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ORIGINAL ARTICLE

Annual GPS tracking reveals unexpected wintering area in a long-distance migratory songbird

Lykke Pedersen[1] · Kasper Thorup[1] · Anders P. Tøttrup[1]

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Abstract
Recent technological development has made it possible to pinpoint precise locations of small migratory songbirds throughout their annual cycle, providing the opportunity for improving our understanding of year-round habitat use. Here, we use GPS loggers to map the exact location and habitat use at stationary sites throughout the annual cycle of a long-distance migratory songbird, the Red-backed Shrike *Lanius collurio*. Although the main staging sites confirmed previous findings from light-level geolocation studies, one individual wintered in south-western Chad, an area with only a few historical records of this species. This study highlights opportunities for answering new questions and gaining more knowledge using fine-scale tracking of migratory songbirds.

Keywords GPS pinpoint · Habitat use · Red-backed shrike · Lanius collurio · Migration · Annual cycle

Zusammenfassung
Ganzjahres-GPS Tracking deckte ein bisher unbekanntes Wintergebiet einer langstreckenziehenden Singvogelart auf
Die derzeitigen technologischen Entwicklungen haben es ermöglicht, kleine ziehende Singvogelarten im Verlauf ihres Jahreszyklus präzise lokalisieren zu können. Dies eröffnet die Möglichkeit eines verbesserten Verständnisses zur ganzjährigen Habitatwahl dieser Arten. In der vorliegenden Studie nutzten wir GPS-Logger für die exakte Lokalisierung und Habitatwahl von Neuntötern *Lanius collurio*, einer langstreckenziehenden Singvogelart in den im Jahresverlauf genutzten Gebieten. Obwohl die Hauptrastgebiete dieser Art bereits durch frühere Ergebnisse aus sogenannten Hell-Dunkel-Geolokationsstudien bestätigt wurden, überwinterte ein Individuum im südwestlichen Tschad, in einem Gebiet mit nur einzelnen historischen Nachweisen dieser Art. Die Studie erlangt weitere Kenntnisse zur ganzjährigen Habitatwahl ziehender Singvögel durch detaillierte Ortungsmethoden und stellt die Möglichkeiten zur Beantwortung neuer Fragen heraus.

Introduction

The miniaturization of light-level geolocators has revolutionized our understanding of songbird migration throughout the annual cycle (McKinnon and Love 2018). However, due to the coarse spatial resolution of light-level geolocator data (~50–200 km, Fudickar et al. 2012), an evaluation of the specific sites and habitats encountered by individuals during their migration cycle has previously been unattainable.

Recently, the use of GPS loggers has allowed for identifying the location of individual migratory songbirds across the annual cycle (Hallworth and Marra 2015; Siegel et al. 2016). This technology enables us to pinpoint the location of the individual bird at an accuracy of less than 10 meters at any point in time during the annual cycle. Thus, it provides the opportunity to validate positions of staging sites obtained by

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✉ Lykke Pedersen
lypedersen@snm.ku.dk

✉ Anders P. Tøttrup
aptottrup@snm.ku.dk

[1] Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

light-level geolocators and for exploring the specific habitats that birds are experiencing outside their breeding range (Hallworth and Marra 2015; Siegel et al. 2016; Fraser et al. 2017).

The Red-backed Shrike, *Lanius collurio* is a long-distance migratory songbird that breeds across the Palearctic and spends the non-breeding season in southern Africa. Recent studies using light-level geolocators have identified the main staging sites and timing of migration for individual Red-backed Shrikes in the European-Afrotropical migration system (Tøttrup et al. 2012, 2017).

In this study, we use GPS loggers to map the main staging sites and non-breeding areas and describe the habitat encountered by Red-backed Shrikes at these sites throughout the annual cycle. We discuss our findings in relation to previous light-level geolocator studies.

Methods

During the breeding season (May–July) 2015 and 2016 we deployed 21 PinPoint-8 archival GPS loggers (1.1 g, Biotrack Ltd.) on Red-backed Shrikes in Gribskov forest, Denmark (55.98°N, 12.33°E). In the following years, four birds (two males and two females) returned with the loggers (return rate: 20%). The return rate is similar to a control group (27% $n = 15$) and corresponds to return rates from light-level geolocator tracking studies (Tøttrup et al. 2012). At tag deployment birds weighed 25–31.5 g (mean: 28, SD: 1.87). Thus, the logger represented a maximum of 4.4% of the body mass. We retrieved loggers from three individuals (two females and one male). One tag had failed, resulting in data for two females.

The loggers record the location of birds at a pre-programmed schedule with an accuracy of up to ~ 10 m, depending on the number of satellites available at the given site and time. Considering an annual schedule with discrete recordings, an estimated 10 positions can be expected within the lifetime of the battery. We programmed the logger to record two locations from stationary periods, based on geolocator trackings (Tøttrup et al. 2012, Online Resource 1), and assumed that the bird would be staging if no or little movement (< 1 km) had occurred between the two consecutive fixes at each site. The tags recorded 9 and 11 positions for the two individuals, respectively. The number of satellites ranged from 4 to 10 (median: 7) and Dilution of Precision (DOP, a measure of the accuracy of positions) ranged from 0.6 to 13.8 (mean: 2.29, SD: 2.98), a low value indicating a higher probability of accuracy (Table 1).

To evaluate whether pinpointed staging areas deviated from the expected general area obtained from light-level geolocators, we calculated the nearest neighbour great circle

Table 1 Locations with precision (number of satellites and DOP) for the two individual Red-backed Shrikes throughout the annual cycle

Id	Date	Site	Longitude	Latitude	DOP	Satellites	Distance
88	2015-08-31	Turkey	29.2601681	38.8959985	13.8	4	–
88	2015-09-03	Turkey	29.2609574	38.8960839	1.2	7	69 m
88	2015-10-06	Sudan	24.1315613	13.0323497	1	6	2910 km
88	2015-10-09	Sudan	24.1315165	13.0322359	0.8	9	13 m
88	2015-12-15	Botswana 1	21.6149975	– 18.7501902	0.8	10	3526 km
88	2016-02-15	Botswana 2	21.2497027	– 19.4408425	5.6	5	86 km
88	2016-04-14	Migration	42.8759256	9.0641490	0.8	8	3945 km
88	2016-04-17	Migration	42.5810326	9.0873545	4	7	33 km
88	2016-04-20	Migration	42.5952107	16.0210648	2	6	767 km
310	2015-08-31	Migration	26.2680137	41.3690850	3	4	–
310	2015-09-03	Migration	27.3935856	38.7523302	1.4	5	306 km
310	2015-10-06	Sudan	23.6090039	14.7142667	1.2	8	2689 km
310	2015-10-09	Sudan	23.6090052	14.7141121	1	7	17 m
310	2015-12-15	Chad	14.9095361	9.8053774	1.4	7	1091 km
310	2016-02-15	Chad	14.9091402	9.8062467	1	8	106 m
310	2016-04-14	Migration	38.6269148	0.3803672	1.4	7	2826 km
310	2016-04-17	Kenya	38.8506831	0.8529256	2.4	4	58 km
310	2016-04-20	Kenya	38.8532539	0.8514114	0.6	10	332 m
310	2016-04-23	Migration	40.4063706	2.2091984	1.6	5	229 km
310	2016-04-26	Migration	43.2244046	6.1751003	0.8	7	539 km

All positions were recorded at 06:00 AM GMT. Distance is measured from previous position for each individual distances for all individual average positions at each site, using the *distm* function in the R-package *geosphere* version 1.5-5 (Hijmans 2016). We then used Tukey's rule of quartiles to identify outlying positions (interquartile range, IQR*1.5). In addition, we used a one-tailed Grubbs' test for single outliers from the R-package *outlier* version 0.14 (Komsta 2011) to test whether the longitude of an identified staging site in southern Europe could be considered an outlier.

Distances between consecutive pinpoint positions for each individual were calculated as great circle distances using the function *distVincentyEllipsoid* in the R-package *geosphere* version 1.5-5 (Hijmans 2016). We extracted information on elevation, habitat type and local NDVI from all pinpointed staging sites and non-breeding areas (Online Resource 1). All analyses were conducted in the statistical software R 3.4.2 (R Core Team 2017).

Results

Recorded staging sites and non-breeding areas throughout the annual cycle of Red-backed Shrikes generally overlapped with the overall areas estimated by light-level geolocators. Additionally, some positions were logged while the birds were on migration, confirming the general migration route (Fig. 1, Table 1). Surprisingly, one female shrike (id: 310) showed an unexpected non-breeding area strategy by spending the second part of the non-breeding season in south-western Chad, Central Africa (Fig. 1). This was confirmed by two high-quality positions taken on the 15 December and 15 February, respectively, which were located 106 meters apart.

During autumn migration one individual was recorded at a staging site in Turkey (id: 88). This staging site was located further East than expected, but was still within the overall range of longitudinal light-level geolocator estimates (Grubbs' test: $G = 1.77$, $P = 1$, Fig. 1). The second individual (id: 310) likewise seemed to migrate east via Turkey. Both individuals then migrated to south-western Sudan, to spend the first part of the non-breeding season around 200 kilometers apart. The second non-breeding area, similar to light-level geolocator tracking data, was identified for one individual (id: 88) in north-western Botswana, although the two positions for this individual in December and February, respectively, were located 86 kilometers apart. During the spring migration route across the Arabian Peninsula, a staging site was mapped to northern Kenya (id: 310), within the expected range estimated from light-level geolocator data (Fig. 1).

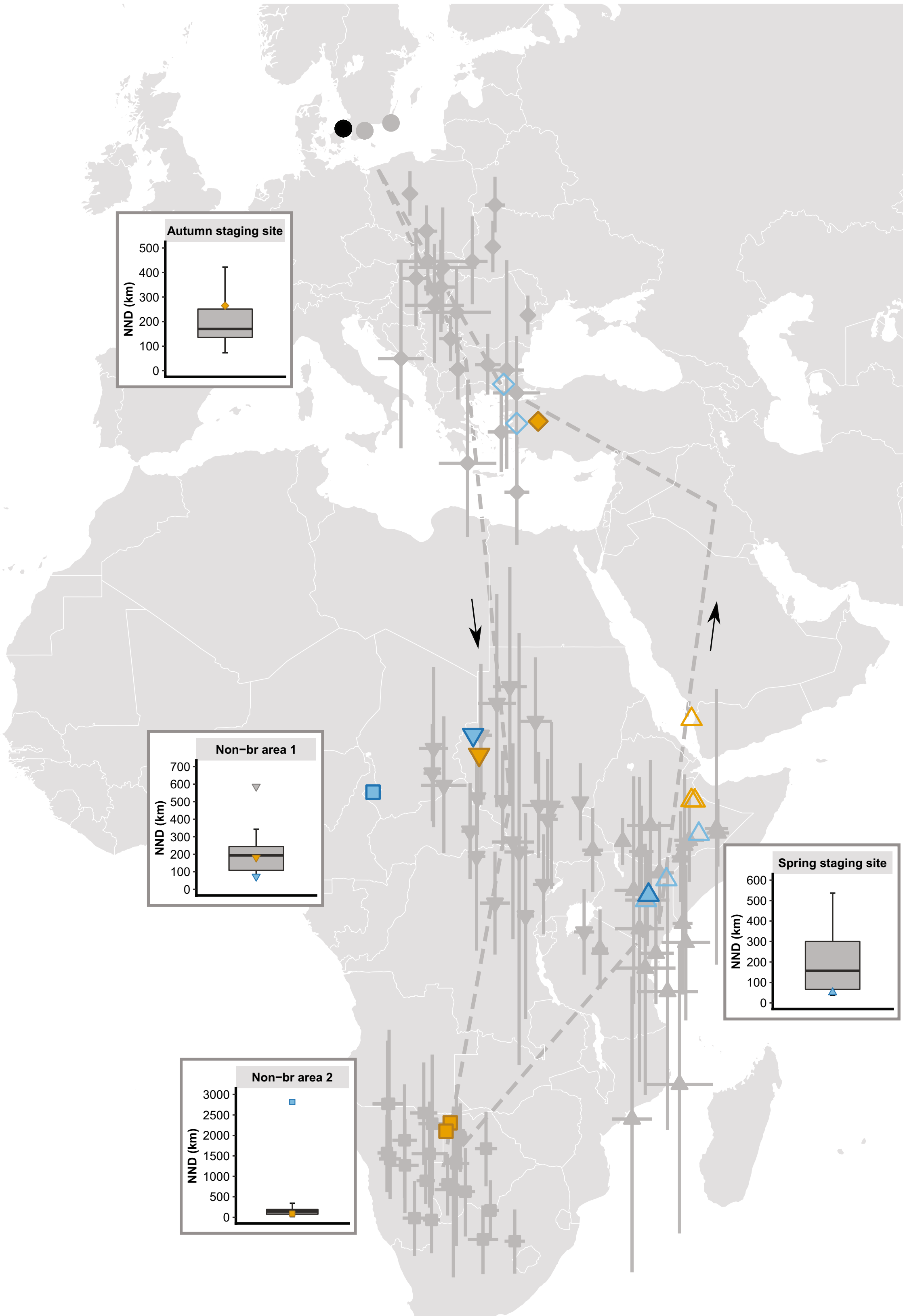
While the southern European staging site was located in an agricultural landscape in Turkey, all positions of staging sites within Africa fell within the same overall landcover classes: 'Shrubland and Grassland' and 'Desert and Semi-Desert' covering a wide altitudinal range (322–1422 m a.s.l, Table 2). Local NDVI decreased over the period when the birds were in Sudan while it increased during the main non-breeding period in Botswana (Online Resource 2).

Discussion

Here, we mapped the precise location of staging sites throughout the annual cycle of two red-backed shrikes. We show that the individuals spent the non-breeding season in overall similar habitat types, although one individual spent the main part of the non-breeding season in south-western Chad, around 3000 km north of the established wintering grounds of Red-backed Shrikes (Tøttrup et al. 2012; BirdLife International 2016).

Although distribution maps are often found to be incomplete, the finding that one individual spent the non-breeding season in Chad was surprising, as only a few observations of Red-backed Shrikes have been recorded from outside of the known non-breeding range during November to March (Fig. 2, Online Resource 3). The unexpected behaviour could represent a different phenotype or an exploratory search for an alternative non-breeding area. An inherent limitation of all tags currently available for tracking migration in songbirds is that individuals need to be recaptured in order to receive the data. Thus, only migration of successful individuals that manage to return to the breeding area is recorded. Given the dynamic nature of migration (Alerstam et al. 2003), one could speculate that such unexpected behaviour is not uncommon in migratory songbirds, but may in many cases be unsuccessful such as described for juveniles (Cresswell 2014). We found no indication that the positions were caused by a technical error of the logger, as the number of satellites was high and DOP values low for both positions (Table 1). Furthermore, an estimated altitude from the tag data corresponded to the expected value of the area (Biotrack Ltd, G. Fowler *pers. comm.*). Due to the coarse temporal resolution of our data, we cannot rule out that substantial movements have occurred between the two observations in December and February. Likewise, the individual may have visited the established non-breeding area of Red-backed Shrikes in southern Africa before taking off on spring migration.

Large-scale itinerant movement of individuals within the non-breeding season has been documented for many


Autumn staging site
NND (km)
500
400
300
200
100
0
Non−br area 1
NND (km)
700
600
500
400
300
200
100
0
Spring staging site
NND (km)
600
500
400
300
200
100
0
Non−br area 2
NND (km)
3000
2500
2000
1500
1000
500
0

◂**Fig. 1** Positions of Red-backed Shrikes throughout the annual cycle. Yellow (id: 88) and blue (id: 310) symbols represent the two females tracked with GPS loggers and grey symbols show the main staging sites (mean ± SD) of all individuals (males and females) tracked with light-level geolocators from the same breeding area, including two additional sites in southern Sweden. Symbols represent staging sites (circle: breeding area, diamonds: autumn staging area, inverted pyramids: non-breeding area 1, squares: non-breeding area 2, pyramids: spring staging area). Open symbols denote positions recorded while the individual was on migration. Dashed lines illustrate overall migration route of the population based on light-level geolocator data and black arrows indicate direction. Inserted boxplots show the Nearest Neighbor Distance (NND) of all points in kilometers and highlight the distance of the pinpointed positions in relation to distances between the light-level geolocator positions (color figure online)

migratory songbirds using geolocators (Mckinnon and Love 2018). Here, the small-scale movements of one individual (ca. 80 km) during the main non-breeding period in Botswana suggest a local change in non-breeding area. This kind of local itinerant movement may be more general, as it was also shown for a red-backed shrike using activity loggers (Bäckman et al. 2017) and was recently found in an American songbird, the Black-headed Grosbeak (Siegel et al. 2016). The finding highlights the advantage of the GPS tracking technology, as such fine-scale movements cannot be discerned from light-level geolocator data. The movements could be due to degrading habitat conditions, exploration of more suitable areas or competition for resources. Here, we find no obvious differences in the habitat type between the two locations. Likewise, both locations are experiencing a general increase in NDVI over the non-breeding season. Overall, this indicates that local studies of behaviour of migratory birds at the non-breeding grounds are important, as movements may be related to factors that cannot be detected by remote sensing data.

Continuous advancement in tracking technology has made it possible to track precise locations during the annual

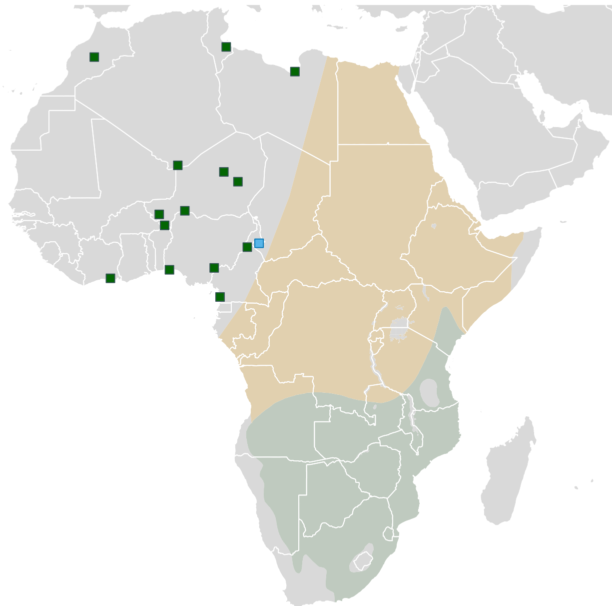


Fig. 2 Observations of Red-backed Shrikes outside of the species' known passage and non-breeding range in November to March (green squares) as well as the non-breeding area position (December and February) of the individual tracked with a GPSlogger (id: 310, blue square). Orange and green polygons represent Birdlife International distribution maps of passage and non-breeding range, respectively (BirdLife International 2016) (color figure online)

cycle of migratory songbirds. With ongoing developments, we can expect tracking at even finer temporal scales in the nearby future (Pennisi 2011; McKinnon and Love 2018). In combination with local studies at the non-breeding areas and at staging sites, our understanding of habitat preferences and the ecology of these birds outside their breeding range will increase, directing applied conservation efforts of migratory birds. Here, we provide the first insight into the habitat use

Table 2 Landcover classes and elevation of identified staging sites throughout the annual cycle of two red-backed shrikes

Id	Site	Landcover class	Landcover sub-class	Elevation (m a.s.l)
88	Turkey	Non-irrigated arable land		903
88	Sudan	Shrubland and grassland	Afromontane grassland	1422
310	Sudan	Desert and semi-desert	North Sahel herbaceous steppe	895
88	Botswana 1	Shrubland and grassland	Baikiaea woodland and savanna	1019
88	Botswana 2	Shrubland and grassland	Baikiaea woodland and savanna	1066
310	Chad	Shrubland and grassland	Sudano-Sahelian treed savanna	346
310	Kenya	Desert and semi-desert	Eastern African bushland and thicket	334

of Red-backed Shrikes throughout the annual cycle, demonstrating future research opportunities.

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