

Local weather, food resources and breeding stage influence Thrush Nightingale movement

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Insectivorous migrants breeding at northern latitudes often time the breeding period with the seasonal peak of food resources. Whether this general pattern transfers to movement behaviour during the breeding season requires detailed study from a local perspective. We investigated fine-scale environmental correlates of movements by six actively-breeding adult Thrush Nightingales (*Luscinia luscinia*) at a breeding site in Denmark, using radio tracking and multiple regression models. Overall, the chick-rearing period coincided with the peak of vegetation greenness at the site. Adults flew further from nesting areas during stable weather and as vegetation greenness decreased. Adults were more active at higher environmental temperatures and when fledglings were older but still dependent on adults. These changes in local movements likely reflect adjustments to chick developmental needs and to specific local environmental conditions, including resource availability.



1. Introduction

Long-distance bird migrants respond broadly to seasonality of weather and food resources (MacArthur 1959, Somville *et al.* 2015). Some insectivorous long-distance migrants attune their annual movement to coincide with surplus food resources throughout the annual cycle, as measured through vegetation greenness (Thorup *et al.* 2017). However, to assess the specific role of environmental cues in shaping timing of annual events, it is important to establish the link with behaviour at the local scale.

Studies of the environment's influence on timing of breeding and breeding performance in insectivorous songbirds suggest that breeding takes place during peaks of food resources (van Noord-

wijk *et al.* 1995, Both *et al.* 2005, Studds & Marra 2011, Emmenegger *et al.* 2014). For example, temperature and food availability enhance breeding performance by increasing chick growth (e.g., McCarty & Winkler 1999). However, research has shown little attention to how local movements of breeding insectivorous birds are affected by short-term as well as seasonal resource availability. For example, radio tracking studies have mainly looked into habitat use and selection (Streby & Andersen 2013, Dittmar *et al.* 2014, Jirinec *et al.* 2016), territory and mate selection (Amrhein *et al.* 2004, Roth *et al.* 2009), or fitness consequences (Grüebler & Naef-Daenzer 2008).

Here, we study movements of Thrush Nightingales (*Luscinia luscinia*) during chick rearing in relation to local environmental conditions at a

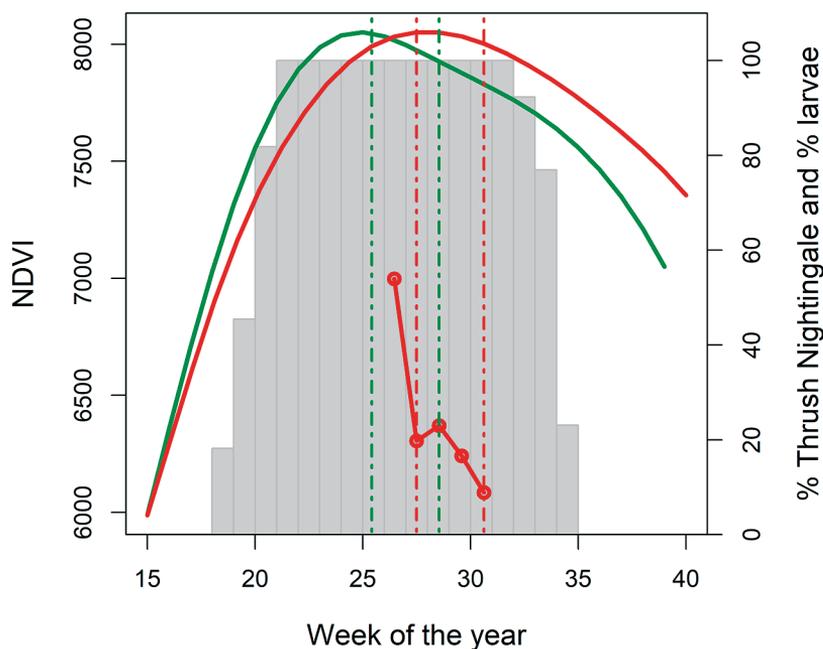


Fig. 1. Normalized Difference Vegetation Index (NDVI) in 2014 (green curve), in 2015 (red curve), percentage of larvae sampled during five weeks in 2015 (red line combined with dots) and percentage of Thrush Nightingale present in the area (bar plot; source from geolocator data, Thorup *et al.* 2017) with week of the year. The dotted lines represent the tracking periods of eight actively breeding Thrush Nightingales in 2014 (green colour) and 2015 (red colour) that were carried out right after the NDVI peak in each season.

Danish breeding site. Thrush Nightingales are insectivorous, long-distance migrants that breed from northeastern Europe to part of central Asia and winter in southeastern Africa (Collar 2017). Geolocator data show that the main breeding period at the same study site in Denmark is from the end of May to the beginning of August (Fig. 1, using geolocator data from Thorup *et al.* 2017). Thrush Nightingales are very secretive, generally requiring labour-intensive tracking to sample accurate locations with limited bias. Thus, movement data from the breeding season are scarce and difficult to obtain.

We used radio tracking to estimate positions of eight individuals of which only six provided enough data for analyses. Using two movement variables derived from radio tracking – activity and distance to home-range centre – we investigate (1) whether Thrush Nightingales time chick rearing with the peak of food resources and, (2) how weather conditions and chick development may affect local movement during the course of the breeding season. We hypothesise that birds adjust chick rearing – brooding and early fledgling stages – to the peak of food resources to optimise chick survival. Further, we expect that local movement is related to weather and chick development, such that there is more movement (more activity

and longer flights) during warmer and stable weather, coinciding with high availability of insects. Finally, we expect to find an influence of developmental stage of the chicks on the adult movement patterns, with increasing levels of activity when chicks are older but still dependent, and with longer flights when the chicks become independent.

2. Material and methods

2.1. Field work

We fitted eight (seven females and one male) adult Thrush Nightingales with 0.4 g VHF radio transmitters (PicoPip Ag379, Biotrack Ltd.) at a breeding site in Copenhagen (55° 39' 18.72" N, 12° 34' 43.14" E) where two females were tagged in June 2014 and the remaining six birds were tagged in June–July 2015. The total tracking period was week 25–28 in 2014, and week 27–30 in 2015. We used $N = 6$ birds in the analyses as one female showed very short-time parental care (one day) and another failed to breed. The tagged male was the mate of one of the tagged females. The site was an urban green-area with patches of thick shrubs and trees distributed among semi-open grassland

and water areas. Nightingales mainly used very dense tall shrubs (≤ 3 m height *Crataegus laevigata* and *Salix* sp.) in a mean home range area of 1.7 ha ($SD = 2.2$ ha, $N = 6$).

Individuals displaying breeding behaviour were caught with mist nets, using playback at breeding territories. Tags were adhered on a bare skin patch of the birds' backs using mild glue after cutting off some back feathers. A small piece of fabric was sewn to the tags to facilitate adherence. This system allowed radio tracking of individuals for a three-week period (mean = 18 days, $SD = 2$, $N = 5$, excluding one female that supposedly suffered predation after being tracked for 8 days), after which tags would fall off. Positions were collected with hand-held Yagi antennae (on 151 MHz) and Sika receivers (Biotrack Ltd.) by triangulation and with a GPS. We tracked each bird approximately six days per week (mean tracking time = 12 hours/bird, $SD = 4$, $N = 6$) mainly during morning hours (6–12 h). We collected positions separated by at least one hour to calculate home ranges and recorded positions approximately every five minutes to estimate bird activity.

It was not possible to find the exact position of the nests. Thrush Nightingales breed in very dense vegetation and nests are extremely difficult to locate without extensive disturbance. We estimated the location of the nests by observing feeding behaviour (e.g., adults carrying food and feeding fledglings in the same area). Thus, we determined that each bird's home range had its own nesting-site. Three-level chick developmental-stage (incubating or brooding, pre-fledgling and fledgling) was inferred from the brood patch index in females at catching and from behavioural observations of adults and young, and counting the days that young require to develop (Cramp 1992). From these observations, we estimated that all the tagged birds were actively breeding, and that at tagging, one of them was possibly at the last stage of incubation (a female of 2014) and the rest were brooding or already with recently fledged young. Due to the difficulty of assigning the transition from pre-fledgling to fledgling stage, the transition time was somewhat uncertain.

Relative abundance of larvae was estimated by sampling larvae of *Lepidoptera* and *Coleoptera* orders and was used as a direct measure of chick food availability. Larvae sampling was done in

four transects at four breeding sites, once per week, during weeks 26–30 of the year 2015. The sampled transects were representative of the breeding-site vegetation and contained similar vegetation type per breeding site: a proportionate mix of *Crataegus* and *Salix* sp., shaded or exposed to sunlight. Larvae sampling was carried out by beating the vegetation up to 2.5 m from the ground, collecting the falling larvae with 1 m² beating sheet and counting number of items.

2.2. Data processing

To investigate local correlates of nightingale movement we defined two measures as response variables: activity and distance to home-range centre. We defined activity as individual flight distance per radio-tracking hour, and used it as a measure of the activity detected at a finer time-scale ($N = 64$, after excluding $NAs = 6$, of which 5 were due to data points with unknown chick developmental-stage and 1 with unknown stable/showers variable).

We calculated the activity by adding up the distances in meters between consecutive radio-tracking positions that were collected within one radio-tracking hour. We defined distance to home-range centre as the distance in meters from the Centre of Mass of each bird's home range to independent positions (positions separated by at least one hour: mean = 28, $SD = 14$, $N = 6$ birds), and we used it as a measure of how far birds flew from the nesting area ($N = 134$). Ideally, we would have used the nests to measure this distance, but finding Thrush Nightingale nests was not possible without causing disturbance. To obtain the Centres of Mass we calculated the home ranges (using the 95% minimum convex polygons; Fig. 2). We visualised the positions through mapping the radio-tracking data on Google Earth images (<http://www.google.com/earth/download/ge/>).

We used information about the environment as well as developmental stage of the chicks and time as explanatory variables. Food resource levels were measured indirectly with a vegetation index (Normalized Difference Vegetation Index, *NDVI*; Sanz *et al.* 2003, Pettorelli *et al.* 2005), in addition to the direct measure of food resources obtained through larvae sampling. *NDVI* was processed

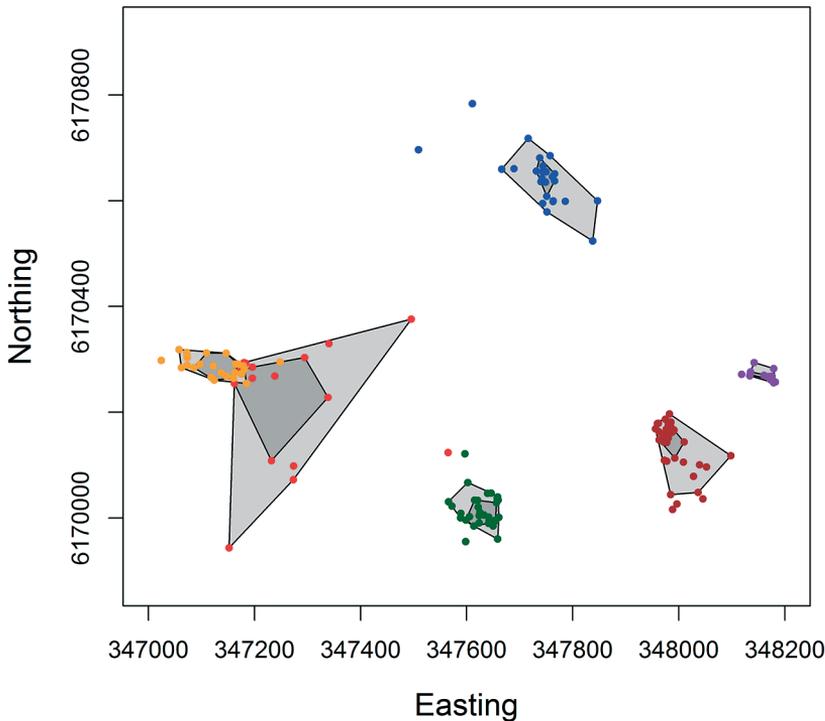


Fig. 2. 95% (light grey shadings) and 50% (dark grey shadings) minimum convex polygon per individual Thrush Nightingale ($N = 6$) with all independent positions identified as dots (radio-tracking positions separated by more than one hour). Brown and purple dots correspond to the two birds tracked in 2014, and orange, red, green and blue dots to the four birds tracked in 2015. Of the radio-tracked pair, male and female positions are represented with orange and red dots, respectively.

with data from the University of Natural Resources and Life Sciences, Vienna (BOKU, <http://ivfl-info.boku.ac.at/index.php/eo-data-processing/dataprocess-global>). These data corresponded to the total area of 11.5 ha used by the birds and were collected as weekly values at 250 m resolution. Weather data were obtained from Meteorological Aerodrome Reports (METAR) of a station 6 km from the site. These data consisted of temperature in centigrade degrees, relative humidity in percentage, and wind speed in km/h, and were collected with resolution every 20 minutes and every week.

Radio-tracking data points were assigned weather conditions from the nearest observation. Weekly means of weather data were used for additional analyses at a comparable resolution with the weekly sampling of *NDVI* and larvae. A measure of rain was added *in situ* for every position with two categories: stable (including no rain and drizzle) and showers. To account for other temporal dynamics, as chick development stage, we included day or week of the year and year as nuisance variables. We included bird identity (bird *ID*) as grouping variable to account for individual behavioural patterns and home ranges.

2.3. Statistical analyses

To investigate the associative effect of chick development and environment on local movement we used multiple linear regressions with either activity or distance to home-range centre as response variables. We used box-cox transformation with an exponent of 0.4 for activity and log transformation for distance to home-range centre. This improved residual plots of full models and thus normality assumptions. We ran model-averaging analysis with all models with combinations of non-correlated explanatory variables (256 models per response variable). To obtain the relative importance of each variable we used Akaike weights, Σw_i , calculated with Akaike Information Criterion corrected for small sample size (*AICc*; Burnham & Anderson 2002). As we were especially interested in investigating the association between chick development and movement, we ran a separate model-averaging analysis with developmental stage alone as the time variable. To assess the association with larvae availability we performed model averaging with the data set of 2015 (with $N = 48$ for activity and $N = 98$ for distance to home-range centre).

Table 1. Summary of results after model averaging showing the effects of bird identity (*ID*), environmental factors, chick development and other temporal variables on activity ($N = 64$) and distance to home-range centre ($N = 134$) of breeding Thrush Nightingales ($N = 6$). For each variable, model averaged parameter estimates, standard errors (*SE*), confidence intervals (*CI*: 2.5%, 97.5%) and relative importance (Akaike weights, Σwi) are shown (conditional average method). The reference categories are: *ID* – individual “151.024”; developmental stage – “Incubating or Brooding”; year – 2014, and rain – “Stable”. Highest Σwi values are shown in bold.

Parameter	Activity					Distance to home-range centre				
	Estimate	SE	CI 2.5%	CI 97.5%	Σwi	Estimate	SE	CI 2.5%	CI 97.5%	Σwi
Intercept	7.10	5.49	-3.75	17.94		6.05	1.81	2.49	9.62	
<i>ID</i> 151.063	-1.53	1.47	-4.49	1.42	0.99	-1.18	0.20	-1.59	-0.78	1.00
<i>ID</i> 151.149	-4.55	1.51	-7.58	-1.52	0.99	-1.31	0.20	-1.71	-0.90	1.00
<i>ID</i> 151.494	-1.87	1.52	-4.90	1.17	0.99	-1.27	0.22	-1.70	-0.84	1.00
<i>ID</i> FN1	1.27	3.79	-6.23	8.77	0.99	-2.11	0.94	-3.95	-0.26	1.00
<i>ID</i> FN2	-2.73	3.71	-10.09	4.63	0.99	-2.34	0.92	-4.16	-0.52	1.00
Temperature	5.43	1.98	1.47	9.39	0.94	0.15	0.34	-0.53	0.83	0.34
Pre-fledgling	3.10	1.55	-0.01	6.20	0.70	0.11	0.24	-0.36	0.59	0.05
Fledgling	5.67	2.07	1.52	9.82	0.70	-0.01	0.37	-0.75	0.73	0.05
Year	-2.09	5.57	-13.06	8.88	0.50	1.50	1.28	-1.01	4.01	0.50
<i>NDVI</i>	-2.39	4.47	-11.27	6.48	0.24	-1.78	1.38	-4.49	0.94	0.58
Showers	-0.29	1.14	-2.58	2.01	0.20	-0.28	0.16	-0.59	0.03	0.62
Wind	-0.24	1.82	-3.89	3.41	0.19	-0.10	0.20	-0.50	0.30	0.27
Week	-1.73	5.20	-12.03	8.57	0.06	-0.77	1.12	-2.98	1.44	0.29
Day	-1.78	4.12	-9.96	6.41	0.06	-0.48	0.78	-2.02	1.05	0.24

We used R 3.3.2 (R Development Core Team 2011) and several R packages for all analyses, including packages *sigloc* for bird position estimate, *raster* and *MODIS* for *NDVI* data processing, *adehabitatHR* for home range calculation, *SDMTools* for Centre of Mass calculation, *stats* for linear models and *MuMIn* for model averaging.

3. Results

Based on radio-tracking movements and observations of tracked Thrush Nightingales and their young throughout the tracking period, young likely hatched approximately a week before the peak of vegetation greenness (Fig. 1). Radio-tracked Thrush Nightingales reared their young when the vegetation greenness peaked and started to decline, and larvae abundance had a declining trend during the sampling period (Fig. 1). Nightingale movement and home-range size varied among individuals (Figs. 2–4), such that the bird identity, among all variables, had the strongest effect on movement ($\Sigma wi = 1$; Table 1).

Despite individual differences, we found support for associations between temperature, devel-

opmental stage and activity, and between rain and vegetation greenness and distance to home-range centre (Table 1). Parents were more active during the last two developmental stages than in the earliest stage ($\Sigma wi = 0.70$) and with increasing temperature ($\Sigma wi = 0.94$, Table 1, Fig. 3). Longer distance to the home-range centre was associated with lower vegetation greenness ($\Sigma wi = 0.58$) and stable weather ($\Sigma wi = 0.62$; Table 1, Fig. 4).

In the analysis on the association between developmental stage and movement we found no support for an effect on distance to home-range centre, but did find support for an association with activity (Table 1). There was a similar relative importance for larvae and vegetation greenness using the larvae data set, for both activity ($\Sigma wi = 0.2$) and distance to home-range centre ($\Sigma wi = 0.3$) indicating equivalent support for an effect on movement. All analyses showed some support for a year effect ($\Sigma wi = 0.5$; Table 1, Figs. 3 and 4).

4. Discussion

Our radio tracking of Thrush Nightingales indicated some associations between vegetation

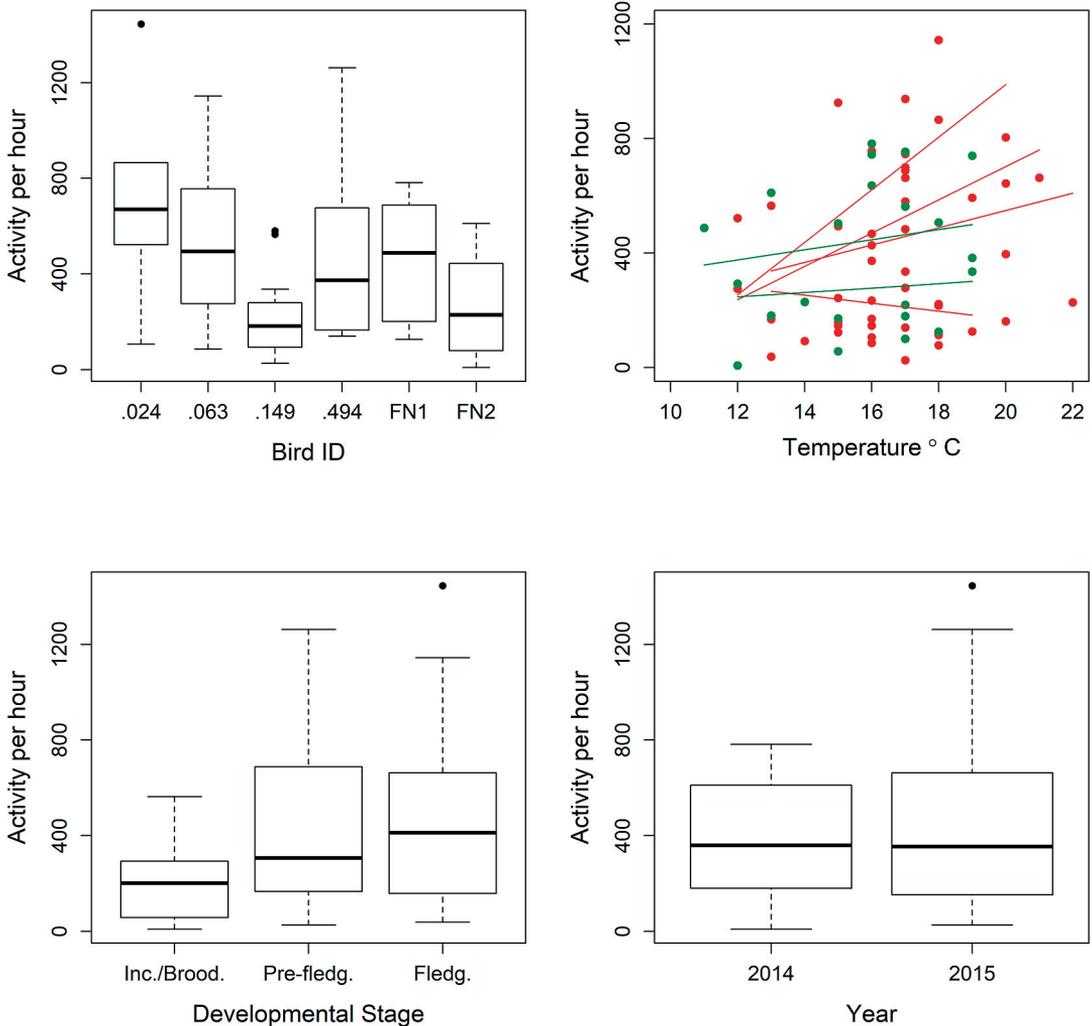


Fig. 3. Activity change (measured as flight distance in meters per radio-tracking hour) with bird identity (bird ID which male is .063; *Adjusted R*² = 0.20, *P* = 0.003), temperature (*Adjusted R*² = 0.10, *P* = 0.014; 2014 and 2015 values are represented in green and red colours, respectively; lines represent each bird ID with the colour of their tracking year), developmental stage (*Adjusted R*² = 0.03, *P* = 0.137) and year (*Adjusted R*² = -0.01, *P* = 0.56). Category sample-size (and overlap) is, for Incubating or Brooding stage two bird IDs out of six (overlap with Pre-fledgling, two; with Fledgling, zero); for Pre-fledgling, four bird IDs out of six (overlap with Incubating or Brooding, two; with Fledgling, two) and for Fledgling, four bird IDs out of 6 (overlap with Incubating or Brooding, zero; with Pre-fledgling, two). The sampling effort was during four weeks in 2014 and 2015, respectively, with week range = 25–28 in 2014, and 27–30 in 2015.

greenness, weather and chick development with the two measures of breeding movement despite individual variation in these two measures. Thrush Nightingales flew longer distances as vegetation greenness decreased with the advancement of the breeding season. In terms of weather, activity increased with temperature, and distance to home-range centre increased with more stable weather.

Finally, parents were more active when fledglings were older.

The uncertainty in exact nesting positions and breeding status were likely a main contributor to the noise in our data and thus potentially masking more direct causal relationships between stages and behaviour. Furthermore, our relatively small sample size necessarily restricts general inference

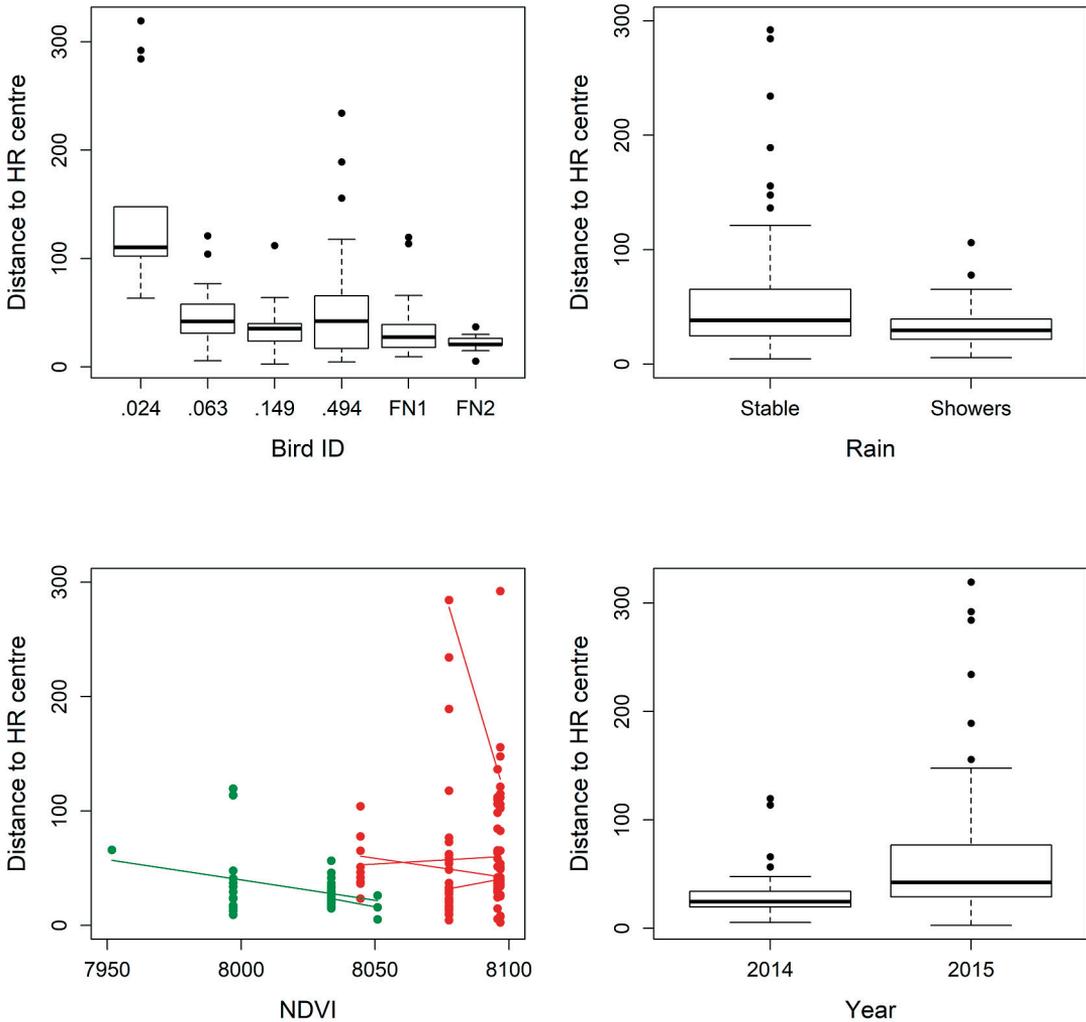


Fig. 4. Distance to home-range (HR) centre in meters with bird identity (bird ID which male is .063; *Adjusted R2* = 0.42, *P* < 0.001), rain (*Adjusted R2* = 0.02, *P* = 0.047; category Stable represents dry or drizzle), weekly Normalized Difference Vegetation Index (*NDVI*; *Adjusted R2* = 0.10, *P* = 0.003; 2014 and 2015 values are represented with green and red colours, respectively; lines represent each bird ID with the colour of their tracking year) and year (*Adjusted R2* = 0.10, *P* = 0.001). The sampling effort was during four weeks in 2014 and 2015, respectively, with week range = 25–28 in 2014, and 27–30 in 2015.

but, nevertheless, provides valuable and difficult-to-attain indications on the role of different environmental factors and chick development on migrants' local movement during a specific period of the annual cycle.

Chick rearing at this site coincided with the local peak of vegetation greenness, which gradually declined during the breeding season together with the relative abundance of larvae. This suggests that potentially the global-resource tracking pattern shown in Thorup *et al.* (2017) was traced also to

the local scale during the breeding season at this site. We also found some support for an association between vegetation greenness and local movements as distance to home-range centre increased with decreasing vegetation greenness for the tracked birds. This association suggests that at least some breeding nightingales may be forced to undertake longer flights to find food as the season advances. At the same time, adults may be more capable of flying longer distances to find local resource peaks as fledglings become more inde-

pendent, possibly moving with them in the habitat. The idea that juvenile Thrush Nightingales would be capable of moving to habitat patches with more food resources is supported by analogous radio-tracking data of independent juvenile Swainson's Thrushes (*Catharus ustulatus*, White *et al.* 2005) and Black-capped Vireos (*Vireo atricapilla*, Dittmar *et al.* 2014).

Increasing movements during good weather conditions, such as higher temperature and no rain, can likely be linked to food availability. For example, higher temperatures after summer rains trigger arthropod productivity (Brust *et al.* 2009, Jarošik *et al.* 2011) and birds could then feed more actively, taking advantage of higher food availability. Further, fledgling growth and survival in swallows (*Tachycineta bicolor*) suggest strong effects of weather conditions through the influence on food abundance (McCarty & Winkler 1999, Gruebler & Naef-Daenzer 2008). Thus, if spells of rain and low temperature are short, birds may be able to optimise their energy expenditure through low activity during these spells. Taken together, this suggests that feeding activity of insectivores could be positively correlated with higher temperature and food availability.

Developmental stage was associated with activity but not with distance to home-range centre in our data. The low relative importance obtained in the distance to home-range centre analysis could be because *NDVI* and weather stability had more influence on this kind of movement. It is certainly possible that distance to home-range centres did not reflect well enough how far birds flew from the nesting areas during chick development, as home ranges may change during the season. Ideally, one would use nest sites instead of home-range centres but searching for nests cause much disturbance to the birds. In addition, assigning the two last developmental stages (pre-fledgling and fledgling stages) was difficult and somewhat uncertain. Nevertheless, the positive effect on activity of the tracked birds could be linked to increase of energy needs while fledglings are still dependent.

The individual differences in movement may be related to different habitat characteristics (Holt *et al.* 2012) of the different nesting locations, but we did not explicitly aim to explore the effects of habitat in the study. The fact that home ranges were very different for some birds can indirectly indi-

cate nesting habitat differences. However, home ranges could also be influenced by number of young or task partitioning between parents. For example, for the radio-tracked pair, we observed that the female had the largest home range of all the birds and did not show parental care during the last part of the season, while the male had a smaller home range and showed parental care to the fledglings throughout (we frequently observed male feeding-behaviour while the female was away).

In conclusion, the Thrush Nightingales that we observed adjusted local movements during the breeding season to specific local environmental conditions and developmental needs of their young, rapidly reacting to local weather changes and progressively adjusting to intra-seasonal changes in food resources. Whether these patterns are more general will require tracking more individuals at more sites. Studying movement at the local scale and the mechanisms associated with movement flexibility can contribute new process-based insights to improve our understanding of the capacity of birds to adapt movement patterns to large-scale changes in environmental conditions.

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Paikallinen sää, ravinnonsaatavuus ja pesinnän vaihe vaikuttavat satakielien paikalliseen liikkuvuuteen

Monet lintulajit ajoittavat lisääntymiskautensa hyönteisravinnon saatavuuden mukaan. Ei ole selvää, vaikuttaako hyönteisten saatavuus myös lintujen liikkuvuuteen paikallisesti. Tutkimme ympäristötekijöitä, jotka selittävät satakielien pesinnänaikaista paikallista liikkuvuutta kuudella revii-

rillä Tanskassa. Lintujen liikkumista seurattiin radiolähettimien avulla. Havaittiin, että pesäpoikas-aika sijoittui kasvillisuuden vehreimpään aikaan. Emolinnut lensivät kauemmaksi pesästä kun sääolosuhteet olivat vakaat ja kun ympäristön vehreys väheni. Emolinnut liikkuivat aktiivisemmin korkeammassa lämpötiloissa ja poikasten ollessa vanhempia. Nämä muutokset emojen liikkumisessa ovat luultavasti selitettävissä paikallisten ympäristöolosuhteiden muutoksilla (ml ravinnonsaataavuus) ja sillä että poikaset tarvitsevat erilaista ravintoa eri ikäisinä.

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