locally and are joined by birds from Scandinavia and Russia (e.g. Venema 2001, SOVON 2002), but also that most breeding birds migrate (e.g. Lensink 1993, Vergeer & van Zuylen 1994, Hustings *et al.* 2006, van Dijk *et al.* 2008) with France as the most important wintering destination (van Beusekom 2006). Yet, these ideas have not been verified using ringing data, stable isotopes, radio-telemetry or other tracking methods, even though such knowledge is essential to develop a more powerful conservation strategy (Sutherland *et al.* 2004, van Beusekom 2006, Bos *et al.* 2009).

Skylark populations from northern Europe migrate to south-west Europe, mainly to France and Spain, whereas southern European and British populations are thought to be resident (Spaepen & Van Cauteren 1962, 1968; Zink 1975, Glutz von Blotzheim 1985, Spaepen 1995). Birds that are wintering on the northern edge of the wintering range react to cold spells, and winter movements occur especially when snow fall restricts access to food (Glutz von Blotzheim 1985, Donald 2004). However, the geographical border between resident and migratory populations remains unclear (Glutz von Blotzheim 1985, Bauer *et al.* 2005).

Futhermore, it is unclear whether resident and migratory strategies occur within a single Skylark population. Partial migration is defined as occurring when one part of the population remains in the breeding area year round and another part migrates (Gauthreaux 1982, Terril & Able 1988, Alerstam 1990, Berthold 1993, Newton 2008). The mechanism for partial migration is thought to be a mixture of environmental and genetic factors, with the latter being more prominent in obligate partial migrants and environmental factors like food supply being more important in facultative partial migration (Schwabl & Silverin 1990, Berthold 1993, Newton 2008). Partial migration has been described for several temperate breeding birds, with European Robin *Erithacus rubecula*, Blackbird *Turdus merula* and Blue Tit *Cyanistes caeruleus* being the most prominent examples (e.g. Schwabl *et al.* 1984, Smith & Nilsson 1987, Adriaensen & Dhondt 1990, Nilsson *et al.* 2006, Partecke & Gwinner 2007). Data on Skylarks are lacking so far.

In this study we investigated migration strategies of Skylarks in The Netherlands using two different approaches. First, we analysed all ring recoveries of Skylarks from the database of the Dutch ringing centre "Vogeltrekstation". Second, we conducted a radio-telemetry study in a local breeding population of Skylarks in the northern Netherlands. We combine the results of both approaches to evaluate whether Skylarks that breed in The Netherlands migrate or winter locally. Additionally, we analyse the ring recoveries of Skylarks that spend the winter in The Netherlands, to trace their origin. Finally, we present data on natal and breeding dispersal of Skylarks ringed in The Netherlands during the breeding season to verify that our results on the migratory strategies of Skylarks are not in fact influenced by long-distance dispersal.

METHODS

Ring recoveries

Since 1911 more than 88,000 Skylarks have been ringed in The Netherlands (Vogeltrekstation data until November 2008), of which 497 were recovered. The database contains an additional 35 recoveries of birds ringed in other countries and found in The Netherlands.

We selected all cases where distinction between migration strategies (resident in winter vs. migrant) is possible (n = 25, Appendix 1). These include birds that were (1) ringed during the breeding season in The Netherlands (either as nestling or as breeding adult) and recovered in any winter, or during any autumn or spring migration; (2) ringed during winter and reported during the breeding season in The Netherlands; and (3) ringed during migration and recovered during the breeding season within The Netherlands. We define migration based on distance between ringing and recovery site by visually deriving a divide in travelled distance between residents and migrants (see Fig. 1). Skylarks recovered closer to the inferred breeding area than the divide are regarded as residents, and birds that flew further as migrants (see Helm *et al.* 2006). Birds either ringed or recovered during active migration in the main migration period in October were classified into a third category 'probable migrants' (n = 3).

We defined the migration periods as 30 Jan – 25 Mar for spring migration and 24 Sep – 19 Nov for southward migration. These periods are based on diurnal migration as observed during more than 67,000 observation hours in the years 1976–1993 at 121 observation stations throughout The Netherlands (LWVT/SOVON 2002). Accordingly, the wintering season is defined as the period 20 Nov – 29 Jan and the breeding season (including the moulting period) as 26 Mar – 23 Sep.

To evaluate whether, in addition to Dutch birds, Skylarks from northern origins also winter in The Netherlands, we selected all birds that were ringed during winter (20 Nov – 29 Jan) in The Netherlands and were later recovered further north. We additionally checked for the origin of late migrants (1 Nov – 19 Nov).

If long-distance natal or breeding dispersal occurs in Skylarks, this could potentially influence our results given the selection criteria we used to classify migrants. Therefore we performed an analysis of natal and breeding dispersal by selecting all recoveries from birds ringed during the breeding season as either nestlings or adults and that were recovered during any subsequent breeding season (n = 43). Of these 43 recoveries, 23 birds were found by the ringer and 20 by another person, and thus estimated dispersal is not only based on birds recaptured by a ringer within a study population.

Study area for radiotelemetry

We obtained detailed information on a breeding population in the "Aekingerzand", part of the National Park Drents-Friese Wold in the northern Netherlands (52°55'N; 6°18'E). The area is a mixture of open sand, groups of trees, heath- and grasslands on nutrient-poor soil and surrounded by a thin belt of forests. The wider surroundings are characterised by agricultural fields and small villages. The study population consists of about 100 pairs; the vast majority of individuals are colour-ringed.

Radio-tracking

We equipped 28 Skylarks with radio-transmitters. Eight birds (3 adult males, 4 adult females, 1 juvenile female) received the transmitter in the period 13 Jul – 26 Sep 2007 and another 20 (9 adult males, 4 adult females, 4 juvenile males, 2 juvenile females and 1 male of unknown age) in the period 3 Aug – 22 Sep 2008 when all birds showed active moult. Ageing of the birds was based on previous ringing or on plumage characteristics; sex was determined by wing length and in doubtful cases confirmed by molecular sexing.

The radio-transmitters (172 MHz-band) were specifically designed for this project by JDJC Corp. d.b.a. Sparrow Systems, United States. The life-time was assumed by the manufacturer to be at least 6–7 months. In fact, in all cases where birds returned to the breeding grounds, transmitters continued to work for longer than this expected life-span and one transmitter was still working one year after attachment. Transmitters were fixed on the back of a bird using figure-eight-harnesses (Rappole & Tipton 1991) made from elasticated cotton thread. Transmitters, including harness, ranged in weight from 1.29 to 1.50 g, equalling 3.1–5.2% of a bird's body weight at time of attachment. During the period when transmitters were attached, Skylarks in this study population are close to their minimum weight in the annual cycle (A. Hegemann, unpubl.). From when transmitters were attached until the end of September we carried out repeated searches for birds in the study area to check if birds were still present and to determine if transmitters produced regular signals on the supposed frequency. One transmitter attached to a bird in 2007 failed to work properly due to an antenna that was broken two weeks after attachment. Therefore we excluded this bird from further analysis.

Starting in October when birds left the Aekingerzand, we searched for radio-tagged birds using two portable ICOM IC-R20-receivers with hand-held 5-element yagi-antennas. In a radius of up to 8 km around the Aekingerzand, the agricultural landscape was checked for the presence of radio-tagged birds by one person searching for 4–5 days per week and about five hours per day. In the open landscape (excluding villages and wooded areas) we scanned for all used frequencies, conducting scans at regular distances of not more than 1 km apart. In addition we used a dipole antenna mounted on the roof of a car with a automatically scanning receiver to search for birds while driving around the search area. During winter 2008/09 the hand-held antenna was mounted on a 4-m long plastic pole to increase reception. Furthermore we conducted telemetry from a small aircraft (Cessna skyhawk), flying for 2–4 hours at a height of 250–300 m and with a speed of 100–110 km/h in circles over the study area. Flights were completed once in winter 2007/08 (on 8 December) and twice in winter 2008/09 (on 16 January and 6 February). With these flights we covered an area with a radius of about 12 km around the Aekingerzand. During the flight on 8 December 2007 we received signals from one bird we did not find previously by ground telemetry. During the two flights in winter 2008/09 we did not find any additional birds. During all flights radio-tagged birds with known location, or one additional transmitter that was not attached to a

bird, were used as references values. From the air we were able to detect these references signals from a distance of at least 2 km. Another search flight was flown in spring 2009 (on 3 March) to search for potentially dispersed birds, but none were found.

RESULTS

Migration strategies from ringing data

Based on 25 ring recoveries, we classified 12 birds as residents, 10 as migrants and three as probable migrants (Fig. 1). Eight birds had been ringed as nestlings and six of these were migratory, with three being recovered in their first winter and three in their second or third winter respectively (Table 1). All birds ringed as adults (n = 17) had been ringed outside the breeding season, and four were classified as migrants, and another two as probable migrants. Migratory birds (n = 10) travelled on average 713.0 km ± SD 531.3 (median 437 km) between ringing and recovery location. Most likely these migrants were still on migration when caught/recovered (eight out of ten during the migratory period), and therefore this is not an estimate of the total migration distance. Migratory birds ringed as nestlings and recovered as first-year birds or as adults did not differ in the distance travelled between ringing and recovery location (Wilcoxon-Test, W = 4, P = 0.18). The furthest distance was covered by a bird ringed as a nestling in 1968 and hunted the same autumn in Spain at 1900 km.

Origin of birds wintering in The Netherlands

Eleven birds ringed in winter in The Netherlands were recovered in or on their way towards breeding areas outside The Netherlands, in Denmark (n = 8), Russia (n = 1), Sweden (n = 1) and Norway (n = 1) (Appendix 2). Additionally two birds ringed during the breeding season in Denmark and Norway, respectively, were found in winter in The Netherlands. Furthermore, birds that were ringed during the last part of the southward migration period in The Netherlands (1 Nov – 19 Nov) were later reported in Denmark (n = 8) and Russia (n = 1) (Appendix 2).

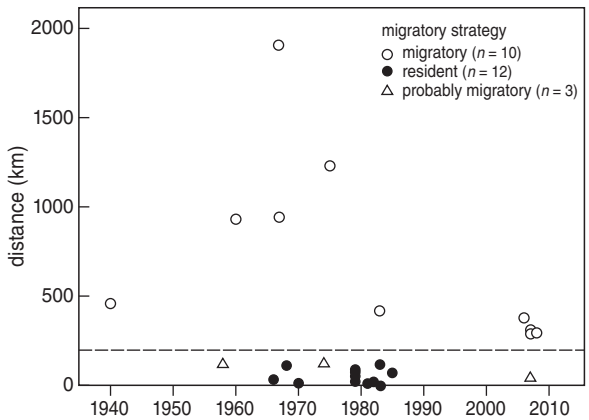

Figure 1. Distance between ringing and recovery location in Skylarks from The Netherlands by year of recovery. The dotted line (visually drawn) separates resident and migratory birds. For further details see Methods.

Natal and breeding philopatry

Thirty Skylarks ringed as nestlings were reported during a later year as breeding birds. Twenty-six of these birds (1 male, 18 female, 7 unknown) were found within 4 km of the ringing site, and four (all unknown sex) had dispersed further than 10 km from the place of hatching. The furthest recovery was found in a fresh pellet of a Montagu's Harrier *Circus pygargus* one year after being ringed as a nestling, at a distance of 41 km

Table 1. Distance between ringing and recovery location for Skylarks of the Dutch breeding population with known migration strategy (n = 25) by age and sex. Adults were ringed outside the breeding season.

			Sex			Distance			
Ringed as	Recovered as	Migration strategy	Male	Female	Unknown	Max	Min	Median	Average
Nestling	First-year	Migratory			3	1900	295	459	884.7
	First-year	Resident			1			73	73.0
	Adult	Migratory		1	2	937	415	925	759.0
	Adult	Probably migratory			1			47	47.0
Adult		Migratory		2	2	1219	294	343	549.8
		Resident			11	116	0	28	48.7
		Probably migratory			2	122	46	84	84.0

from its place of hatching (H.J. Ottens, pers. comm.). Because Montagu's Harriers of this specific population hunt over distances of more than 18 km from their nest site (C. Trierweiler, pers. comm.), the actual dispersal distance of this bird remains uncertain. Of the 13 birds ringed as adults (5 males, 7 females, 1 unknown) during the breeding season all were reported in subsequent years within 2 km of the site of ringing.

Radio-telemetry of Aekingerzand population

In the winter of 2007/08 all radio-tagged birds had left the Aekingerzand by 2 October. In the course of the winter we detected signals from three of the seven radio-tagged birds (43%) at distances of 0–9 km from the Aekingerzand. These included two adult males and one adult female (Table 2). One of these males stayed from 9 October till 12 November on an agricultural field just outside the Aekingerzand before it moved a few kilometres further. Both males returned to the breeding site in the following breeding season, while we lost track of the female during winter. Two birds (both adult females; 29% of all birds) were not detected during the winter in the surroundings of the Aekingerzand, but returned to the area in the following breeding season. One of them stayed from 12–20 October on an agricultural field 3.5 km from the original breeding site, before moving out of our study area. Two birds were never located during winter and did not return to the breeding site. Their migratory strategy remains unknown (Table 2).

In the winter of 2008/09 we located only one of the 20 radio-tagged birds in the search area around the Aekingerzand (5%, Table 2). This adult male (transmitter frequency 172.475) was still in the Aekingerzand on 3 October, but was not detected in the breeding area after this date (Table 3). He was located again on 24 November in a group of about 60 Skylarks on harvested potato fields 4 km from the breeding site. He stayed in this vicinity for several weeks and the last signal was detected from this bird on 16 January 2009. However, this bird did not return to the original breeding area the following spring. All other radio-tagged Skylarks left the Aekingerzand in October, with the last radio-tagged male detected there on 30 October (Table 3). Twelve of the 19 birds (60%) which we did not detect in winter returned during the following breeding season, with the first two males being in their territories on 12 February and one more male being there on 24 February. On 7 March a total of nine birds (8 males, 1 female) were present, and two more females on 13 March and on 29 March, respectively (Table 3). We did not receive any signals from seven birds (35%) after they left the Aekingerzand and their migratory strategy remains unknown.

Both winters combined, we found three of 17 males and one of 10 females to winter locally (Fisher's Exact Test, $P = 1$). Four adults were found to winter locally, while we did not detect any of the seven juveniles in winter (Fisher's Exact Test, $P = 0.55$). The proportion of birds we found in our study area during winter, differed between the two years (Fisher's Exact Test, $P = 0.04$).

DISCUSSION

Ring recoveries from the entire Netherlands for the past 100 years clearly demonstrate that Dutch Skylarks are partial migrants; some birds migrate to the southwest and others winter close to their breeding grounds. Our radio-telemetry study on a local breeding population in the northern part of The Netherlands confirmed that some birds winter very close to the breeding location while others were not found in winter in the immediate

Table 2. Radio-tagged Skylarks from the Aekingerzand population. Numbers in brackets give percentage of birds in relation to total number of tagged birds.

Age	Sex	Total 2007/08	Detected winter 2007/08	Not detected but returned summer 2008	Total 2008/09	Detected winter 2008/09	Not detected but returned summer 2009
Adult	Male	3	2		9	1	7
Adult	Female	3	1	2	4		3
Juvenile	Male				4		2
Juvenile	Female	1			2		0
Unknown	Male				1		0
Total		7	3 (43%)	2 (29%)	20	1 (5%)	12 (60%)

Table 3. Presence of radio-tagged Skylarks in the Aekingerzand during autumn 2008 and in early spring 2009. Grey cells indicate days when particular transmitters were not applied yet. X marks presence of birds. M=male, F=female, ad=adult, juv=juvenile. During winter no birds were detected in the area on 3 and 12 December 2008 and 15 January 2009. The male with transmitter frequency 172.475 MHz wintered outside the study area.

Frequency 172 MHz + KHz	183	214	564	495	593	187	335	539	517	132	475	697	575	661	669	636	414	611	437	460
Sex	M	M	M	F	F	M	M	M	M	M	M	M	M	M	M	F	F	F	F	M
Age	Juv	Juv	Juv	Juv	Juv	Juv	Ad	Ad	Ad	Ad	Ad	Ad	Ad	Ad	Ad	Ad	Ad	Ad	Ad	?
Date of capture	03/08	04/08	13/09	09/08	10/09	05/08	09/09	09/09	10/09	13/09	19/09	19/09	20/09	20/09	22/09	04/08	09/09	10/09	19/09	13/09
Date of control																				
06/08/2008	X	X				X														
10/08/2008	X	X				X										X				
08/09/2008	X	X		X		X										X				
09/09/2008		X		X		X										X				
17/09/2008	X	X	X		X	X	X	X	X	X						X	X	X		X
03/10/2008	X							X			X		X						X	X
24/10/2008	X							X						X					X	X
27/10/2008	X							X												
28/10/2008	X							X												
29/10/2008													X							
30/10/2008													X							
12/11/2008																				
											**									
12/02/2009													X							
14/02/2009										X			X							
07/03/2009		X					X	X		X		X	X	X	X			X		
13/03/2009		X					X	X		X		X	X	X	X			X	X	
29/03/2009		X					X	X		X		X	X	X	X		X	X	X	
02/04/2009		X	X*				X	X		X			X	X			X	X	X	

*This bird established a territory outside the study area. Even though we often were able to receive signals in the study area, we likely missed it during earlier controls.
**This bird wintered a few km outside the study area on agricultural fields. We received the last signal on 16 Jan 2009.

surroundings, but returned in spring. Our results provide the first evidence for the simultaneous occurrence of migratory and resident strategies in the Dutch Skylark population. Our data suggest that both natal and breeding dispersal occur over limited distances in Dutch Skylarks and thus our conclusions on migration strategies are unlikely influenced by long dispersal distances. High site fidelity in Skylarks to both natal and breeding area has been described earlier (Duncan 1987, Wolfenden 1990 cited in Dougall 1999, Dougall 1996, Paradis *et al.* 1998, Wernham *et al.* 2002).

Locally-wintering Dutch-breeding Skylarks are accompanied during winter by birds from the north and east, as shown by recoveries of birds ringed in winter. Eleven such recoveries were of birds breeding in The Netherlands and 11 were of birds found in breeding areas to the north or east. Thus The Netherlands also serve as wintering grounds for Skylarks from the northeast. Resident birds and wintering birds from the north probably use the same habitats and potentially join the same flocks. Indeed, we captured birds with a wing length of up to 122 mm in fields where colour-ringed and radio-tagged birds from our local study population were also present. Birds from the study population have a maximum wing length of 117 mm (A. Hegemann, unpubl.) suggesting that these longer-winged birds are coming from northern populations (Glutz von Blotzheim 1985). Our data do not allow us to make quantitative statements about the frequencies of the different migration strategies because we lack the crucial information on ringing efforts, recovery rates and reporting rates in The Netherlands relative to those in other countries (see Körner-Nievergelt *et al.* 2010).

We are also not yet able to say whether the migration strategy of an individual bird is fixed or flexible between years because we did not track any individual twice. Nonetheless, different proportions of birds undertaking local wintering among the radio-tagged birds in the two years of our study could indicate that migration strategies are not fixed. Our study population thus might consist of facultative partial migrants, where some individuals migrate in some years and not in others, depending on conditions at the time (Terril & Able 1988, Newton 2008). A switch in migratory strategy in individual birds has been shown for European Robins (Harper 1985 but see Adriaensen & Dhondt 1990), rarely occurred in American Dippers *Cinclus mexicanus* (Gillis *et al.* 2008), and was age and sex-dependant in Blackbirds (Schwabl & Silverin 1990).

Our telemetry study showed that some birds wintered very close to their breeding territory and made use of the surrounding agricultural fields. This is also confirmed by the sighting of three colour-ringed individuals from the Aekingerzand breeding population on 26 November 2007 and two resightings on 30 January 2008. Further resightings are lacking because of the difficulty in reading colour-rings on Skylarks in winter.

Combining data from both winters, 15 of the 23 birds with radio-transmitters that were undetected during winter returned to the original breeding grounds during the subsequent breeding season. Since all transmitters still worked in spring, this suggests that these birds migrated out of our search area. We cannot exclude the possibility that we missed some birds or that birds wintered just outside the search area. Despite this uncertainty, we have unequivocal evidence for true migration, because two individuals captured during breeding were originally ringed during migration in Belgium. The disappearance of the radio-tagged birds in the autumn also fits the timing of migration of the two birds from our study population captured in Belgium. We therefore assume that at least a subset of the birds that we did not find during winter truly migrated.

Our sample sizes are currently too small to draw definite conclusions about age-differences in migration strategies. Age-related migration patterns are hard to document, as both adult and young Skylarks undergo a complete post-breeding moult and are impossible to age in autumn based on field characteristics. Nevertheless, van Dobben & Mörzer Bruyns (1939) suggested that first-year birds migrate later than adults based on dissection of birds killed at lighthouses. Different timing and travel distances between age classes have been shown for a number of other short-distance migratory species in Europe (Newton 2008).

We found both males and females to winter locally, but sample sizes are small. In the 1970s it was suggested that Skylarks wintering in north-western Europe were mainly males (Niethammer 1970, Senk *et al.* 1972, Vauk 1972, Zink 1987) and during cold weather movements in winter in The Netherlands more than 70% of all caught Skylarks were males (Levering & Keijl 2008). Females were significantly over-represented in migrating Skylarks in southern Italy (Scebba 2001) suggesting that female Skylarks migrate further south as shown for many other European partial migrants (reviewed by e.g. Gauthreaux 1982 and Newton 2008). Only in Scotland the sex ratio among Skylarks is equal during winter (Dougall 1997). If such a sex-bias in migration strategies exists, this could have important implications for conservation measures.

In light of ongoing discussions about reversing negative population trends and how to improve the

winter situation for farmland birds, our findings provide important information for conservation plans and activities. The change in agricultural practices from summer to winter cereals and thus the loss of overwintering stubble fields as a food source for Skylarks in winter might be an important problem associated with the decline in Skylark numbers (Donald *et al.* 2001, Newton 2004, Siriwardena *et al.* 2008). Despite the enormous decline in the Dutch breeding population, the migratory tendency has not disappeared, which might have been expected if migration depends on competition for limited available winter food. Identifying where Skylarks from the Dutch breeding population spend the winter is therefore an essential question to answer if we are to develop more effective conservation measures (see van Beusekom 2006). Our data suggest that a two-pronged wintering conservation strategy is necessary: the situation for wintering birds needs to be improved not only in SW Europe, where Skylarks are still hunted (European Communities 2007) but also in The Netherlands itself.

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REFERENCES

Adriaensen F. & Dhondt A.A. 1990. Population dynamics and partial migration of the European Robin (*Erithacus rubicula*) in different habitats. J. Anim. Ecol. 59: 1077–1090.

Alerstam T. 1990. Bird Migration. Cambridge University Press. Cambridge.

Bauer H.-G., Bezzel E. & Fiedler W. 2005. Das Kompendium der Vögel Mitteleuropas. Aula, Wiebelsheim.

Berthold P. 1993. Bird Migration. Oxford University Press, Oxford.

Bijlsma R.G., Hustings F. & Camphuysen C.J. 2001. Algemene en schaarse vogels van Nederland (Avifauna van Nederland 2). KNNV uitgeverij, Utrecht.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge.

Bos J., Koks B., Kragten S. & Schroeder J. 2009. Akkervogels alleen te redden met een koerswijziging van het Gemeenschappelijk Landbouwbeleid. Levende Natuur 110: 192–197.

Donald P.F. 2004. The Skylark. Poyser, London.

Donald P.F., Buckingham D.L., Moorcroft D., Muirhead L.B., Evans A.D. & Kirby W.B. 2001. Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in southern Britain. J. Appl. Ecol. 38: 536–547.

Donald P.F, Sanderson F.J., Burfield I.J. & van Bommel F.P.J. 2006. Further evidence of continent-wide impacts of agriculture intensification on European farmland birds, 1990–2000. Agric. Ecosyst. Environ. 116: 189–196.

Dougall T.W. 1996. Movement and mortality of British-ringed Skylarks (*Alauda arvensis*). Ring. Migrat. 17: 81–92.

Dougall T.W. 1997. Biometrics and sex ratios of Skylarks (*Alauda arvensis*) in winter in south-east Scotland. Ring. Migrat. 18: 37–49.

Dougall T.W. 1999. Mass and visible fat scores of Skylarks (*Alauda arvensis*) in winter in south-east Scotland. Ring. Migrat. 19: 283–297.

Duncan R. 1987. Breeding Skylarks in Aberdeen. Grampian Ringing Group 5: 49–55.

European Bird Census Council (EBCC) 2009. European wild bird indicators, 2009 update.

European Communities 2007. Management plan for Skylark (*Alauda arvensis*) 2007 –2009. Directive 79/409/EEC on the conservation of wild birds.

Gauthreaux S.A. 1982. The ecology and evolution of avian migration systems. In: Farner D.S. & King J.R. (eds) Avian Biology, 6. Academic Press, New York, pp. 93–167.

Gillis E.A., Green D.J., Middleton H.A. & Morrissey C.A. 2008. Life history correlates of alternative migratory strategies in American Dippers. Ecology 89: 1687–1695.

Glutz von Blotzheim U.N. 1985. Handbuch der Vögel Mitteleuropas. Passeriformes (1. Teil). Aula, Wiesbaden.

Harper D.G.C. 1985. Pairing strategies and mate choice in female robins *Erithacus rubecula*. Anim. Behav. 33: 862–875.

Helm B., Fiedler W. & Callion J. 2006. Movements of European Stonechats *Saxicola torquata* according to ringing recoveries. Ardea 94: 33–44.

Hustings F., van der Coelen J., van Noorden B., Schols R. & Voskamp P. 2006. Avifauna van Limburg. Stichting Natuurpublicaties, Roermond.

Körner-Nievergelt F., Sauter A., Atkinson P.W., Guélat J., Kania W., Kéry M., Köppen U., Robinson R.A., Schaub M., Thorup K., van der Jeugd H. & van Noordwijk A.J. 2010. Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. J. Avian Biol. 41: 8–17.

Landelijke Werkgroep Vogeltrektellen/SOVON 2002. Vogeltrek over Nederland. Schuyt, Haarlem.

Lensink R. 1993. Vogels in het Hart van Gelderland. KNNV Uitgeverij, Utrecht.

Levering H.P.A. & Keijl G.O. 2008. Vinkenbaan Castricum 1960–2006 – een halve eeuw vogels ringen. VRS Castricum, Castricum.

Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146: 579–600.

Newton I. 2008. The migration ecology of birds. Academic Press, London.

Niethammer G. 1970. Überwintern nur männliche Feldlerchen in Westdeutschland? Vogelwarte 25: 356–357.
Nilsson A.L.K., Linstrom A., Jonzen N., Nilsson S.G. & Karlsson L. 2006. The effect of climate change on partial migration - the blue tit paradox. Global Change Biol. 12: 2014–2022.
Paradis E., Baillie S.R., Sutherland W.J. & Gregory R.D. 1998. Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67: 518–536.
Partecke J. & Gwinner E. 2007. Increased sedentariness in European Blackbirds following urbanization: A consequence of local adaptation? Ecology 88: 882–890.
PECBMS 2009. The State of Europe's Common Birds 2008. CSO/RSPB, Prague.
Poelmans W. & van Diemen J. 1997. Broedvogels in Midden- en Oostbraband. Provincie Noord-Brabant, 's-Hertogenbosch.
Rappole J.H.& Tipton A.R. 1991. New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol. 62: 335–337.
Schwabl H. & Silverin B. 1990. Control of partial migration and Autumnal Behaviour. In: Gwinner E. (ed.) Bird Migration: physiology and ecophysiology. Springer-Verlag, Berlin, pp. 144–155.
Schwabl H., Wingfield J.C. & Farner D.S. 1984. Endocrine correlates of autumnal behaviour in sedentary and migratory individuals of a partial migratory population of the European Blackbird (*Turdus merula*). Auk 101: 499–507.
Scebba S. 2001. Biometrics and sex ratios of Skylarks (*Alauda arvensis*) during migration in southern Italy. Ring. Migrat. 20: 364–370.
Senk R., Senk A. & Wörbner H. 1972. Zur Frage: Überwintern nur männliche Feldlerchen in Westdeutschland. Vogelwarte 26: 314.
Siriwardena G.M., Stevens D.K., Anderson G.Q.A., Vickery J.A., Calbrade N.A. & Dodd S. 2007. The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two largescale experiments. J. Appl. Ecol. 44: 920–932.
Siriwardena G.M., Calbrade N.A. & Vickery J.A. 2008. Farmland birds and late winter food: does seed supply fail to meet demand? Ibis 150: 585–595.
Smith H.G. & Nilsson J.-A. 1987. Intraspecific variation in migratory patterns of a partial migrant, the Blue Tit (*Parus caeruleus*): an evaluation of different hypothesis. Auk 104: 109–115.
SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse Broedvogels 1998 – 2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden.
Spaepen J.F. 1995. A study of the migration of the Skylark *Alauda arvensis*, based on European ringing data. Gerfaut 85: 63–89.
Spaepen J. & Van Cauteren F. 1962. Migration of the Skylark. Gerfaut 52: 275–297.
Spaepen J. & Van Cauteren F. 1968. Migration of the Skylark (New results). Gerfaut 58: 24–77.
Speek B.J. & Speek G. 1984. Thiemes's Vogeltrekatlas. Thieme, Zutphen.
Sutherland W.J., Pullin A.S., Dolman P.M. & Knight T.M. 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19: 305–308.
Terril S.B. & Able K.P. 1988. Bird migration terminology. Auk 105: 205–206.
Teixeira R.M. (ed.) 1979. Atlas van de Nederlandse broedvogels. Natuurmonumenten, 's-Graveland.
van Beusekom R. 2006. Is er hoop voor de Veldleeuwerik in het agrarisch gebied? Levende Natuur 107: 138–140.
van Dijk A.J., Boele A., Hustings F., Koffijberg K. & Plate C.L. 2008. Broedvogels in Nederland in 2006. SOVON-monitoringrapport 2008/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
van Dobben W.H. & Mörzer Bruyna M.F. 1939. Zug nach Alter und Geschlecht an niederländischen Leuchttürmen. Ardea 28: 61–71.
Vauk G. 1972. Welches Geschlecht haben in W-Deutschland überwinternde Feldlerchen (*Alauda arvensis*)? J. Ornithol. 113: 105–106
Venema P. 2001. Wintervogels in Drenthe. Stichting Werkgroep Avifauna Drenthe.
Vergeer J.-W. & van Zuylen G.J.C. 1994. Broedvogels van Zeeland. KNNV Uitgeverij, Utrecht.
Wernham C., Toms M., Marchant J., Clark J., Siriwardena G. & Baillie S. 2002. The Migration Atlas. Movements of the birds of Britain and Ireland. Poyser, London.
Wolfenden I.H. 1990. Some results from a Skylark colour-ringing project. Bird Ringing in south-west Lancashire. 1988–89: 42–47.
Zink G. 1975. Der Zug europäischer Singvögel – ein Atlas der Wiederfunde beringter Vögel. 2. Lieferung. Vogelzug-Verlag, Moeggingen
Zink G. 1987. Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel. Aula, Wiesbaden.

SAMENVATTING

We hebben onderzocht of de Nederlandse Veldleeuwerik *Alauda arvensis* in de winter in het broedgebied blijft of wegtrekt. Van de 532 terugmeldingen die bij het Vogeltrekstation bekend zijn, kunnen er 25 gebruikt worden om trekvogels en standvogels te onderscheiden. Er blijken 12 Veldleeuweriken standvogel te zijn, 10 waren trekvogel en 3 waarschijnlijke trekvogel. In de winter krijgen de Nederlandse standvogels gezelschap van leeuweriken uit het noorden en oosten van Europa. De ringgegevens vergeleken we met trekpatronen van Veldleeuweriken die we door de seizoenen probeerden te volgen. Daartoe werden 27 Veldleeuweriken op het "Aekingerzand" in het Nationale Park Drents-Friese Wold voorzien van een zendertje. Vier van deze vogels bleven in het gebied overwinteren. Van de vogels die niet in de winter werden gevonden kwamen er 14 in het volgende voorjaar terug, wat er op duidt dat ze elders hebben overwinterd. De waarnemingen laten zien dat de Nederlandse Veldleeuweriken er verschillende overwinteringstrategieën op na houden. Een deel trekt weg terwijl een ander deel in de buurt van het broedgebied blijft hangen. Voor de bescherming en instandhouding van de Veldleeuweriken is dit een belangrijk gegeven.

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Appendix 1. List of all 25 birds that were used to distinguish between resident and migratory strategies. M=migrant, R=resident, PM=presumably migrant, M=Male, F=female, ?=unknown; accuracy of finding: 0=accurate to day, 1=accurate within 3 days either side of the date coded, 4=accurate within 2 weeks either side of the date coded; recovery condition: 0=unknown, 1=dead, but no information on how recently, 2=freshly dead, within about a week, 3=not freshly dead, more than about a week, 5=sick, wounded, fate unknown, 7=alive and probably healthy and certainly released, 8=alive and probably healthy and released by a ringer; finding circumstances: 1= found, bird or body mentioned, 10=shot, 19='hunted', likely shot, 20= hunted, trapped, poisoned intentionally by man, 28=ring read in the field, 40=killed by traffic, 43=collision with wire, 44=collision with windows, 47=attracted to light, 61=taken by cat, 64=taken by owl or raptor, identity predator available, 99=no information at all; direction: direction between ringing and recovery site in degrees.

			Ringing			Finding								
Strategy	Sex	Age at ringing	Ringing date	North	East	Finding date	Accurancy	Country	North	East	Condition	Circum-stances	Distance (km)	Direction
M	?	Full-grown	15/10/1974	43°24'	01°36'	12/05/1975	0	Netherlands	52°48'	06°54'	2	44	1219	31
M	?	Full-grown	29/10/2002	51°07'	02°41'	30/05/2006	0	Netherlands	53°12'	07°04'	2	64	380	52
M	F	Full-grown	13/10/2003	50°53'	03°18'	01/05/2007	0	Netherlands	52°55'	06°18'	8	20	306	42
M	F	Full-grown	19/10/2007	51°04'	03°16'	14/05/2008	0	Netherlands	52°56'	06°19'	8	20	294	45
M	?	Nestling	17/07/1939	53°00'	04°48'	11/02/1940	0	England	52°36'	02°00'	0	99	459	264
M	?	Nestling	17/05/1960	51°54'	05°06'	06/10/1960	0	France	44°42'	01°12'	1	1	925	210
M	?	Nestling	01/06/1966	51°19'	06°06'	25/10/1967	0	France	44°12'	00°54'	7	20	937	214
M	?	Nestling	09/05/1968	51°00'	05°48'	15/09/1968	4	Spain	36°00'	-05°36'	0	19	1900	209
M	?	Nestling	25/05/1982	52°17'	06°54'	11/12/1983	0	France	49°53'	02°21'	2	10	415	230
M	F	Nestling	27/06/2006	52°53	06°37	08/10/2007	0	Belgium	50°43'	04°12'	8	20	295	215
PM	?	Full-grown	08/10/1972	51°06'	04°00'	15/09/1974	0	Netherlands	51°54'	05°12'	1	40	122	43
PM	?	Full-grown	17/10/2003	51°20'	04°58'	02/09/2007	0	Netherlands	51°19'	05°38'	3	0	46	92
PM	?	Nestling	15/06/1956	52°36'	04°42'	12/10/1958	2	Netherlands	51°42'	03°42'	2	47	121	214
R	?	Full-grown	15/01/1966	52°24'	04°30'	30/03/1968	0	Netherlands	53°18'	05°06'	8	20	108	22
R	?	Full-grown	19/01/1966	51°24'	03°24'	22/05/1966	0	Netherlands	51°24'	03°48'	3	1	28	90
R	?	Full-grown	07/01/1970	52°24'	043°6'	01/04/1970	0	Netherlands	52°18'	04°24'	1	1	18	231
R	?	Full-grown	29/12/1976	52°25'	04°34'	23/07/1979	0	Netherlands	52°15'	04°27'	3	64	20	203
R	?	Full-grown	01/01/1979	52°33'	04°37'	07/04/1979	0	Netherlands	51°59'	04°07'	2	64	72	208
R	?	Full-grown	04/01/1979	52°25'	04°34'	15/04/1979	4	Netherlands	52°03'	04°13'	3	1	47	210
R	?	Full-grown	27/01/1979	52°33'	04°37'	30/05/1979	0	Netherlands	51°49'	04°08'	1	1	88	202
R	?	Full-grown	07/12/1980	52°08'	04°20'	23/06/1981	0	Netherlands	52°15'	04°28'	3	64	16	35
R	?	Full-grown	16/12/1981	52°33'	04°37'	08/05/1982	0	Netherlands	52°21'	04°32'	1	64	23	194
R	?	Full-grown	08/01/1982	52°21'	04°32'	21/05/1983	0	Netherlands	52°21'	04°32'	1	64	0	0
R	?	Full-grown	10/02/1982	52°25'	04°34'	03/05/1983	0	Netherlands	53°11'	05°44'	3	1	116	43
R	?	Nestling	05/07/1985	53°04'	04°44'	18/11/1985	0	Netherlands	52°25'	04°34'	8	20	73	189

Appendix 2. List of all 12 birds that were used to evaluate the origin of birds wintering in The Netherlands (classification W= wintering) and the 10 birds that were present in The Netherlands during the late autumn migration period (classification LM=late migration period). For abbreviations see Appendix 1.

			Ringing				Finding							
Classif-ication	Age at ringing	Sex	Ringing date	Ringing date	North	East	Finding date	Country	North	East	Condition	Circum-stances	Distance (km)	Direction
LM	full-grown	M	02/11/1967	Netherlands	51°42'	03°42'	25/07/1969	Denmark	56°24'	10°54'	2	40	702	42
LM	full-grown	?	13/11/1967	Netherlands	52°24'	04°36'	28/07/1969	Denmark	56°12'	08°06'	0	1	479	28
LM	full-grown	?	06/11/1969	Netherlands	52°24'	04°30'	27/07/1970	Denmark	57°06'	10°24'	1	1	645	36
LM	full-grown	M	01/11/1977	Netherlands	52°08'	04°20'	09/04/1979	Denmark	56°00'	08°24'	1	1	505	32
LM	full-grown	?	17/11/1977	Netherlands	52°24'	04°36'	16/06/1978	Denmark	56°30'	10°30'	1	40	594	40
LM	full-grown	?	04/08/1978	Norway	70°09'	28°52'	15/11/1978	Netherlands	53°05'	06°35'	1	1	2214	211
LM	full-grown	?	11/11/1979	Netherlands	52°25'	04°34'	21/03/1981	Denmark	55°39'	09°10'	3	1	468	40
LM	full-grown	M	02/11/1989	Netherlands	52°51'	04°32'	12/07/1992	Denmark	57°15'	11°01'	1	43	684	37
LM	full-grown	M	03/11/1994	Netherlands	51°51'	05°59'	28/05/1996	Denmark	55°12'	09°32'	1	64	347	42
LM	full-grown	M	01/11/2002	Netherlands	51°40'	03°41'	15/03/2004	Russia	54°57'	19°47'	7	20	1128	71
W	full-grown	?	10/12/1967	Netherlands	52°24'	04°30'	03/04/1969	Norway	59°18'	09°12'	5	1	821	21
W	full-grown	?	12/01/1968	Netherlands	52°24'	04°30'	02/04/1969	Denmark	56°36'	09°36'	1	1	571	35
W	full-grown	?	30/12/1968	Netherlands	52°24'	04°36'	28/09/1972	Denmark	55°36'	10°06'	2	19	505	45
W	full-grown	F	24/12/1970	Netherlands	52°36'	04°36'	04/06/1971	Sweden	59°18'	15°24'	1	1	1002	42
W	full-grown	?	29/12/1970	Netherlands	52°24'	04°36'	30/08/1971	Russia	57°48'	29°30'	1	1	1691	69
W	full-grown	?	30/11/1973	Netherlands	52°24'	04°36'	14/05/1974	Denmark	55°30'	11°12'	1	1	552	51
W	full-grown	M	01/12/1973	Netherlands	52°36'	04°36'	10/07/1974	Denmark	55°24'	09°00'	1	1	424	43
W	full-grown	?	02/12/1973	Netherlands	52°24'	04°30'	11/09/1974	Denmark	55°18'	09°36'	2	43	464	46
W	full-grown	?	27/11/1977	Netherlands	52°25'	04°34'	03/07/1980	Denmark	56°10'	09°21'	2	61	519	37
W	full-grown	?	03/01/1985	Netherlands	52°21'	04°32'	11/05/1986	Denmark	57°22'	09°43'	7	28	648	31
W	nestling	?	28/05/1993	Denmark	56°18'	10°30'	25/11/1993	Netherlands	52°24'	04°32'	8	20	578	222
W	full-grown	M	23/12/2001	Netherlands	52°21'	04°31'	22/07/2002	Denmark	56°31'	09°37'	2	61	568	35