Drought in Africa Caused Delayed Arrival of European Songbirds

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Advancement in phenological events such as spring arrival of songbirds at their breeding grounds is well documented (*1*). Despite this, the arrival in 2011 at northern European breeding grounds of several trans-Saharan migratory bird species was among the latest documented since 1950 (Fig. 1A). Local nonbreeding conditions can affect subsequent life-cycle stages at the level of individual birds (*2*). Here, we confirm this by showing a link of causality between the drought at the Horn of Africa (*3*) and the migratory behavior of individual birds resulting in subsequent delayed arrival at breeding grounds thousands of km away.

Photoperiod (*4*) and local environmental conditions (*5*) control timing of life-history events in migratory animals. Timing may also be affected by events during migration, e.g., on stopover sites. We followed individual movements of two long-distance migratory songbird species [18 red-backed shrikes (RS) and eight thrush nightingales (TN)] during three consecutive annual cycles (2009 to 2012) by miniature light-level geolocators (*6*) with the purpose of assessing the impacts of environmental conditions at different life-history stages. Breeding area arrival was documented by using 63 years of monitoring data and related to en route conditions by using remote-sensing data (31-year vegetation index series).

The exceptional 2011 delay in spring arrival could be traced back to a significant prolongation of stopover time during northward migration at the Horn of Africa, which was at that time affected by extreme drought (Fig. 1C). Mean stopover time in this region was longer during the drought year 2011 (18 days, SE = 1.72, *n* = 5 for RS and 29 days, SE = 4, *n* = 3 for TN) compared with the mean stopover time for the adjoining years, 2010 and 2012, combined (9 days, SE = 0.90, *n* = 13 for RS and 21 days, SE = 5, *n* = 5 for TN). This carried over to a corresponding delay in spring arrival and breeding start in Europe (Fig. 1A and fig. S1) even apparent at the individual level (two individuals tracked during two consecutive years; supplementary materials). There was no significant difference in the timing of migration between 2010/2012 and 2011 up to the spring stopover period in northeast Africa.

The extent of the catastrophic drought (*3*) at the refueling area (*6*) is illustrated by vegetation indices (Fig. 1C and fig. S2). The drought probably caused food shortage, which slowed down refueling rate and increased time needed to reach the necessary fuel loads. Other southeast African migrants were also delayed, whereas species not relying on the Horn of Africa for refueling were not (table S1). Thus, this demonstrates cross-season interactions in individual migratory animals (*2*).

Advances in tracking technology currently revolutionize migration research. Our results elucidate how new technology helps establish a direct link between local climate during migration and arrival/breeding conditions. Still, improvements in small-animal tracking are required to provide better precision globally (*7*).

Migration delay may have cascading effects on breeding success, mortality, and timing of later life-history stages. Start of breeding of RS was delayed in 2011, but population sizes and reproductive success were reported to be close to average (supplementary materials). However, the implications of our results are that even very local stopover conditions during short time periods have crucial importance for the entire migration system, emphasizing the challenges in conserving migration routes and systems (*8*).

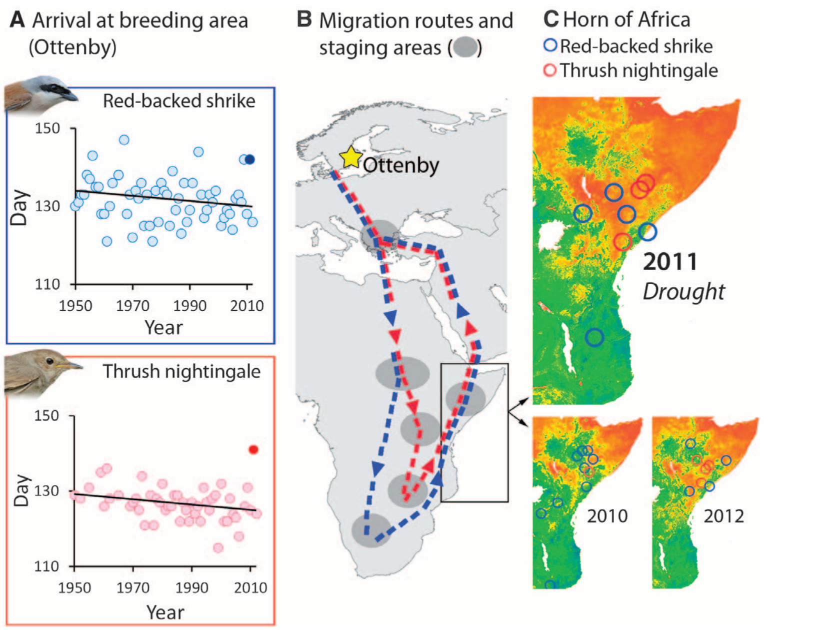

Fig. 1. (**A**) Trends in first-arrival day of RS and TN at Ottenby, Sweden, during 1950 to 2012 (solid dots are 2011 arrivals). (**B**) Migration revealed by year-round tracking of individuals during 2009 to 2012. (**C**) Horn of Africa staging positions of individual RS (blue; *n* = 9 in 2010, *n* = 5 in 2011, *n* = 4 in 2012) and TN (red; *n* = 1 in 2010, *n* = 3 in 2011, *n* = 4 in 2012). Background maps show eMODIS normalized difference vegetation index (NDVI) (15 to 30 April); color range (red to green) indicates increasing presence of green vegetation. The difference in number of northeast African staging days between 2010/12 and 2011 was significant for both species combined ($P = 0.006$, $n = 26$) as well as RS alone ($P < 0.002$, $n = 18$), but not the small sample of TN ($P = 0.46$, $n = 8$; Kruskal-Wallis).

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Supplementary Materials

www.sciencemag.org/cgi/content/full/338/6112/1307/DC1
Materials and Methods
Supplementary Text
Figs. S1 and S2
Table S1
References (*9–17*)

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Supplementary Materials for

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Materials and Methods

During four consecutive breeding seasons (2009-12), 151 red-backed shrikes *Lanius collurio* (RS) and 44 thrush nightingales *Luscinia luscinia* (TN) were fitted with 1-g geolocators (Mk10-S/Mk12-S). A total of 26 RS and 10 TN were re-trapped the following year of which 18 and 8, respectively contained useful data. Study sites were located in southern Scandinavia: Gribskov (55.988°N, 12.338°E), Vittskövle (55.858°N, 14.188°E), Ottenby (56.238°N, 16.468°E) and Amager Fælled (55.653°N, 12.580°E). See also recent study of TN fall migration (*9*).

Geographical positions are generated using continuously stored light levels from which sunrise and sunset times can be converted to day length and local apparent noon and midnight, respectively (*8*). Each position is associated with large inaccuracy (up to 1000 km for latitude) and average positions have been shown to deviate by up to 200 and 50 km for latitude and longitude, respectively (*10*).

Supplementary Text

Two individual red-backed shrikes tracked in both 2010 (year before drought) and 2011 (year of drought) increased Horn of African stopover time from 6 to 18 days and 6 to 20 days, respectively, confirming our overall findings at the individual level.

Delay in spring arrival time in 2011 among RS, TN and other species using the East African spring migration route was recorded and widely recognized by bird observatories and the ornithological community in northern Europe, causing much concern (*11,* Table S1). This delay caused a late breeding start as indicated by RS populations in the Netherlands showing the latest breeding start (31 May) since recording started in 1993 (Mean: 22 May, SE=1.12 (*12*)) while in Denmark, first hatch date was seven days later in 2011 (22 June) compared to 2010 (*13*). Still, reproductive success was average (the Netherlands, 2011: equal to ten-year mean: 2.9 young/pair (range: 1.9-3.7) (*12*); Denmark, 2011: 3.67±0.15 SE young/pair, five-year mean: 3.39±0.05 SE young/pair (*13*)). Furthermore, the percentage of young birds recorded during autumn migration in Sweden was similar to former years (RS, 2011: 88%, Mean=90%, SE=1%; TN, 2011: 81%, Mean=80%, SE=3% (*14*)). Populations were of average size in 2011 (the Netherlands, RS: 54 pairs in 2011, 10-year mean=50 pairs (*13*)); Denmark, RS: 99 pairs in 2011, seven-year mean=97 pairs (*13*); Sweden, RS: population index in 2010 = 1.03, 2011 = 1.22; TN: population index 2010 = 0.77, 2011 = 0.94; and breeding censuses across northern Europe (*12*, *15*, *16*, *17*). With delayed breeding start we expect later autumn departure, which was seen in median departure day of TN (+10 days, SE: 0.60), but not of RS (-2 days, SE=0.59) (*14*).

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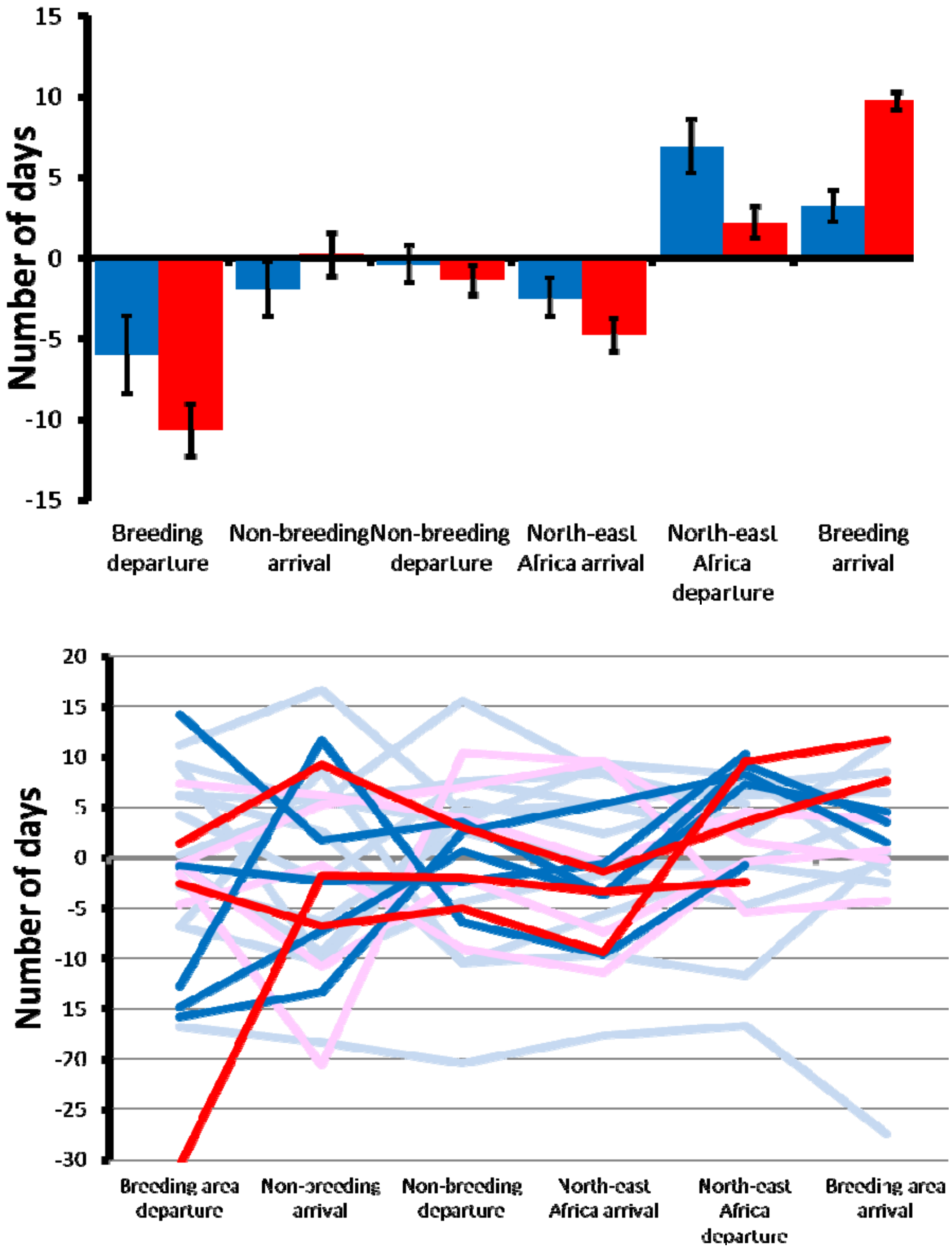

Fig. S1.

Temporal patterns of year-round migration in red-backed shrike (blue: n=12 in 2009-10/2011-12; n=5 in 2010-11) and thrush nightingale (red: n=5 in 2009-10/2011-12; n=3 in 2010-11) at three main staging areas (breeding, wintering and north-east African stopover area). **(A)** Mean timing in 2011 given as number of days relative to the mean for 2010 and 2012 combined. Vertical bars indicate standard error. **(B)** Individual time tracks in 2011 (darker colors) relative to the mean for 2010 and 2012 (lighter colors). Positive values on the y-axis indicate later than average movement.

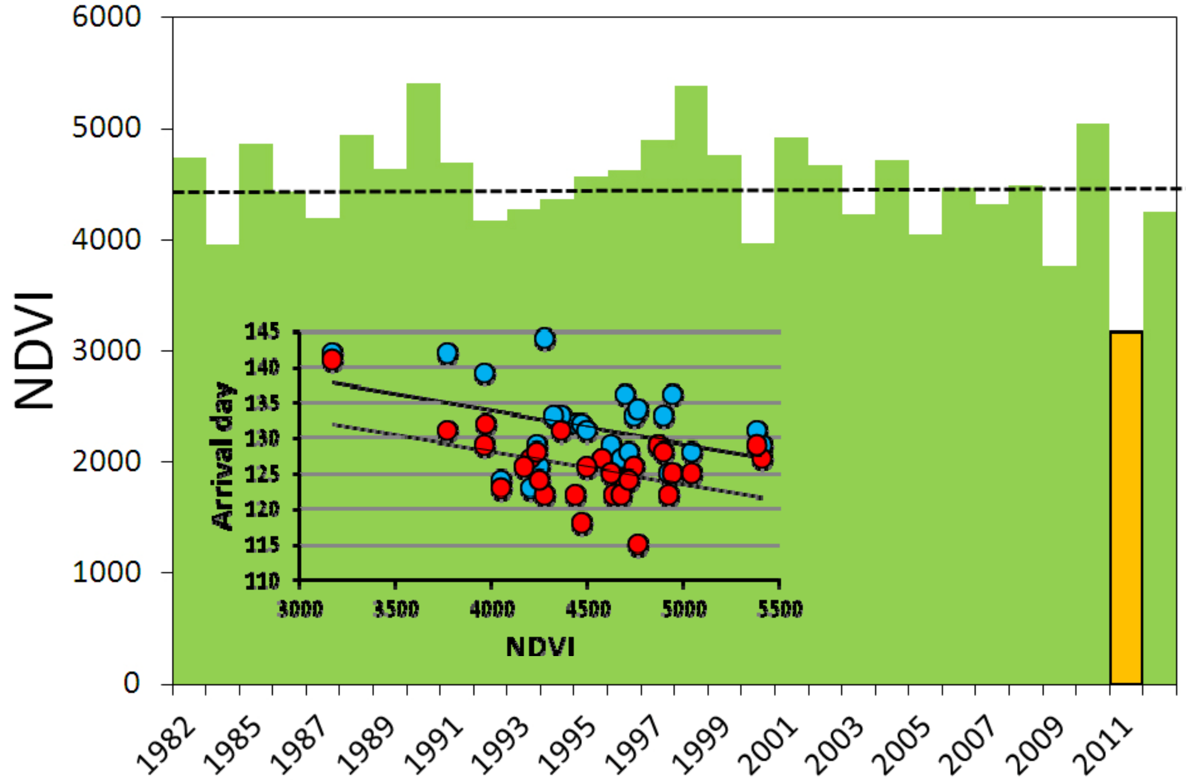

Fig. S2

Normalized Difference Vegetation Index (NDVI; eMODIS and AVHRR) from Horn of Africa for the stop-over period 15-30 April during 1982-2012. Yellow bar indicates the 2011 drought condition and the dotted line indicates the overall mean. Insert figure shows the correlation between Horn of Africa conditions and first arrival day (RS (blue dots): $R^2 = 0.16$, P=0.035; TN (red dots): R^2=0.21, P=0.013). A similar negative relationship holds also for median arrival day in relation to NDVI, however not being statistically significant (RS: $R^2 = 0.11$, P=0.071; TN: R^2=0.10, P=0.093).

Species		**Wintering region**	**ΔFirst**	**ΔMedian**
Lesser whitethroat	*Sylvia curruca*	Northern Africa	1	-1
Whitethroat	*Sylvia communis*	Northern Africa	1	-1
Icterine warbler	*Hippolais icterina*	Central/South Africa	1	4
Spotted flycatcher	*Muscicapa striata*	Central/South Africa	3	-2
Barred warbler	***Sylvia nisoria***	**South/Eastern Africa**	**17**	**14**
Red-backed shrike	***Lanius collurio***	**South/Eastern Africa**	**12**	**-1**
Thrush nightingale	***Luscinia luscinia***	**South/Eastern Africa**	**16**	**7**

Table S1.

Deviation in 2011 arrival time in number of days (positive values are later arrival) from the 63-year mean for first and median arrival in seven common sub-Saharan migrants trapped at spring arrival in southern Scandinavia (Ottenby; *4*). Species in bold are crossing the Horn of Africa during spring migration (wintering region also indicates approximate migration route).

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