Departure directions, migratory timing and non-breeding distribution of the Red-backed Shrike Lanius collurio: do ring re-encounters and light-based geolocator data tell the same story?

Fränzi Korner-Nievergelt [a] [b], Lukas Jenni [a], Anders P. Tøttrup [c] & Gilberto Pasinelli [a]

[a] Swiss Ornithological Institute, Sempach, Switzerland

[b] oikostat GmbH, Ettiswil, Switzerland

[c] Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen, Denmark
Version of record first published: 18 Dec 2012.

PLEASE SCROLL DOWN FOR ARTICLE

Departure directions, migratory timing and non-breeding distribution of the Red-backed Shrike *Lanius collurio*: do ring re-encounters and light-based geolocator data tell the same story?

FRÄNZI KORNER-NIEVERGELT[1,2]*, LUKAS JENNI[1], ANDERS P. TØTTRUP[3] and GILBERTO PASINELLI[1]

[1]*Swiss Ornithological Institute, Sempach, Switzerland* [2]*oikostat GmbH, Ettiswil, Switzerland* [3]*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark*

This study explores differences and consistencies between ring re-encounter and light-based geolocator data from Red-backed Shrike when used for studying three aspects of bird migration: departure direction and its relationship with longitude and latitude, non-breeding distribution, and timing of migration. Departure directions were consistent between the two methods. They indicate a funnel-shaped migration with individuals from southwest Europe taking a detour via the eastern Mediterranean rather than migrating via Gibraltar. This indicates that an original migration route has been retained after colonisation of the breeding range. Non-breeding distributions differed substantially between birds ringed and re-encountered and birds tracked by geolocators. This difference may be due to spatio-temporal heterogeneity in ring re-encounter probability and/or due to the two samples of birds belonging to different populations. The monthly average ring re-encounter location moved later southward during autumn and earlier northward during spring migration than the geolocator positions, because of an over-representation of re-encounters in the north. The results emphasise the importance of combining different sources of data when analysing migration patterns of animals that are difficult to track.

Migration towards subtropical or tropical areas in winter is a characteristic life-history trait of many bird species breeding in temperate climate zones (Alerstam 1990). Energy-demanding long-distance flights and the stages in stopover or wintering areas, where the habitat may be completely different from the breeding grounds, may have important implications for the ecology, behaviour and population dynamics of species (Webster *et al* 2002, Helm *et al* 2006, Norris & Marra 2007). To understand the ecology and population dynamics of a species or a population, it is therefore important to know when and where individuals are migrating.

Migration directions are heritable (Helbig 1991). They are often adapted to the specific locations of breeding and wintering areas in relation to topography such as mountains, seas, or deserts (Bruderer 1997a). When environmental conditions change or a species expands to new breeding areas, migratory direction may evolve rapidly. Such a rapid evolution of migration direction

has been observed in southern German and Austrian populations of Blackcap *Sylvia atricapilla* that started to migrate towards the UK in the 1960s (Helbig 1994). Subsequently, temporal segregation of spring migration led to reproductive isolation and genetic and phenotypic divergence into two sympatric populations (Rolshausen *et al* 2009). Observing such changes in migratory behaviour may thus allow insight into the evolutionary mechanisms of bird migration. However, the unbiased measurement of migratory direction is a prerequisite for detecting changes in migratory behaviour.

Knowledge of the distribution of bird populations during the non-breeding period is important for various reasons, including the study of carry-over effects (Norris 2005, Norris & Marra 2007) or migratory connectivity (Webster *et al* 2002), as well as for conservation purposes (*eg* Fox & Salmon 1988). Ecological conditions at stopover or wintering sites can affect breeding success and population dynamics (Norris & Marra 2007). As an example, in the Red-backed Shrike *Lanius collurio*, low breeding success is associated with dry weather at the autumn stopover sites (Schaub *et al* 2011) and fluctuations in breeding population size are positively related to rainfall in the

* Correspondence author
  Email: fraenzi.korner@vogelwarte.ch

autumn stopover sites and in the wintering areas (Pasinelli *et al* 2011). To detect such carry-over effects of factors acting at large spatial scales, it is sufficient to know the approximate locations of stopover and wintering sites. However, to study the effects of local factors such as management and human impacts, stopover sites and wintering areas need to be accurately identified.

In addition to identifying the stopover and wintering locations, it is important to know when and how long these areas are used. When the temporal and spatial occurrence of favourable ecological conditions change in the non-breeding area, we expect that birds should also adjust their movement behaviour. Such behavioural changes can be detected only when the timing of migration can be measured accurately. The study of the timing of migration by observing departure, passage or arrival of birds has recently provided clear evidence of climate change affecting bird migratory behaviour (Hüppop & Hüppop 2003, Jenni & Kéry 2003). In the Red-backed Shrike, arrival in the breeding area has shifted earlier during the last century in western Poland (Tryjanowski *et al* 2002) and in Scandinavia (Tøttrup *et al* 2006). Furthermore, knowledge of the timing of migration and of the duration of active migration may provide insights into the energetics of bird migration (Moore & Kerlinger 1987, Bayly 2006).

Unfortunately, the study of migration in small birds is hampered because of their body size. Several methods have been used to study small-bird migration: visual daytime observation (*eg* Bednarz *et al* 1990), moon watching (*eg* Liechti *et al* 1996), infrared and radar observation (*eg* Bruderer 1997b, Zehnder *et al* 2002), ringing (*eg* Zink 1973–85, Wernham *et al* 2002), and tracking by light-based geolocators (*eg* Stutchbury *et al* 2009). All these methods have their pros and cons. All observation methods (*ie* visual observation including moon watching, infrared and radar) produce counts of actively migrating birds at one or several sites but neither the origin nor the destination of these birds are known. Ringing usually reveals two positions (ringing and recovery position) of the same individual bird during its life cycle, but not the whereabouts of the bird in-between. Tracking small birds by light-based geolocators allows reconstructing the entire migration journey, but requires that the bird is recaptured to extract the data (Hill 1994). This leads to a non-random sample of individuals available for analysis. Given the limitations of each method, it is surprising that only a few studies have combined different methods, even though it is acknowledged that combinations have great potential for migration studies of birds and other animals (Norris *et al* 2006).

Ring re-encounters have improved our knowledge of bird migration hugely (Zink 1973–85, Zink & Bairlein 1995, Wernham *et al* 2002). However, almost every study based on ring re-encounter data has struggled against bias caused by spatial and temporal heterogeneity in ring re-encounter probability (Perdeck 1977, Siriwardena *et al* 2004, Korner-Nievergelt *et al* 2010). To draw unbiased inference on bird migration behaviour from ring re-encounters, precise information on the spatial and temporal patterns of ring re-encounter probability is needed. Comparing results from ring re-encounters with those from alternative technologies such as satellite telemetry or light-based geolocation may allow detection of inconsistencies between the methods and may thus inform us about spatial and temporal patterns of ring re-encounter probability. Whereas results from ring re-encounters are susceptible to spatial and temporal heterogeneity in ring re-encounter probability, tracked birds might not constitute a random sample of the populations of interest. Furthermore, when estimating locations using light-based geolocators, topography, habitat, weather and behaviour of the bird can produce substantial errors, especially in the estimated latitude (Lisovski *et al* 2012), whereas locations of ring re-encounters can, in most cases, be assumed to be accurate. Conversely, the date of geolocated birds is known exactly, while the date of ring re-encounters may be inexact. A combination of these two approaches may yield a more comprehensive understanding of migratory behavior than either method alone.

We here combine ring re-encounter data and geolocator data from a long-distance migratory songbird, the Red-backed Shrike, and analyse these data with respect to three aspects of bird migration: departure direction, non-breeding distribution and timing of migration. We aim to describe the migration of Red-backed Shrike and to delineate consistencies and inconsistences between the two data sets. More specifically, we investigated the following questions: (1) How do autumn departure directions change in relation to latitude and longitude of the breeding area? (2) Does the spatial distribution of ring recoveries during the non-breeding period match the spatial distribution of birds tracked by geolocators? (3) Does the timing of migration measured by ringing data match the timing observed at ringing stations and the timing of the birds tracked with geolocators?

METHODS

Data sources
Data from the EURING Data Bank (www.euring.org; received November 2007) contained 2,382 re-encounter

records of Red-backed Shrike. We complemented this data set with 101 long-distance recovery records of Zink (1973–85) that were not included in the EURING database. These recovery records were kindly provided by the Max-Planck Institute of Ornithology, Radolfzell, Germany. In addition, we included 18 records kindly provided by the French and Aranzadi Ringing Schemes (see Acknowledgements). We discarded 54 records because the uncertainty of the re-encounter date was larger than ± two weeks. A total of 2,447 records from 1,983 individuals were then available for analysis. Of these, 432 re-encounters were from more than 50 km from the place of ringing and 2,015 were from shorter distances.

From the study on nine adult Red-backed Shrikes tracked using light-based geolocators by Tøttrup *et al* (2012), individual locations during four stationary periods and individual arrival and departure dates from these locations were extracted.

Data on the timing of occurrence of Red-backed Shrike at ringing stations were extracted from the literature (see Appendix).

Data analyses

Departure direction

We selected recoveries of birds ringed during the breeding season and re-encountered north of the Mediterranean within the same year in the months July, August and September (and October for birds from France and the Iberian Peninsula) at least 200 km distant from the place of ringing. Breeding season was defined to last from 15 May to 30 June for central, northern and eastern Europe (Bauer *et al* 2005) and from 15 May to 15 July in France and the Iberian Peninsula, respectively. Had we included only birds ringed up to 30 June in France and on the Iberian Peninsula, no re-encounter from these regions would have been included in the analyses. We excluded one recovery (from Sweden) which was very likely to have been moved by a vehicle before recovery. This yielded 34 re-encounters of which the loxodromic direction (Imboden & Imboden 1972) between place of ringing and place of re-encounter was used as departure direction. From the birds tracked by geolocators, departure direction was determined as the direction from the breeding sites (in northeastern Denmark and southern Sweden) to the location of their first stationary period (end of August to beginning of September; Tøttrup *et al* 2012). Data from ring re-encounters and geolocators were pooled to analyse departure directions.

The departure direction in degrees was used as the dependent variable in a linear model with latitude (ºN), longitude (ºE) and the interaction between latitude and longitude as predictors. Age (first year *v* older) and the origin of departure direction (*ie* from ring re-encounter data or geolocator data) were also included as predictors in the model. Departure directions clustered around a median of 150° with a range of 85° to 197°. Therefore, we treated the departure direction variable as linear instead of circular and assumed the normal distribution as the error distribution for the model. For the same reason, latitude and longitude were also treated as linear predictor variables. We used standard diagnostic residual plots to assess the fit of the model.

Spatial distribution during the non-breeding period

To describe the spatial distribution of ring re-encounters during the non-breeding period, we selected re-encounters during each of the four stationary periods identified by Tøttrup *et al* (2012) based on the nine birds tracked with geolocators. We defined a stationary period to last from the mean arrival date to the mean departure date of the nine birds. 188 ring re-encounters were available from these stationary periods: 48 from the first stationary period (22 August – 6 September), 111 from the second (13 September – 5 November), 22 from the third (19 November – 28 March) and seven from the last (18 April – 26 April). Locations of ring re-encounters and of the nine birds tracked by geolocators were plotted.

Timing of migration

To describe the temporal pattern of migration based on ring re-encounters, we selected all re-encounters during the non-breeding period (*ie* outside the breeding period) at least 200 km distant from the place of ringing (n = 302). The running monthly means of the latitudes of the ring re-encounter locations were then calculated and compared graphically with the average track of the nine geolocator birds. The latter was obtained from the average departure and arrival dates and the average latitudes of the starting sites given by Tøttrup *et al* (2012). In this plot we also visualised the passage times of Red-backed Shrikes at observatories described in the Appendix (Fig ii).

RESULTS

Departure directions

Departure direction was significantly related neither to age ($F_{1, 37}$ = 0.03, P = 0.86) nor to method ($F_{1, 37}$ = 0.00, P = 0.99). Departure direction gradually shifted from east (93.4° ± 12.3, mean ± sd) for Spanish birds to south (163.7° ± 12.3) for Scandinavian birds with increasing

longitude (Table 1, Fig 1). This shift was more pronounced in southern populations than in northern ones (significant interaction, latitude x longitude). Northern and eastern populations had more southerly departure directions than southern and western populations, which departed towards the east (Fig 2). These changes in departure direction with latitude and longitude corroborate the hypothesis that most Red-backed Shrikes from European populations circumvent the Mediterranean eastwards to enter Africa at its northeastern edge.

Spatial distribution during the non-breeding period

Locations of ring re-encounters corresponded in principle to the locations of the geolocator birds during the first stationary period (22 August – 6 September) in southeast Europe (Fig 3). In contrast, there was a striking discrepancy between the ring re-encounter and geolocator locations during the three subsequent stationary periods. During the second staging period (13 September – 5 November), the geolocator birds were in Sudan and Chad, whereas with two exceptions all ring re-encounters originated from the North African coast or even from Europe. During the third stationary period (19 November – 28 March), geolocator birds were located in Namibia, Botswana and Angola, whereas rings were reported from Zambia, Zaire and Tanzania as well as from Europe. During the fourth stationary period (18 April – 26 April), only one of seven ring re-encounters originated from the staging area of geolocator birds, which corresponded to the southeastern African countries (Mozambique to Ethiopia). All other ring re-encounters were from further north, in the Arabian Peninsula or Greece.

The mean locations of ring re-encounters during the second, third and fourth stationary period were consistently closer to Europe than the mean locations of the geolocator birds. Ring re-encounters from Europe seem to be over-represented in the data throughout the year.

Table 1. Parameter estimates of the linear model of departure direction. The model explained 78% of the variance in departure direction (adjusted R^2, $F_{3, 39} = 50.0$, $P < 0.001$).

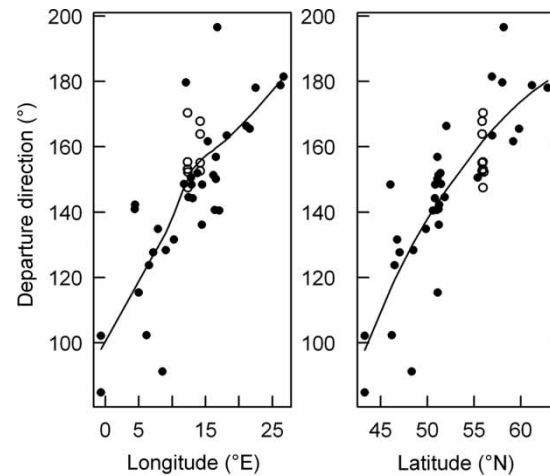| parameter	estimate	se	t	P
intercept	−94.59	40.05	−2.36	0.023
latitude	4.27	0.82	5.21	<0.001
longitude	7.22	2.53	2.85	0.007
latitude x longitude	−0.11	0.05	−2.27	0.029

Figure 1. Departure directions of Red-backed Shrikes in relation to the longitude and latitude of the site of origin. Closed circles (n = 34): birds ringed or controlled during the breeding season and re-encountered from July to September at least 200 km from the ringing or control site. Open circles (n = 9): directions of birds with geolocators from breeding site to location of first stationary period. The line in each graph is a loess smoother.

Timing of migration

Autumn migration measured by average latitude ring re-encounter location per month lagged behind the migration of the geolocator birds, whereas in spring northward displacement of the average ring re-encounter locations took place before the geolocator birds moved northward (Fig 4). Ringed birds were re-encountered until later in the year than the passage observed at the ringing stations located along the migration route of Red-backed Shrike during autumn migration (Fig 4 and Appendix).

DISCUSSION

On the basis of combined data for ring re-encounters and birds with geolocators, this study suggests that Red-backed Shrikes from northern and eastern populations have more southerly departure directions whereas birds from the southern and western populations depart towards the east. This gradual shift in migration departure direction from east to south with increasing latitude and longitude results in a (half-) funnel-shaped migration pattern. The European populations of Red-backed Shrikes primarily migrate to Africa across the eastern Mediterranean.

The comparison of ring re-encounters and geolocator data revealed that the identification of staging areas

Figure 2. Re-encounter locations (open circles) and ringing location (start of solid lines) of Red-backed Shrikes that were ringed or controlled during the breeding season and re-encountered during the same year, north of the Mediterranean, between July and September. Directions of birds with geolocators from breeding site to location of first stationary period (closed circles) are given as dotted lines. Model predictions of departure direction for each bird are shown in the right-hand graph.
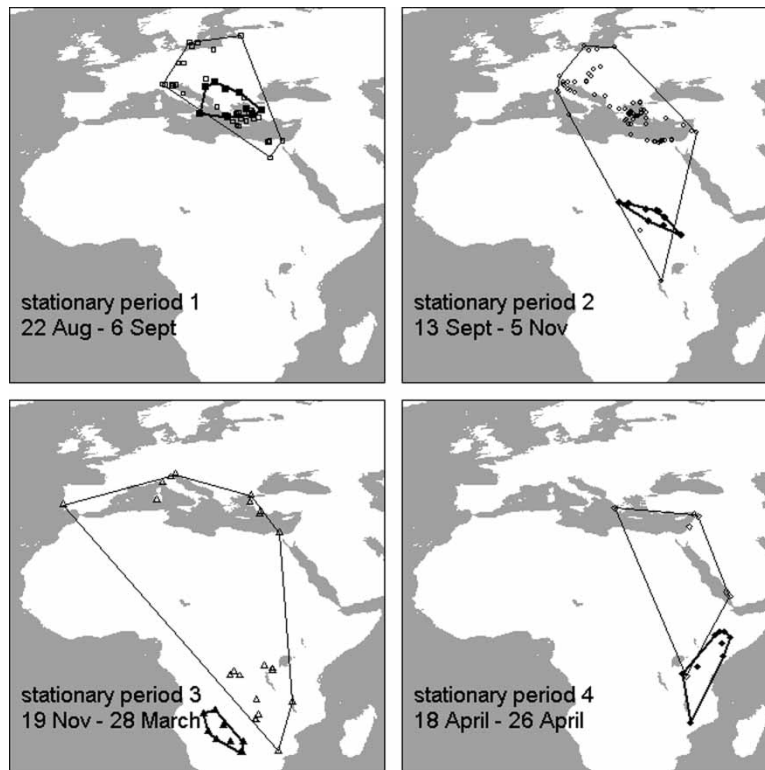

Figure 3. Distribution of ring re-encounters and the nine birds tracked by geolocators during the four stationary periods identified by the geolocator data. Open symbols are ring re-encounters and filled symbols the locations of geolocator birds. To facilitate interpretation, minimum convex polygons were drawn separately for ring re-encounters and geolocator birds.
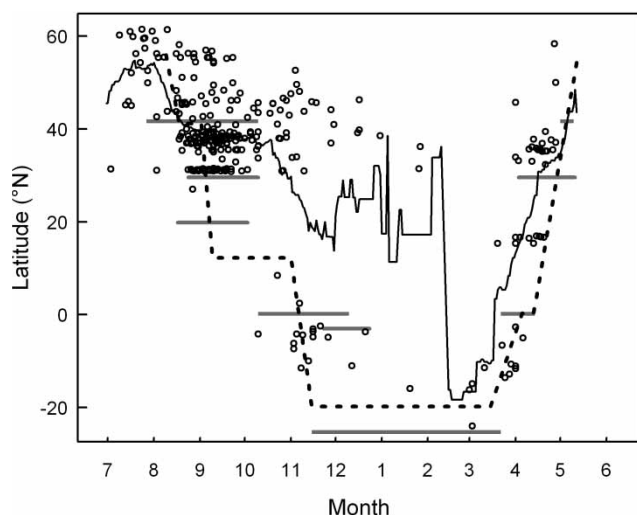
Figure 4. Latitude vs time for ring re-encounters (open circles, n = 302; the solid line indicates the running mean with a one-month window), for geolocator birds (dotted line shows the average of nine birds), and passage time of Red-backed Shrikes at observatories (horizontal grey bars). The nine individual tracks for the geolocator birds are given in the Appendix (Fig ii). The passage times at observatories are given either as span from begin to end of passage/wintering or as median passage day with 95% confidence interval. Details of passage times are given in the Appendix (Figs i, ii).

during the migratory journey and the timing of migration may differ substantially, depending on the method considered. These results suggest that approaches combining several methods are necessary to provide a comprehensive understanding of the migration strategies of species such as Red-backed Shrike.

Departure direction

A funnel-shaped migration pattern is known from soaring species, such as the White Stork *Ciconia ciconia*, which require thermal uplift for saving energy during flight and therefore concentrate during migration at the edges of large water bodies, *eg* the Strait of Gibraltar, the Bosphorus or the eastern coast of the Black Sea (Spaar 1997). Funnel-shaped migration patterns are also displayed by species which have breeding ranges largely exceeding the longitudinal extent of wintering areas (Berthold 2000). Although the departure directions of Red-backed Shrike indicate a funnel-shaped migration pattern, this pattern can hardly be explained by the requirements for thermal uplift or a concentration in a relatively small wintering area. Red-backed Shrike regularly cross the Mediterranean in the east (departing from Greece; Biebach *et al* 1983), and wintering areas seem to be dispersed throughout southern Africa. Red-backed Shrikes from most European populations seem

to migrate first towards Greece and then use a common migration route towards the African wintering areas.

It is remarkable that the southwestern European populations seem to follow this general pattern, thus taking a considerable detour. If the southwestern populations of Red-backed Shrikes were to take the shortest (western) route to the wintering area, we would expect them to migrate via Gibraltar and thus to depart towards the southwest. However, our data show an easterly departure direction for breeding birds from the Iberian Peninsula and France agreeing with the general opinion that western Red-backed Shrikes fly towards the eastern Mediterranean to enter Africa at its northeastern edge (Dorst 1956, Vaurie 1959, Moreau 1961, Zink 1973–85, Mead 1983). A few Red-backed Shrikes have recently been reported from Gibraltar and northwest Africa during autumn migration (Finlayson 1992). Among more than 18,000 migrating birds (of all species) captured and ringed in the western Sahara desert, only one Red-backed Shrike was caught (a first-year bird captured at Nouakchott, Mauritania, on 22 October 2003; Appendix Fig i). However, it remains unclear to what extent Red-backed Shrikes from the western populations take the western route. Our study constitutes an update of the ring re-encounter analyses of Zink (1973–85).

The conclusion that Red-backed Shrikes from southwestern populations mainly depart eastward is supported by own anecdotal data (unpublished) from nighttime captures during active migration at the alpine pass Col de Bretolet (southwest Switzerland). The side from where the birds entered the mist-nets was recorded for seven individuals (out of 85 captures during autumn migration from 1976 to 2010). Six of the seven individuals entered the mist-nets from the south, which is extremely rare in other night-migrating species, indicating a northeasterly migration direction. Of the 85 Red-backed Shrikes, 56 (66%) were caught during northerly wind directions whereas only 26 (31%) were caught during southwesterly wind directions (three were caught in calm conditions). Because birds are predominantly caught during headwind situations at Col de Bretolet (Komenda-Zehnder *et al* 2010), the dominance of Red-backed Shrike captures during northerly winds indicates that the general migration direction at Col de Bretolet may be northeast rather than southwest. Thus, these somewhat anecdotal data from captures on Col de Bretolet and the re-encounter data analysed in this paper both suggest that Red-backed Shrikes breeding in southwestern populations take a longer migration route to their African wintering area than seemingly necessary.

Taking longer migration routes than seemingly necessary has also been found in other bird species; Sutherland (1998) gives a non-exhaustive list of 14 species that fall into this category. For most of these, the migration route follows that of a recent range expansion. For example, the Paddyfield Warbler *Acrocephalus agricola* has recently expanded its range and established breeding areas in the Balkans. Individuals from these new breeding sites still winter in Hindustan and migrate along the route of breeding-range expansion, that is, they depart from the breeding area in northeasterly directions, travelling around the Black Sea northward instead of taking a shorter route south of the Black Sea (Zehtindjiev *et al* 2010). However, unlike the Paddyfield Warbler, the Red-backed Shrike has not expanded its breeding range during the last 100 years into the southwest of Europe (Vaurie 1959, Glutz von Blotzheim & Bauer 1993). The Red-backed Shrike, therefore, has either retained an old migratory route over more than 100 years, or the western (shorter) migration route is associated with such low individual fitness that this behaviour is strongly selected against.

Spatial distribution during the non-breeding period

Surprisingly, there was almost no overlap between the ring re-encounter distribution and the distribution of birds tracked with geolocators during their stationary periods in Africa, even though the geolocator birds originated from within the breeding range of the ringed birds (Appendix, Fig iii). If Red-backed Shrikes from the western breeding area were also wintering in the western part of the wintering area and individuals from the eastern breeding area were wintering in the eastern parts of the wintering area, we would expect to find the geolocator birds surrounded by ring re-encounters in winter. However, the winter distributions of the two samples of birds (geolocator birds and ringed birds) were completely separated. This could be due to low sample size or to the methodology.

The geolocator birds belonged to two small populations situated close to each other and they were tracked in the same single year (2009/10). Therefore, these birds were probably not independent of each other and the effective sample size might be lower than nine. This would reduce the relevance of the observed difference in the spatial distribution somewhat. Nevertheless, the large distance between re-encounter locations and geolocator positions found here during winter is surprising. Such distances may be unlikely to arise only from measurement errors of the light-based geolocation. For example, during winter

(stationary period 3), the ring re-encounters were situated on average 800 km more to the east and 1000 km more to the north than the geolocator positions. These differences exceed the average measurement errors reported for geolocator positions, which are around 50 km in longitude and between 150 and 200 km in latitude (Fudickar *et al* 2012, Lisovski *et al* 2012). Thus, the difference in spatial distribution of ring re-encounters and geolocator positions may result from the different nature of the two data sets.

To obtain a location during the non-breeding period by a light-based geolocator, the tracked bird has to survive until the next breeding season, return to the breeding site and then to be recaptured by the researcher. Therefore, geolocator data show sites from where birds successfully returned to their breeding area. In contrast, ring re-encounter data are generated when a ringed bird is found and the number on the ring is reported to a ringing scheme. Thus, a bird has to be captured or found dead by someone (such as a hunter) who knows that such a ring can be reported to a ringing scheme and who has the ability to do so either via the internet or by paying the postal charges. Ring re-encounters therefore occur more frequently in areas where birds die (*eg* due to high hunting pressure) and in areas with high human densities and with a high socio-economic standard (Korner-Nievergelt *et al* 2010). It may be indicative that 84% of our ring re-encounters from Africa were from former British colonies, where ornithology might have had a high profile in educational programmes. In contrast, among the geolocator localisations in Africa only 30% were from former British colonies, whereas 44% were from countries that gained independence before 1950 (Sudan, Ethiopia). Therefore, geolocator data should be analysed together with ring re-encounter data to describe the non-breeding distribution of a species.

Timing of migration

The average ring re-encounter location seemed to be shifted towards the north compared to the geolocator locations year-round, resulting in an apparent delay of autumn migration and an advance of spring migration, as estimated by ring re-encounters compared to geolocator birds. Strandberg *et al* (2009) also found a delay in autumn migration of raptors when estimated from ring re-encounters compared to satellite-tracking data. Average re-encounter locations were shifted towards Europe, presumably because ring re-encounter probabilities are higher in Europe than in Africa or in the Middle East, leading to an over-representation of birds in or near Europe in the ring re-encounter sample. This produces

an apparent delay of migration in autumn and an apparent advance in spring. The apparent delay in autumn migration observed in ring re-encounters may be enhanced by recoveries of individuals in poor condition that do not migrate, or stop migrating, and then are found with a higher probability (also later in the year) compared to individuals in good condition that rapidly migrate towards the wintering areas where ring re-encounter probabilities are low.

Data from ringing stations and from geolocators provide evidence that male Red-backed Shrikes migrate earlier in spring than females, whereas no such difference has been found during autumn migration (Tryjanowski & Yosef 2002, Tøttrup & Thorup 2008, Tøttrup *et al* 2012). Insufficient sample size and/or strong influence of temporal and spatial variance in ring re-encounter probability precluded analysing sex- or age-specific differences in the timing of migration.

In summary, geolocator data inform us only about birds that successfully return to their breeding site, whereas ring re-encounter data mainly tell us where birds have died. The two data sets thus contain different, perhaps complementary samples of birds. Therefore, the combined analyses of both types of data can reveal migration patterns of birds more accurately than can separate analyses of each.

ACKNOWLEDGEMENTS

REFERENCES

Alerstam, T. (1990) *Bird Migration*. Cambridge University Press, Cambridge.

Bauer, H.-G., Bezzel, E. & Fiedler, W. (2005) *Das Kompendium der Vögel Mitteleuropas. Alles über Biologie, Gefährdung und Schutz. Passeriformes – Sperlingsvögel*. AULA-Verlag, Wiebelsheim.

Bayly, N.J. (2006) Optimality in avian migratory fuelling. *Animal Behaviour* **71**, 173–182.

Bednarz, J.C., Klem, D. Jr., Goodrich, L.J. & Senner, S.E. (1990) Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934–1986. *The Auk* **107**, 96–109.

Berthold, P. (2000) *Vogelzug: eine aktuelle Gesamtübersicht*. Wissenschaftliche Buchgesellschaft, Darmstadt.

Biebach, H., Dallmann, M., Schuy, W. & Siebenrock, K.-H. (1983) Die Herbstzugrichtung von Neuntötern (*Lanius collurio*) auf Karpathos (Griechenland). *Journal of Ornithology* **124**, 251–257.

Bruderer, B. (1997a) Migratory directions of birds under the influence of wind and topography. In *RIN 1997: Orientation & Navigation – Birds, Humans and Other Animals* **27**, 1–10. Royal Institution of Navigation, Oxford.

Bruderer, B. (1997b) The study of bird migration by radar. Part 1: The technical basis. *Die Naturwissenschaften* **84**, 1–8.

Bruderer, B. & Bruderer, H. (2008) Der Neuntöter *Lanius collurio* im Winterquartier. *Der Ornithologische Beobachter* **105**, 231–266.

Dorst, J. (1956) *Les Migrations des Oiseaux*. Petite Bibliothèque Payot, Paris.

Finlayson, C. (1992) *Birds of the Strait of Gibraltar*. Poyser, London.

Fox, A.D. & Salmon, D.G. (1988) Changes in non-breeding distribution and habitat of Pochard *Aythya ferina* in Britain. *Biological Conservation* **46**, 303–316.

Fudickar, A., Wikelski, M. & Partecke, J. (2012) Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution* **3**, 47–52.

Glutz von Blotzheim, U.N. & Bauer, K.M. (1993) *Handbuch der Vögel Mitteleuropas*. AULA-Verlag, Wiesbaden.

Helbig, A.J. (1991) SE- and SW-migrating Blackcap *Sylvia atricapilla*. *Journal of Evolutionary Biology* **4**, 657–670.

Helbig, A.J. (1994) Genetic basis and evolutionary change of migratory directions in a European passerine migrant *Sylvia atricapilla*. *Ostrich* **65**, 157–159.

Helm, B., Piersma, T. & van der Jeugd, H. (2006) Sociable schedules: interplay between avian seasonal and social behaviour. *Animal Behaviour* **72**, 245–262.

Hill, R.D. (1994) Theory of geolocation by light levels. In *Elephant Seals, Population Ecology, Behavior, and Physiology* (eds Le Boeuf, B.J. & Laws, R.M.). University of California Press, Oxford.

Hüppop, O. & Hüppop, K. (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London Series B: Biological Sciences* **270**, 233–240.

Imboden, C. & Imboden, D. (1972) Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs- und Wiederfundort. *Die Vogelwarte* **26**, 336–346.

Jenni, L. & Kéry, M. (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London Series B: Biological Sciences* **270**, 1467–1471.

Komenda-Zehnder, S., Jenni, L. & Liechti, F. (2010) Do bird captures reflect migration intensity? – Trapping numbers on an Alpine pass compared with radar counts. *Journal of Avian Biology* **41**, 434–444.

Korner-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. *Journal of Avian Biology* **41**, 8–17.

Liechti, F., Peter, D., Lardelli, R. & Bruderer, B. (1996) The Alps, an obstacle for nocturnal broad front migration – a survey based on moon-watching. *Journal of Ornithology* **137**, 337–356.

Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W. & Hahn, S. (2012) Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution* **3**, 603–612.

Mead, C. (1983) *Bird Migration*. Newnes Books, Northants.

Moore, F. & Kerlinger, P. (1987) Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* **74**, 47–54.

Moreau, R.E. (1961) Problems of Mediterranean–Saharan migration. *Ibis* **103a**, 373–427.

Nikolaus, G. (1983) An important passerine ringing site near the Sudan Red Sea coast. *Scopus* **7**, 15–18.

Norris, D.R. (2005) Carry-over effects and habitat quality in migratory populations. *Oikos* **109**, 178–186.

Norris, D.R. & Marra, P.P. (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* **109**, 535–547.

Norris, D.R., Wunder, M.B. & Boulet, M. (2006) Perspectives on migratory connectivity. *Ornithological Monographs* **61**, 79–88.

Pasinelli, G., Schaub, M., Häfliger, G., Frey, M., Jakober, H., Müller, M., Stauber, W., Tryjanowski, P., Zollinger, J.-L. & Jenni, L. (2011) Impact of density and environmental factors on population fluctuations in a migratory passerine. *Journal of Animal Ecology* **80**, 225–234.

Pearson, D.J. (1972) The wintering and migration of palaearctic passerines at Kampala, southern Uganda. *Ibis* **114**, 43–60.

Pearson, D.J. & Backhurst, G.C. (1976) The southward migration of palaearctic birds over Ngulia, Kenya. *Ibis* **118**, 78–105.

Perdeck, A.C. (1977) The analysis of ringing data: pitfalls and prospects. *Die Vogelwarte* **29**, 33–44.

Rolshausen, G., Segelbacher, G., Hobson, K.A. & Schaefer, H.M. (2009) Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. *Current Biology* **19**, 2097–2101.

Schaub, M., Jakober, H. & Stauber, W. (2011) Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. *Oecologia* **167**, 445–459.

Siriwardena, G.M., Wernham, C.V. & Baillie, S.R. (2004) Quantifying variation in migratory strategies using ring-recoveries. *Animal Biodiversity and Conservation* **27**, 299–317.

Spaar, R. (1997) Flight strategies of migrating raptors; a comparative study of interspecific variation in flight characteristics. *Ibis* **139**, 523–535.

Strandberg, R., Klaassen, R.H.G. & Thorup, K. (2009) Spatio-temporal distribution of migrating raptors: a comparison of ringing and satellite tracking. *Journal of Avian Biology* **40**, 500–510.

Stutchbury, B.J., Tarof, S.A., Done, T., Gow, E., Kramer, P.M., Tautin, J., Fox, J.W. & Afanasyev, V. (2009) Tracking long-distance songbird migration by using geolocators. *Science* **323**, 896.

Sutherland, W.J. (1998) Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology* **29**, 441–446.

Tøttrup, A.P. & Thorup, K. (2008) Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *Journal of Ornithology* **149**, 161–167.

Tøttrup, A.P., Thorup, K. & Rahbek, C. (2006) Patterns of change in timing of spring migration in North European songbird populations. *Journal of Avian Biology* **37**, 84–92.

Tøttrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Willemoes Kristensen, M., Søgaard Jørgensen, P., Fox, J., Afanasyev, V., Rahbek, C. & Alerstam, T. (2012) The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society Series B: Biological Sciences* **279**, 1008–1016.

Tryjanowski, P. & Yosef, R. (2002) Difference between the spring and autumn migration of the Red-backed Shrike *Lanius collurio*: record from the Eilat stopover (Israel). *Acta Ornithologica* **37**, 85–90.

Tryjanowski, P., Kuzniak, S. & Sparks, T. (2002) Earlier arrival of some farmland migrants in western Poland. *Ibis* **144**, 62–68.

Vaurie, C. (1959) *The birds of the palearctic fauna*. H.F. & G. Witherby, London.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* **17**, 76–83.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (2002) *The Migration Atlas: movements of the birds of Britain and Ireland*. T. & A.D. Poyser, London.

Zehnder, S., Åkesson, S., Liechti, F. & Bruderer, B. (2002) Observation of free-flying nocturnal migrants at Falsterbo: occurrence of reverse flight directions in autumn. *Avian Science* **2**, 103–113.

Zehtindjiev, P., Ilieva, M. & Åkesson, S. (2010) Autumn orientation behaviour of Paddyfield Warblers. *Acrocephalus agricola,* from a recently expanded breeding range on the western Black Sea coast. *Behavioural Processes* **85**, 167–171.

Zink, G. (1973–85) *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel*. Vogelzug-Verlag, Möggingen.

Zink, G. & Bairlein, F. (1995) *Der Zug europäischer Singvögel, Ein Atlas der Wiederfunde beringter Vögel*. Wiesbaden, Aula-Verlag.

APPENDIX

Graphical combination of different data sources to show the timing of migration for the Red-backed Shrike

The following phenological data sets from bird ringing stations were extracted from published sources (Fig i; references in main text):

- median capture date (with 95% confidence interval) for spring and autumn migration at Eilat, Israel, for juveniles, adult males and adult females (Tryjanowski & Yosef 2002)
- spring arrival and autumn departure dates from the Catalonian ornithological information service SIOC (www.sioc.cat), accessed 8 June 2011

- number of birds captured per day at Ngulia Lodge, Tsavo National Park, Kenya (Pearson & Backhurst 1976)
- number of birds captured per day at Kampala, Uganda (Pearson 1972)
- number of birds captured per decade at the Red Sea coast of Sudan (Nikolaus 1983)
- visual observations at a wintering site in the Nylsvley area, South Africa (Bruderer & Bruderer 2008)
- number of birds captured in Mauretania (own data, Swiss Ornithological Institute SOI)
- Strait of Gibraltar: "There are no records of Lesser Grey Shrike [*Lanius minor*] and very few (all autumn) of Red-backed Shrike" (Finlayson 1992)
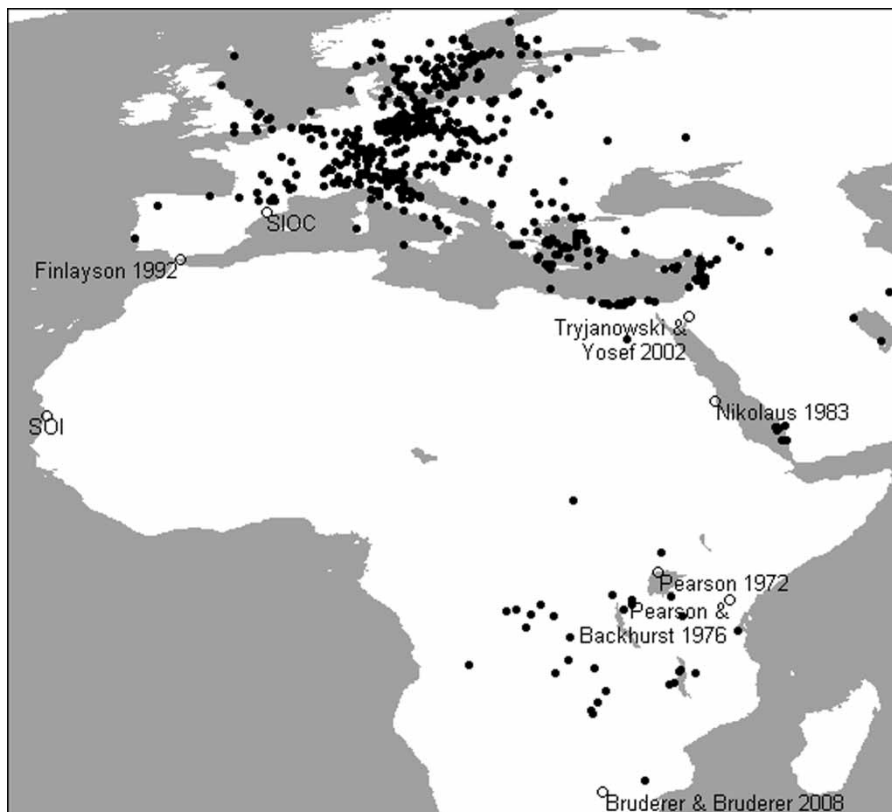

Figure i. Locations (closed symbols) of all 2,447 re-encounters of 1,983 individual Red-backed Shrikes (EURING plus additional records from Zink (1973–85) and from the French and Aranzadi Ringing Schemes). Open symbols indicate locations from which phenological data were available, with sources indicated. SOI = bird captured and ringed at Nouakchott, Mauritania, by the Swiss Ornithological Institute; SIOC = spring arrival and autumn departure dates from the Catalonian ornithological information service.
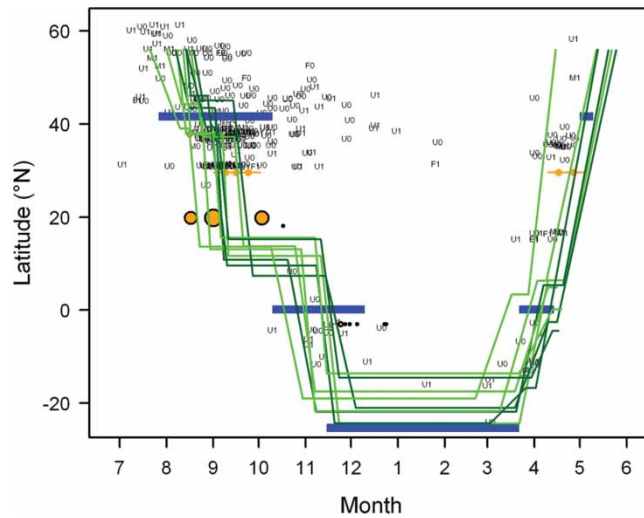
Figure ii. Latitudes of re-encounters of birds during the non-breeding time (1 July – 14 May, n = 302; text codes: 0 = first year, 1 = after first year, M = male, F = female, U = unknown sex) and published phenologies of passage at bird ringing stations. Broad bars connect start and end of spring and autumn migration for Catalonia (SIOC) and Kampala, Uganda (Pearson 1972), as well as arrival and departure in a wintering area in South Africa (Bruderer & Bruderer 2008). Dots with bars indicate median passage times (± standard error) for the different age and sex classes in Eilat (Tryjanowski & Yosef 2002): the age and sex classes are, from left to right, autumn adult males, adult female, juveniles, spring adult males and adult females. Shaded dots of variable sizes give the absolute number of birds caught in Ngulia, Kenya (Pearson & Backhurst 1976) and at the Red Sea coast (Nikolaus 1983). Lines (dark = female, light = male) are tracks of nine adults obtained by geolocators (from Tøttrup *et al* 2012).
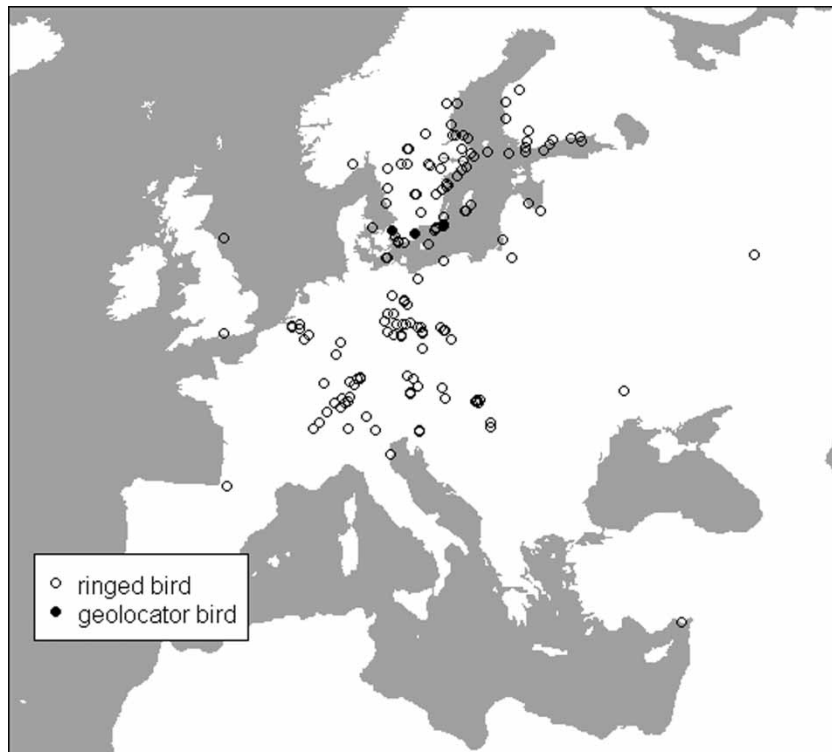

Figure iii. Ringing locations of birds displayed in Fig 3. These birds were ringed on the breeding ground and re-encountered during one of the stationary periods (open symbols) or ringed and tracked by geolocators (closed symbols). The figure shows that the individuals tracked by geolocators originated from within the same general breeding range as the ringed birds analysed in this study.