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**Intra-African movements of the African Cuckoo *Cuculus
gularis* as revealed by satellite telemetry**

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Abstract:	Despite many bird species migrating regularly within the African continent, in response to rainfall and breeding opportunities, documented evidence of the spatiotemporal patterns of such movements is scarce. We use satellite telemetry to document the year round movement of an intra-African migrant breeding in the savannah zone of sub-Saharan Africa, the African Cuckoo. After breeding in central Nigeria, the birds migrated to more forested sites in the Adamawa region of Cameroon (n=2) and western Central African Republic (n=1). Departure from the breeding ground coincided with deteriorating environmental conditions whereas arrival at the non-breeding sites matched period of increasing vegetation greenness. Migratory movements generally occurred during dark hours. In total, an average distance of 748 km in 66 days was covered during the post-breeding migration and 744 km in 27 days during return journey with considerable individual variation and with more stopover sites used during post-breeding migration. The diversity of migration routes followed suggests a relatively variable or flexible initial migration strategy, high individual route consistency as well as high fidelity for non-breeding grounds.

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0 Intra-African movements of the African cuckoo *Cuculus gularis* as revealed by satellite telemetry 53

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15 Despite many bird species migrating regularly within the African continent, in response to rainfall and breeding opportunities, documented evidence of the spatiotemporal patterns of such movements is scarce. We use satellite telemetry to document the year round movement of an intra-African migrant breeding in the savannah zone of sub-Saharan Africa, the African cuckoo. After breeding in central Nigeria, the birds migrated to more forested sites in the Adamawa region of Cameroon (n = 2) and western Central African Republic (n = 1). Departure from the breeding ground coincided with deteriorating environmental conditions whereas arrival at the non-breeding sites matched period of increasing vegetation greenness. Migratory movements generally occurred during dark hours. In total, an average distance of 748 km in 66 d was covered during the post-breeding migration and 744 km in 27 d during return journey with considerable individual variation and with more stopover sites used during post-breeding migration. The diversity of migration routes followed suggests a relatively variable or flexible initial migration strategy, high individual route consistency as well as high fidelity for non-breeding grounds. 70 75

25 Migration is generally thought to occur as a response to seasonal resource availability (Thorup et al. 2017) which varies more in high latitudes than near the tropics. Nevertheless, many bird species show seasonal movements between breeding and non-breeding grounds within Africa, so-called intra-African migration (Moreau 1972). Many of these migratory species are breeding visitors within the savannahs of the region. Yet, only for a few of these species is there detailed information regarding timing and duration of migration between breeding and non-breeding grounds (Meyburg et al. 1995, Jensen et al. 2006). Such knowledge can contribute to understanding migratory behaviour in general as well as to conservation of migrants (Runge et al. 2014) which are declining overall (Bairlein 2016). 80 85

35 Here, we describe the spatiotemporal migration pattern of satellite-tracked African Cuckoos over three annual cycles, focussing on whether there are general population-specific migration routes and winter grounds as well as behaviours such as to-and-fro migration from breeding to non-breeding grounds, facultative migration from breeding grounds, and route and temporal consistency. 90

40 We trapped five African cuckoos (four males; birds no. 126694, no. 126696, no. 126697 and no. 126698 and one female; bird no. 126695; Supplementary material Appendix 1) using mist nets and tape lures on the breeding grounds around the Amurum Forest Reserve in Jos, central Nigeria, sub-Saharan Africa (9.86–9.88°N, 8.93–8.99°E) in June 2013. Individuals were aged and sexed based on plumage characteristics and fitted with Solar PTT-100s 5-g satellite transmitters (Microwave Telemetry) as a back-pack using a 2 mm braided nylon string. Transmitter weight constituted on average 3.7% (3.5–3.9%) of individuals' body weight. Transmitters were on a 10 h on 48 h off cycle. Geographical positions of the transmitters were obtained from ARGOS/CLS Service Argos (Argos 2011). We only included high quality positions (classes 1–3 with standard deviation of 95 100

45 The migration of long-distance, Palearctic–African migrating common cuckoos *Cuculus canorus* has been described in detail recently (Willemoes et al. 2014, Vega et al. 2016) but migration of the closely related intra-African migrant, the African cuckoo *C. gularis* (Payne 2005), is poorly known, except that it occurs in the Savannah region of sub-Saharan Africa mainly during the rains, spending the rest of the year elsewhere. 105 [AQ3]

0	estimated positions less than 1.5 km) during the period of transmission.	
5	From our analyses, we excluded the two transmitters (tag IDs no. 126698 and no. 126695) that stopped transmitting after 252 and 266 days, respectively, preventing conclusive inference caused by transmitter loss or dead bird continuously transmitting. The first excluded cuckoo moved 28 km northeast in mid-August and was then stationary until the last transmission 6 February while the second bird was stationary in Jos until the last transmission 21 February.	
10	Of the remaining three transmitters, only one (bird no. 126694) successfully completed the third journey.	
15	We defined stopover periods as those lasting for a minimum of 3 d and individuals were considered migrating if the distance moved was at least 15 km (based on the distances covered by individuals during daily movements a few days after tagging). Movements of more than 15 km to other areas but returning to the breeding area after some time occurred in two birds and were considered 'pre-migratory' and their final departure from the Jos area was considered as starting of migration. One of these (no. 126696) traversed 355 km 21 October–17 November in the first year, and travelled to the same area 28 October–16 November in the second year traversing 226 km. Another (no. 126697) covered a total distance of about 89 km during 4 June–1 July. The non-breeding ground was determined as the last stopover site from which further movement was not made until return migration.	
20	We estimated the duration of stay of individuals on the breeding ground using data from the second and third year of tracking as the number of days separating the date of arrival and departure at the breeding ground. For individuals with 'pre-migratory' movements, the duration of this movement was not included in the total number of days spent on the breeding ground. Total distance travelled was estimated as the cumulative distance of each leg of migration from the trapping site in Jos. For each individual, we estimated the average travel distance of the post-breeding and pre-breeding (return) journeys over the three annual cycles.	
25	We additionally investigated the daily timing of flights by identifying movements (Supplementary material Appendix 2) and the habitat characteristics and vegetation greenness at stationary locations throughout the year (Supplementary material Appendix 3).	
30	Statistical analyses were conducted in R 3.1.3 (R Development Core Team), except for the circular tests which were conducted in Oriana 3.0.	
35	Data deposition	
40	Tracking data used in this study are available from Movebank Digital Repository: <doi:10.5441/001/1.XXXXXXXX> (Iwajomo et al. 2017).	
45	Results	
50	Migration	
55	Departures from the breeding ground were extremely variable from 29 July–17 January with arrival to non-breeding grounds 18 December–21 January. Return migration started 3 February–13 March, spread over five weeks in both years. However, the dates of arrival at the breeding ground were relatively concentrated; averagely over two weeks (14–31 March) in the first year and over three days (21–24 March) in the second (Fig. 1). One individual arrived at the breeding ground within 9 days over the three years. The distances covered by the three individuals during the post-breeding migration in the first year were 1179, 487 and 590 km and 1272, 487 and 446 km in the second year (for no. 126694, no. 126696, and no. 126697, respectively). In the third year, one (no. 126694) migrated 957 km while another (no. 126697) migrated 401 km before transmissions stopped. The last did not migrate from the breeding ground before transmissions stopped 17 May 2016. During the return journey, the birds covered 1022, 571 and 608 km, respectively, in the first year and 1024, 539 and 716 km, respectively, in the second year.	61 65 70 75
60	The migration speed varied among the three individuals and also between the post- and pre-breeding phases of migration. The fastest migration speed during the post-breeding phase (no. 126696) was 162 and 97 km d ⁻¹ in the first and second year of tracking, respectively, while during the return phase the fastest individual (no. 126694) flew 340 km d ⁻¹ , 34 km d ⁻¹ and 161 km d ⁻¹ in the first, second and third year, respectively (Supplementary material Appendix 1 Table A1).	80 85
65	Stopovers and duration of stay	
70	On average, the birds remained on the breeding ground in central Nigeria for 243 d (192–281 days, n=3). After departing from their breeding ground, two birds made use of one and four stopover sites, respectively, in northeast Nigeria, where they spent about 34 (no. 126694) and 153 d (no. 126697), respectively. The birds spent on average 50 d (16–63 d, n=3) on their non-breeding grounds. While returning to the breeding grounds, two birds (no. 126694, no. 126697) made one stopover in central Nigeria. In two cuckoos (no. 126696, no. 126697), the non-breeding grounds were on the Adamawa Plateau of Cameroon, separated by an average distance of about 67 km. The third individual used two areas in western Central African Republic.	90 95 100
75	Migration routes and repeated journeys	
80	Two cuckoos (no. 126694, no. 126696) followed similar routes during their migration from and to the breeding grounds in the two years, whereas one (no. 126697) took a different, more direct route to the non-breeding stopover site in year two (Fig. 1). One bird (no. 126694) migrated along a narrow loop in both years, another (no. 126696) criss-crossed its own path, while the last bird employed a loop migration in the first year (Fig. 1). In the second year, the sites used were the same or separated by up to about 46 km from that used in the first year (Fig. 1).	105 110 115
85	Discussion	
90	Our study suggests that individuals from the studied population of African cuckoos are nocturnal and likely solitary	121

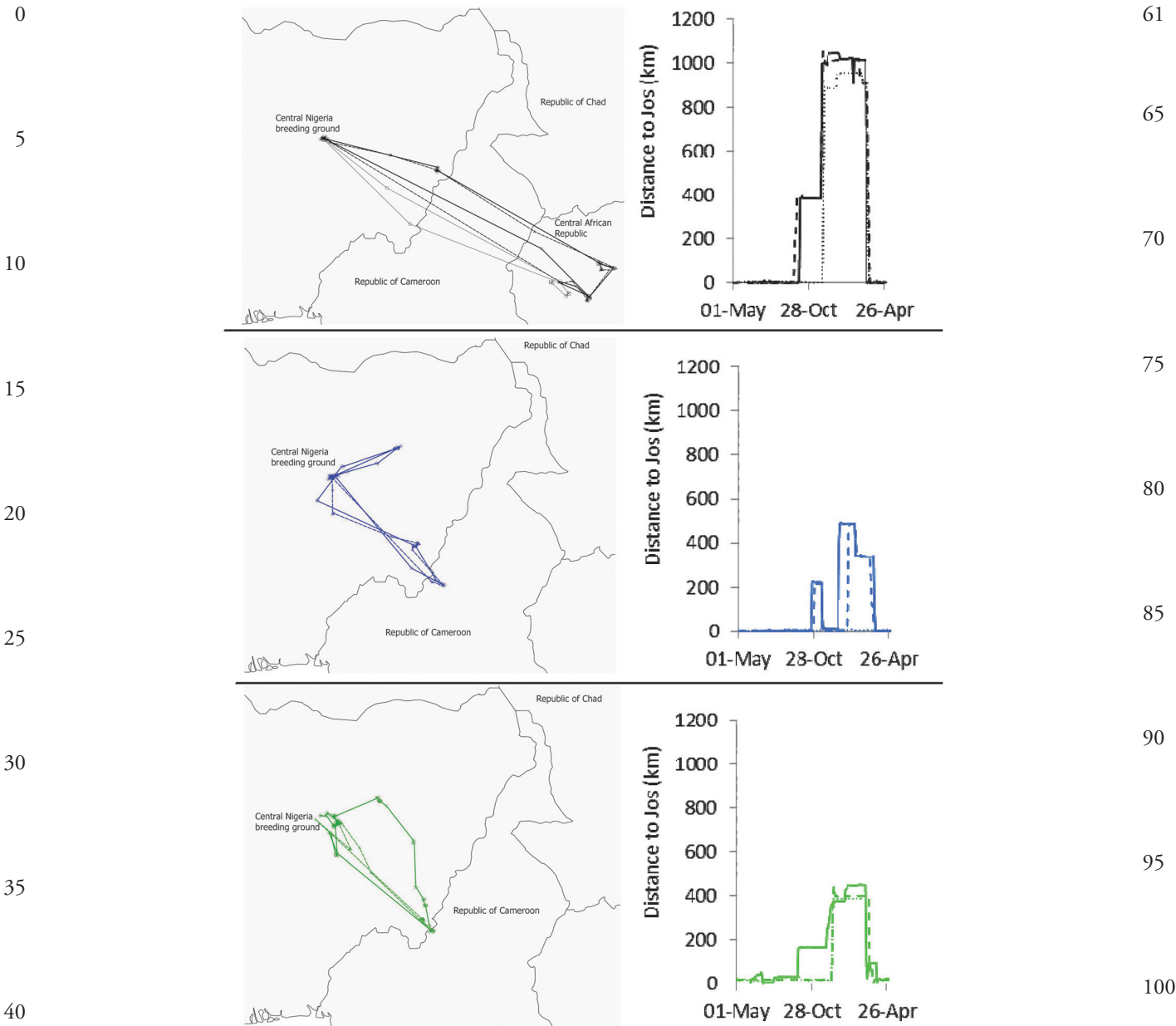


Figure 1. Migration of three satellite-tracked African cuckoos (no. 126694: black, no. 126696: blue, no. 126697: green) from the breeding ground in central Nigeria over three migration seasons. Spatial similarities among individuals (left) and temporal patterns in distance travelled (right). The three panels represent individual tracks. Solid, broken and dashed lines represent migration tracks for the first, second and third seasons, respectively.

intra-African migrants breeding in the savannah zone of sub-Saharan Africa, migrating to wooded savannahs and sub-montane forest sites in central Africa. The migrations were to-and-fro with all birds returning to the same breeding area and our small sample revealed no facultative migrations. The birds showed high route consistency and used the same site as non-breeding ground or the same general area in the second year and third year for one individual, as the one used in the previous year but the non-breeding grounds were very spread out. Overall, timing varied greatly among individuals and individual timing among years was more varied than the spatial component.

Departure from the breeding ground in central Nigeria varied over almost half a year. Arrival on the breeding ground was relatively synchronized among years despite the spread in leaving non-breeding grounds and migration distance. On average, the departures coincided with deteriorating conditions (Supplementary material Appendix 3) that characterize the beginning of the dry season in central Nigeria (Cox et al. 2013). Return to breeding grounds coincides with the end of the dry season and the beginning of the rains. This time fits the peak breeding period of common bulbuls *Pycnonotus barbatus*, a potential host which breeds in all seasons (Cox et al. 2013).

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Supplementary material (Appendix JAV-01616 at <www.avianbiology.org/appendix/jav-01616>). Appendix 1–3.

General migration behavior with nocturnal (Supplementary material Appendix 2), directed movements at specific periods of the year resulting in to-and-fro migration is similar to that found in long-distance Palaearctic migrants. Although we found great flexibility in migration route used by adult African cuckoos, it appears that once the route is set birds predominantly follow a similar route in different years. A genetically-controlled mechanism presumably guides inexperienced migrants (Gwinner 1996, Thorup et al. 2007) whereas adults are able to return to previously visited sites (Thorup and Holland 2009).

The pre-breeding migration from tropical Africa started between January and March in both African and common cuckoos (Willemoes et al. 2014). The main wintering area of the African cuckoos was overshoot by the common cuckoos. Both species migrated into central Africa during the non-breeding season but African cuckoos followed a southeasterly direction whereas common cuckoos flew mostly south and the final non-breeding sites of the African cuckoos were more northerly. Studies have revealed varying patterns in the type of non-breeding grounds used by intra-African migrants with for example a Wahlberg's eagle breeding in savannah woodlands and spending the non-breeding season in Sahelian Africa (Meyburg et al. 1995) and Abdim's storks migrating from Sahelian breeding grounds to mixtures of grasslands and woodlands (Jensen et al. 2006).

Understanding intra-African migration is crucial for identifying the factors influencing the movement of species involved especially in the face of climatic change uncertainties. Given rapid human population growth and the attendant increase in habitat fragmentation and alteration in many parts of Africa, the combination of knowledge from intra-African migration and winter ecology of Palaearctic migrants is urgently needed for determining relevant conservation action on the continent.

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