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Population trends of resident and migrant West African bird species monitored over an 18-year period in central Nigeria‡

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Almost no systematic monitoring of bird population trends occurs in West Africa, despite rapid human population increase, habitat change, and climate change, making conservation planning problematic. We monitored bird population trends using constant-effort mist netting, in a newly protected area (Amurum Forest Reserve) on the outskirts of Jos, central Nigeria, from 2002 to 2019. We modelled the 18-year changes in trends of 10 Palearctic migrant and 41 common resident bird species and related this to any changes in annual environmental site quality using NDVI and rainfall data. The populations of most bird species were stable; 30% of migrants and 7% of residents increased, while 10% of migrants and 29% of residents declined moderately. Primary productivity, measured by NDVI, increased, and rainfall pattern was stable, suggesting that environmental conditions at the site improved slightly during the period. However, only a few species showed significant correlations of population trends with NDVI and rainfall. Overall, our results suggest that population changes were locally similar for both the Afro-Palearctic and resident bird species, being reasonably stable or increasing—although perhaps this reflected the fact that the monitoring was done within a newly protected area, which at present represents the best habitat in the wider locality. Those species that declined were mostly associated with open, grassland areas, which will have decreased as anthropogenic influences were reduced at the study site. Though we only monitored one site, the results are encouraging in that simple protection of a small habitat fragment (~300 ha) in Nigeria yielded generally positive population benefits for both resident and Palearctic migrant species.

Tendances démographiques d'espèces d'oiseaux migrateurs et sédentaires d'Afrique de l'Ouest observées pendant 18 ans dans le centre du Nigeria

Malgré l'augmentation rapide de la population humaine, les changements d'habitats et le changement climatique, il n'existe presqu'aucune surveillance systématique des tendances de la population aviaire en Afrique de l'Ouest, ce qui est problématique pour planifier la conservation. Nous avons suivi les tendances de la population aviaire, en maintenant un effort de capture constant à l'aide de filets japonais, dans une zone nouvellement protégée (réserve forestière d'Amurum), située en périphérie de la ville de Jos, dans le centre du Nigeria, de 2002 à 2019. Nous avons modélisé les évolutions sur 18 ans des tendances de 10 migrateurs paléarctiques et de 41 espèces d'oiseaux sédentaires communs et les avons reliées à tout changement annuel de la qualité environnementale du site en utilisant l'indice de végétation par différence normalisée («NDVI, Normalized Difference Vegetation Index») et les données pluviométriques. La plupart des espèces d'oiseaux était stable; 30% de migrateurs et 7% de sédentaires ont augmenté tandis que 10% des migrateurs et 29% ont connu un déclin modéré. La productivité primaire mesurée par le NDVI a augmenté et le régime de précipitations était stable, ce qui suggère que les conditions environnementales du site se sont légèrement améliorées pendant la période étudiée. Toutefois, seules quelques espèces ont montré une corrélation significative des tendances de population avec les données pluviométriques et l'indice de végétation. Globalement, qu'il s'agisse des migrateurs paléarctiques ou des oiseaux sédentaires, nos résultats laissent à penser que, localement, les changements de population étaient similaires, relativement stables ou en augmentation, reflétant peut-être le fait que le suivi se soit déroulé dans une zone protégée récente, et qui représente actuellement le meilleur habitat dans l'aire d'étude élargie. Les espèces ayant décliné sont généralement associées à des prairies ouvertes, prairies qui ont diminué en raison des influences anthropogéniques réduites sur le site d'étude. Bien que nous n'ayons étudié qu'un site, les résultats sont encourageants dans la mesure où la simple protection d'un petit fragment d'habitat (300ha) au Nigeria a globalement induit des bénéfices positifs pour à la fois les oiseaux sédentaires et les migrateurs paléarctiques.

Keywords: Afro-Palearctic migratory birds, Afrotropical birds, Amurum Forest Reserve, Important Bird Area, NDVI, non-breeding site, stopover site

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Introduction

There is much habitat change, human population change and development occurring in Africa (Lutz and Samir 2010; World Bank 2011). Rapid human population increase has led to growing demand on natural resources, resulting in land-use change (agricultural expansion, urbanisation, and unsustainable resource extraction), placing great pressure on natural areas, biodiversity and ecosystem services (Birdlife International 2018). As a result, wildlife habitats are destroyed or increasingly fragmented causing changes in ecological conditions affecting long-term survival and species population dynamics (Jarošík 2005; Vranken et al. 2011), and reducing genetic diversity and species abundance, richness and distributions (Cresswell et al. 2007; Cooper et al. 2017; Kleinhans et al. 2019).

Such changes are likely to be causing population declines for bird species in Africa. The IUCN Red List of Threatened Species indicates a decrease in many populations of African birds over the past 25 years, implying that some African birds may be prone to extinction (Birdlife International 2018). Of the 2 477 species found in Africa, 276 are globally threatened with extinction because of small and/or declining populations and/or ranges, and 29 are considered Critically Endangered (Birdlife International 2018). Declines in vertebrate species have generally occurred more in Central and West Africa, than in southern or East Africa (Craigie et al. 2010). Despite these apparent declines there is almost no systematic monitoring of bird population trends in West Africa, although Palearctic migrant populations that spend their non-breeding season in Africa are monitored on their breeding grounds. Rapid population declines of long-distance migratory species have been identified in recent times, and some of these declines are attributable to factors operating in Africa (Newton 2004; Sanderson et al. 2006; Zwarts et al. 2009). Yet, the population status is not known for most African species owing to scarce data (Birdlife International 2016). Long-term population trends are essential information for any conservation effort (Donald et al. 2007; Magurran et al. 2010). Estimates of population size and trends are also two of the reliable pointers in identifying species that are vulnerable to human and climate-induced changes (Barshep et al. 2017).

Bird population trends in any local area arise from fluctuations in annual fecundity and survival, and these are determined by changes in local ecological conditions (e.g. Brambilla et al. 2010), although potentially more so for resident birds in the area than for Palearctic migrants (Ockendon et al. 2012, 2014). Although bird population changes in Africa can arise from anthropogenic effects (Cresswell et al. 2020), long-term changes to habitat structure (e.g. vegetation cover) through natural disturbance and succession processes, and climate variability, which is particularly pronounced in Africa (Nicholson 2001; Anhuf et al. 2006), are likely to also be important. It is therefore important to consider the range of potential sources of habitat change as potential drivers of any observed bird population changes.

Here, we present unique long-term monitoring data (spanning 2002–2019) of common resident and Palearctic migrant species at the Amurum Forest Reserve (Amurum), Nigeria, in West Africa. This is an area of regenerating open woodland savanna, located in the Guinea forest savanna belt in central Nigeria. The site is used for foraging activities to build up fat stores used as an energy reserve during long-haul flights for migrants (e.g. Garden Warbler *Slyvia borin*: Ottosson et al. [2005]), as well as a non-breeding site, a breeding site for intra-Africa migrant species, and as a habitat for resident species. It is representative of thousands of small, wooded stop-over/non-breeding/breeding sites that remain in the otherwise increasingly anthropogenic landscape of West Africa. In combination, such sites are probably crucial to the survival of both Afro-Palearctic and resident bird species. However, Amurum is vulnerable because of its small size (~300 ha) and its proximity to Jos, a major urban centre (Ezealor 2002). The area is threatened by a range of anthropogenic activities, such as wood-cutting, human habitation, arable farming and cattle-grazing (Hulme and Cresswell 2012). Amurum has been a protected site since 2002, since the start of the population data reported here, although it still has small-scale firewood removal and periodic fires affect sections of the site (at a frequency of about 2 or 3 times in the dry season every year).

Therefore, we also measured changes in ecological conditions using the normalised difference vegetation index (NDVI) and rainfall data to help interpret overall trends. Remote-sensing data can help measure changes in vegetation cover at a site (Ockendon et al. 2014). In particular, NDVI data measure vegetation parameters, and so are useful for assessing the extent of land-use change and to monitor photosynthetic activity to indicate productivity and ‘good’ and ‘bad’ years (Pettorelli et al. 2011) that may affect bird populations. For example, NDVI provides an index of how food abundance fluctuates in relation to rainfall and changing habitat quality, which then affects bird foraging activities and movements, in time and space (Poulin et al. 1992; Mulwa et al. 2013). Previous studies have linked survival and population growth rates of Afro-Palearctic migrants to the rainfall regime and/or vegetation on their African wintering grounds (Ockendon et al. 2012).

We modelled the population trends of Afro-Palearctic migratory and African resident species over an 18-year period, while considering any changes in quality of the habitat locally, through changes in annual mean NDVI and rainfall pattern. We predicted that:

1) Most resident species will tend to show stable or increasing trends across years, since monitoring was carried out in a protected area with likely improved habitat quality, unless the overall NDVI and the amount of rainfall showed decreases for the site.
2) In contrast, long-distance migratory species may tend to show declines in population trends because of adverse conditions operating throughout their lifecycle at a larger spatial scale.

Materials and methods

Study site

The Amurum Forest Reserve is a globally designated Important Bird Area (IBA), located in the Guinea savanna zone at the AP Leventis Ornithological Research Institute (APLORI) (9°59′ N, 8°53′ E) on the Jos Plateau, Nigeria. Amurum covers approximately 300 ha and is comprised of three main habitat types: Guinea savannah woodland, gallery forest and rocky outcrops surrounded by farmlands, and human settlement (Ezealor 2002). Amurum has a seasonal environment with two distinct seasons (a wet season from May to mid-October and a dry season from end of October to April), with mean total monthly rainfall of >150 mm in the peak months and no rainfall in the dry season. Temperatures vary across the year, with mean monthly temperatures ranging from 16.4 to 26.1 °C. Minimum monthly temperatures range from 8 to 14 °C, and are lowest during the dry, dusty harmattan periods (December to January). Maximum monthly temperatures range from 28 to 32 °C in March and April, before the start of the wet season; relative humidity may be as low as 10% during the dry season (Nwaogu et al. 2017). Afro-Palearctic migrant species arrive between August and October, as the local rainy season ends, and they depart in March to May, at the end of the dry season and the beginning of the next rainy season. Intra-African migrants are present in the wet season, and after breeding they depart in the early dry season.

Bird data and statistical analysis

Bird data from 2002 to 2019 were extracted from the database of the Amurum Constant Effort Sites (ACESs) scheme (see Cox et al. 2011). Presently, the ACESs ringing scheme operates six times a year (in February, April, June, August, October and December), alternating between two sites for six consecutive days. Birds are identified and tagged with unique metal rings, sexed, and aged if possible, and morphometric data are also recorded. There has been some modification in the ACESs ringing efforts (see Appendix) to include wider coverage within a year (Cox et al. 2011). Within each period of different ringing effort, the same netting sites and type of net were used, but with different total length of nets and number of days. Annual ringing effort was included as a variable during analysis to control for this variation.

We utilised data from all species, with sufficient data spread across the years (i.e. >40 observations, to include species with a low capture rate). This included 10 Afro-Palearctic migratory species (2 535 individuals) and 41 resident African species (12 569 individuals) after excluding retraps of individuals ringed the same year to ensure independence of counts. Local trends of Afro-Palearctic migrant and resident species of birds at Amurum were compared with global trends (European trends: https://pecbms.info/trend-2018; and IUCN trends: www.iucn.org), respectively.

The primary productivity of the forest reserve in the period 2002–2019 was measured as NDVI data, with index values ranging from −1.0 to +1.0, collected at 250-m resolution every 16 days. These data were obtained by request from NASA's Earth Observing System Data and Information System (EOSDIS, https: lpdaacsvc.cr.usgs.gov/appears). Annual mean NDVI data were used for analysis. Daily rainfall data were obtained from the Jos Metrological Centre, Plateau State, Nigeria, for 2002–2018, and this was summed for each year.

We built a generalised linear model (GLM) with a family link function Quasi-Poisson because it is suitable for integer data, is bounded at zero, and it deals with moderate overdispersion (Hastie and Pregibon 1992). Population trends of species were estimated using the 18-year overall counts from 2002 to 2019, controlling for variable ringing effort. Annual count in the first year of the series was standardised to zero, and the response variable 'yearly count' was modelled using a GLM, as follows:

Yearly count = year + ringing effort, family = Quasi-Poisson

Next, we built another model to determine whether the annual changes in the populations of the species were explained by NDVI and rainfall, again controlling for ringing effort:

Count = mean NDVI + mean rainfall + ringing effort, family = Quasi-Poisson

The above models were fitted for each species using the statistical software R version 3.2.2 (R Development Core Team 2018). Models were checked for violation of assumptions using plots of residuals, and all models were found to be reasonably robust.

Results

Most populations of resident and Afro-Palearctic bird species were stable, but some declined (Table 1; Figures 1 and 2). For the resident species (Figure 1), 12 of 41 (29%) decreased significantly: Red-billed Firefinch *Lagonosticta senegala*, Lavender Waxbill *Estrilda caerulescens*, Bronze mannikin *Spermestes cucullata*, Red-cheeked Cordon-bleu *Uraeginthus bengalus*, Black-winged Bishop *Euplectes hordeaceus*, Quailfinch *Ortygospiza atricollis*, Vitelline Masked Weaver *Ploceus vitellinus*, Variable Sunbird *Cinnyris venustus*, Common Bulbul *Pycnonotus barbatus*, Red-throated Bee-eater *Merops bulocki*, Black-billed Wood Dove *Turtur abyssinicus* and Greater Honeyguide *Indicator indicator*. Some populations of resident species increased significantly (3 of 41, 7%): Tawny-flanked Prinia *Prinia subflava*, Village Weaver *Ploceus cucullatus* and Moustached Grass Warbler *Melocichla mentalis*. For the Palearctic species (Figure 2), 1 of 10 (10%) decreased significantly, namely Common Whitethroat *Sylvia communis*, whereas 3 of 10 (30%) increased significantly, namely Spotted Flycatcher *Muscicapa striata*, Icterine Warbler *Hippolais icterina* and Common Nightingale *Luscinia megarhynchos*. The relative frequency of species with populations that decreased, increased or remained stable was not significantly different when comparing the groups of resident and Palearctic species (p = 0.11, Fisher's Exact Test).

Overall, annual primary productivity in Amurum using NDVI increased across years but the mean annual rainfall pattern remained stable (Table 2; Figure 3). For resident and Palearctic bird species, NDVI and rainfall influenced

Table 1: Change in the population level of Afro-Palearctic and resident bird species at Amurum Forest Reserve, Nigeria, from 2002 to 2019. Total number of captures is given by *n*. All models controlled for ringing effort. Values are in logarithmic form; LCL and UCL are the lower and upper confidence interval, respectively. T1 = trend based on European classification data for 1980–2016 for common birds in Europe (Pan-African European Common Bird Monitoring Scheme, 2018 update). T2 = trend based on IUCN global population trend with data of BirdLife International 2016 (IUCN Red List of Threatened Species 2016, e.T22719323A94622165). *** = unknown; blank cell = stable; + = increase; – = decrease

	n	Parameters	Estimates	SE	*p*-value	LCL	UCL	T1
Palearctic species								
Garden Warbler	1 047	Intercept	3.70	0.41	<0.001	2.89	4.50	
Sylvia borin		Year	−0.03	0.06	0.61	−0.14	0.08	–
Willow Warbler	174	Intercept	3.39	1.24	<0.01	0.97	5.81	
Phylloscopus torchilus		Year	−0.02	0.07	0.78	−0.16	0.12	–
Spotted Flycatcher	121	Intercept	−0.72	1.24	0.56	−3.14	1.71	
Muscicapa striata		Year	0.18	0.09	0.03	0.01	0.35	–
Tree Pipit	195	Intercept	2.41	1.46	0.10	−0.45	5.27	
Anthus trivalis		Year	−0.11	0.10	0.27	−0.30	0.09	–
Whinchat	205	Intercept	3.55	0.93	<0.001	1.74	5.36	
Saxicola rubreta		Year	0.03	0.08	0.72	−0.14	0.20	–
European Pied Flycatcher	248	Intercept	3.41	0.59	<0.001	2.26	4.56	
Ficedula hypoleuca		Year	0.08	0.04	0.06	0.00	0.17	–
Common Whitethroat	345	Intercept	3.46	0.59	<0.001	2.29	4.62	
Sylvia communis		Year	−0.11	0.04	<0.001	−0.18	−0.04	–
Icterine Warbler	111	Intercept	−0.52	0.89	0.56	−2.27	1.22	
Hippolais icterina		Year	0.19	0.06	<0.001	0.07	0.31	+
Common Nightingale	46	Intercept	0.23	0.51	0.65	−0.77	1.24	
Luscinia megarhynchos		Year	0.09	0.04	<0.001	0.01	0.17	–
Eurasian Wryneck	43	Intercept	0.25	0.76	0.74	−1.24	1.73	
Jynx torquilla		Year	0.06	0.05	0.20	−0.03	0.15	+
Resident species								
Gosling's Bunting	232	Intercept	2.90	1.23	0.02	0.49	5.30	T2
Emberiza goslingi		Year	−0.08	0.07	0.26	−0.21	0.06	
Red-billed Firefinch	469	Intercept	1.32	0.43	<0.001	0.48	2.17	
Lagonosticta senegala		Year	−0.14	0.03	<0.001	−0.21	−0.08	
Rock Firefinch	339	Intercept	1.50	0.34	<0.001	0.82	2.17	
L. sanguinodorsalis		Year	0.02	0.02	0.27	−0.02	0.06	
Black-bellied Firefinch	103	Intercept	1.47	0.81	0.07	−0.13	3.07	
L. rara		Year	0.07	0.06	0.22	−0.04	0.18	
Bronze Mannikin	940	Intercept	2.52	0.42	<0.001	1.69	3.35	
Spermestes cucullata		Year	−0.09	0.05	0.04	−0.18	0.00	
Black-rumped Waxbill	185	Intercept	1.40	0.94	0.14	−0.45	3.25	
*Estrilda troglodyte*s		Year	0.03	0.07	0.62	−0.10	0.17	
Lavender Waxbill	441	Intercept	1.93	0.34	<0.001	1.27	2.59	
E. caerulescens		Year	−0.06	0.02	0.02	−0.11	−0.01	
Red-cheeked Cordon-bleu	560	Intercept	1.48	0.52	<0.01	0.45	2.50	
Uraeginthus bengalus		Year	−0.17	0.05	<0.01	−0.27	−0.07	
Quailfinch	119	Intercept	1.07	1.17	0.36	−1.23	3.37	
Ortygospiza atricollis		Year	−0.21	0.09	0.02	−0.40	−0.03	
Yellow-mantled Widowbird	231	Intercept	1.02	0.59	0.08	−0.14	2.18	
Euplectes macroura		Year	0.06	0.04	0.19	−0.03	0.14	
Northern Red Bishop	2213	Intercept	6.85	1.74	<0.001	3.45	10.26	
Euplectes franciscanus		Year	−0.04	0.09	0.67	−0.21	0.14	
Black-winged Red Bishop	150	Intercept	0.43	1.22	0.73	−1.97	2.83	
E. hordeaceus		Year	−0.26	0.08	<0.001	−0.41	−0.11	
Vitelline Masked Weaver	143	Intercept	0.79	0.64	0.22	−0.47	2.05	
Ploceus vitellinus		Year	−0.17	0.05	<0.01	−0.26	−0.07	
Black-necked Weaver	213	Intercept	1.45	0.44	<0.01	0.59	2.32	
P. nigricollis		Year	−0.01	0.04	0.80	−0.09	0.07	
Village Weaver	1013	Intercept	3.08	0.41	<0.001	2.28	3.89	
P. cucullatus		Year	0.08	0.03	<0.01	0.03	0.14	
Little Weaver	122	Intercept	0.38	0.41	0.36	−0.43	1.19	
*P. luteolu*s		Year	−0.02	0.04	0.66	−0.10	0.06	
Orange-breasted Bushshrike	52	Intercept	0.09	0.47	0.84	−0.82	1.01	
Chlorophoneus sulfureopectus		Year	−0.03	0.06	0.58	−0.14	0.08	
Variable Sunbird	381	Intercept	1.59	0.46	<0.001	0.69	2.49	
Cinnyris venustus		Year	−0.10	0.04	0.02	−0.19	−0.02	

Table 1: (cont.)

	n	Parameters	Estimates	SE	*p*-value	LCL	UCL	T1
Palearctic species								
Scarlet-chested Sunbird	596	Intercept	3.41	0.31	<0.001	2.79	4.02	
Chalcomitra senegalensis		Year	0.01	0.03	0.71	−0.04	0.07	
Green-headed Sunbird	179	Intercept	0.56	0.48	0.24	−0.38	1.50	
Cyanomitra verticalis		Year	−0.07	0.05	0.18	−0.17	0.03	
Northern Yellow White-eye	247	Intercept	1.93	0.41	<0.001	1.11	2.74	
Zosterops senegalensis		Year	−0.06	0.04	0.13	−0.13	0.02	
Senegal Batis	60	Intercept	0.52	0.61	0.40	−0.67	1.70	
Batis senegalensis		Year	−0.03	0.04	0.46	−0.12	0.05	–
Singing Cisticola	120	Intercept	0.40	0.59	0.50	−0.76	1.57	
Cisticola cantans		Year	0.06	0.04	0.10	−0.01	0.13	
Rock-loving Cisticola	95	Intercept	1.14	0.53	0.03	0.11	2.18	
Cisticola eminis		Year	0.08	0.05	0.10	−0.01	0.17	
Tawny-flanked Prinia	104	Intercept	1.42	0.23	<0.001	0.98	1.87	
Prinia subflava		Year	0.12	0.02	<0.001	0.08	0.17	
Northern Crombec	77	Intercept	1.22	0.47	0.01	0.29	2.14	
Sylvietta brachyura		Year	−0.02	0.03	0.54	−0.09	0.05	
Grey-backed Camaroptera	240	Intercept	1.87	0.37	<0.001	1.16	2.59	
Camaroptera brevicaudata		Year	0.05	0.05	0.31	−0.05	0.16	+
Moustached Grass Warbler	81	Intercept	0.90	0.40	0.03	0.11	1.70	
Melocichla mentalis		Year	0.14	0.03	<0.001	0.07	0.20	
Familiar Chat	115	Intercept	1.28	0.38	<0.01	0.53	2.03	
Cercomela familiaris		Year	−0.02	0.03	0.65	−0.08	0.05	
Mocking Cliff Chat	45	Intercept	−1.73	0.66	<0.01	−3.03	−0.43	
Myrmecocichla cinnamomeiventris		Year	0.00	0.06	0.99	−0.11	0.11	
Snowy-crowned Robin-Chat	172	Intercept	1.34	0.35	<0.001	0.65	2.02	
Cossypha niveicapilla		Year	0.00	0.04	0.95	−0.08	0.08	
African Thrush	656	Intercept	2.50	0.32	<0.001	1.89	3.12	
Turdus pelios		Year	0.0002	0.02	0.92	−0.04	0.04	***
Common Bulbul	558	Intercept	2.68	0.42	<0.001	1.84	3.51	
Pycnonotus barbatus		Year	−0.10	0.03	<0.001	−0.15	−0.05	+
Greater Honeyguide	74	Intercept	1.69	0.43	<0.001	0.84	2.53	
Indicator indicator		Year	−0.12	0.03	<0.001	−0.18	−0.05	–
Vieillot’s Barbet	97	Intercept	2.48	0.65	<0.001	1.20	3.75	
Lybius vieilloti		Year	−0.03	0.03	0.29	−0.09	0.03	
Yellow-fronted Tinkerbird	291	Intercept	2.22	0.35	<0.001	1.54	2.91	
Pogoniulus chrysoconus		Year	0.01	0.03	0.87	−0.06	0.07	
Red-throated Bee-eater	149	Intercept	−0.02	0.43	0.95	−0.86	0.81	
Merops bulocki		Year	−0.07	0.03	0.03	−0.13	−0.01	
Speckled Mousebird	385	Intercept	2.39	0.39	<0.001	1.62	3.16	
Colius striatus		Year	0.02	0.03	0.60	−0.05	0.09	+
Black-billed Wood Dove	122	Intercept	1.28	0.68	0.06	−0.05	2.61	
Turtur abyssinicus		Year	−0.09	0.04	<0.01	−0.16	−0.02	
Laughing Dove	78	Intercept	1.89	0.87	0.03	0.19	3.60	
Spilopelia senegalensis		Year	0.01	0.04	0.75	−0.07	0.10	
AdamawaTurtle Dove	122	Intercept	2.07	1.62	0.20	−1.10	5.24	
Streptopelia hypopyrrha		Year	−0.04	0.07	0.57	−0.18	0.10	

Note: The common and scientific names are adopted from the IOC list (https://www.worldbirdnames.org/new/bow/)

population change for only a few species. The populations of 7 (17%) resident species positively correlated with NDVI (Table 3; Figures 4 and 5); these were: Tawny-flanked Prinia, Greater Honeyguide, Little Weaver *Ploceus luteolus*, Orange-breasted Bushshrike *Chlorophoneus sulfureopectus*, Grey-backed Camaroptera *Camaroptera brevicaudata*, Common Bulbul *Pycnonotus barbatus* and Yellow-fronted Tinkerbird *Pogoniulus chrysoconus*. The population of one (10%) Palearctic species Whinchat *Saxicola rubetra* was positively correlated with NDVI (Table 3; Figure 4). The populations of 10 (24%) resident species were positively correlated with increased rainfall: Red-billed Firefinch *Lagonosticta senegala*, Red-cheeked Cordon-bleu *Uraeginthus bengalus*, Lavender Waxbill *Estrilda caerulescens*, Black-winged Red Bishop *Euplectes hordeaceus*, Vitelline Masked Weaver *Ploceus vitellinus*, Variable Sunbird, Common Bulbul, Greater Honeyguide, Vieillot’s Barbet *Lybius vieilloti*, and Black-billed Wood Dove *Turtur abyssinicus* (Table 3; Figure 5). The populations of 3 (7%) resident species correlated negatively with rainfall: Singing Cisticola *Cisticola cantans*, Tawny-flanked Prinia and Moustached Grass Warbler, whereas no populations of Palearctic species correlated positively with rainfall (Table 3; Figure 5).

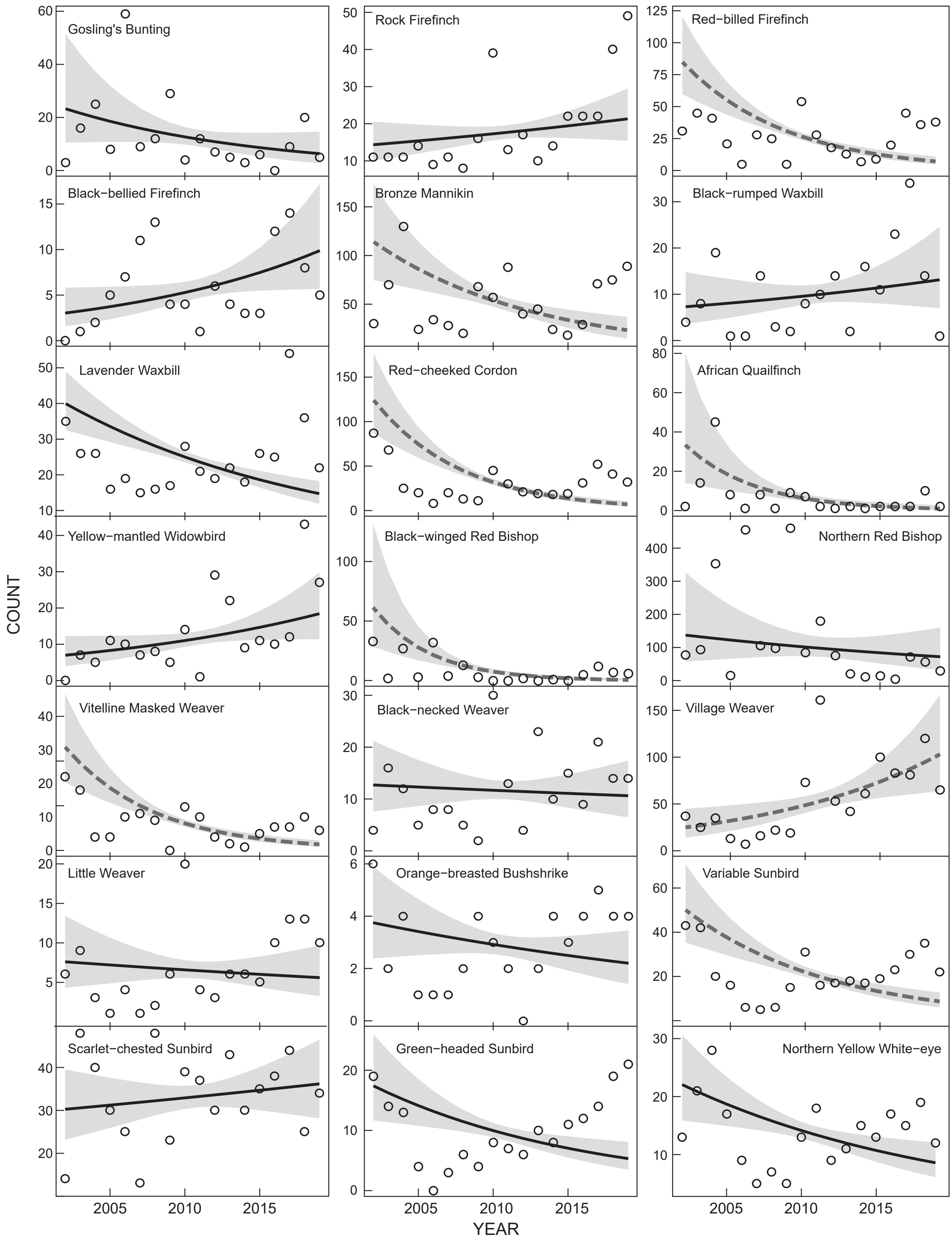
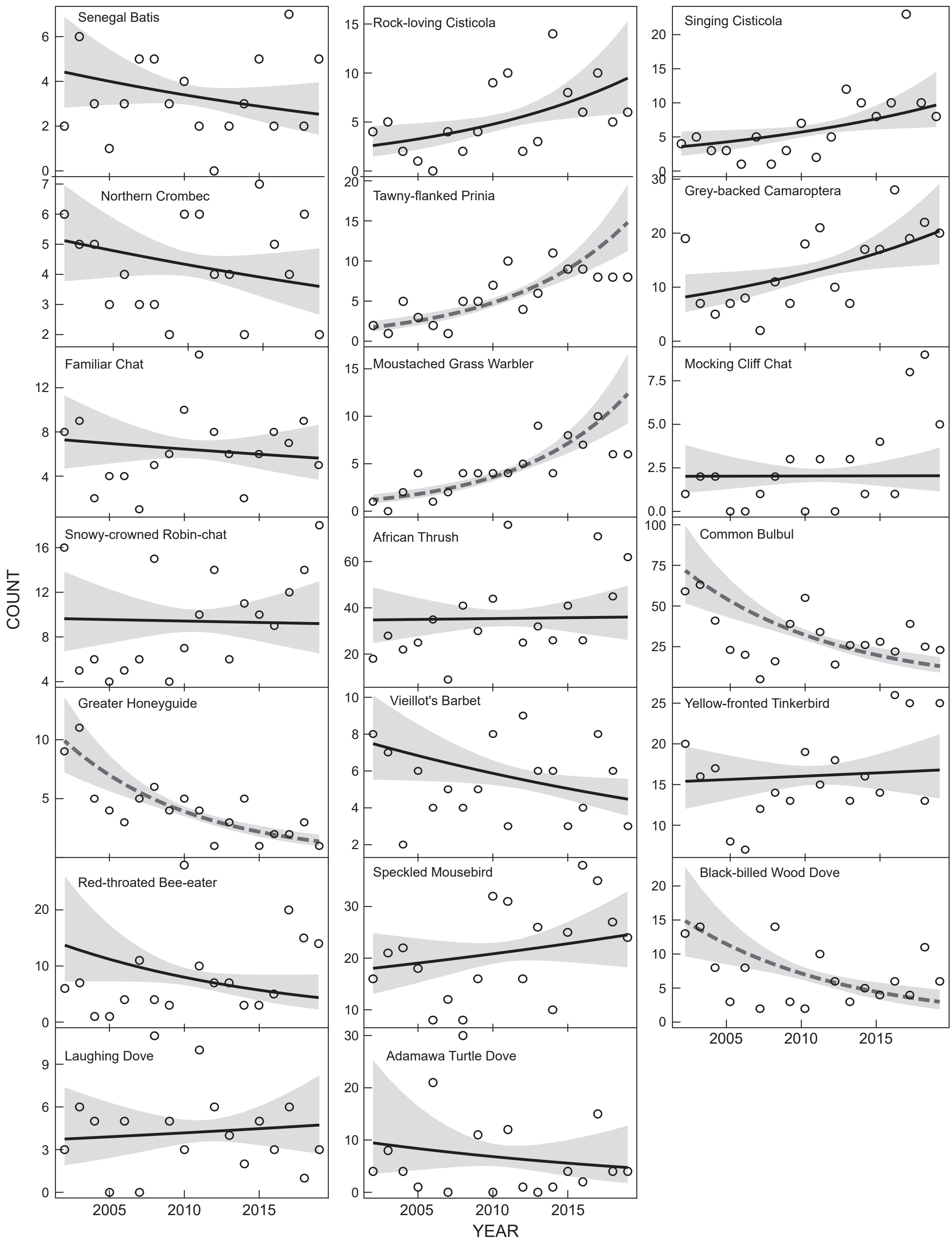


Figure 1: Population trends of African resident bird species at Amurum Forest Reserve, Nigeria, using data for the period 2002–2019. For each species, the total number of birds caught per year is indicated on the y-axis, uncorrected for capture effort. The smooth line is the model fit assuming a constant capture effort based on the median capture effort value (9 720). Grey shading indicates the prediction interval. Species with significant change explained by year are indicated with dashed lines. R Code and example data are provided as Supplementary Material. Note that with a few species there are major discrepancies between the fitted line and the raw data, but these arise because of a significant confounding effect of effort on count for these species: this is controlled for in the GLM (the predicted line), but not the plot which shows count uncorrected for variable annual effort



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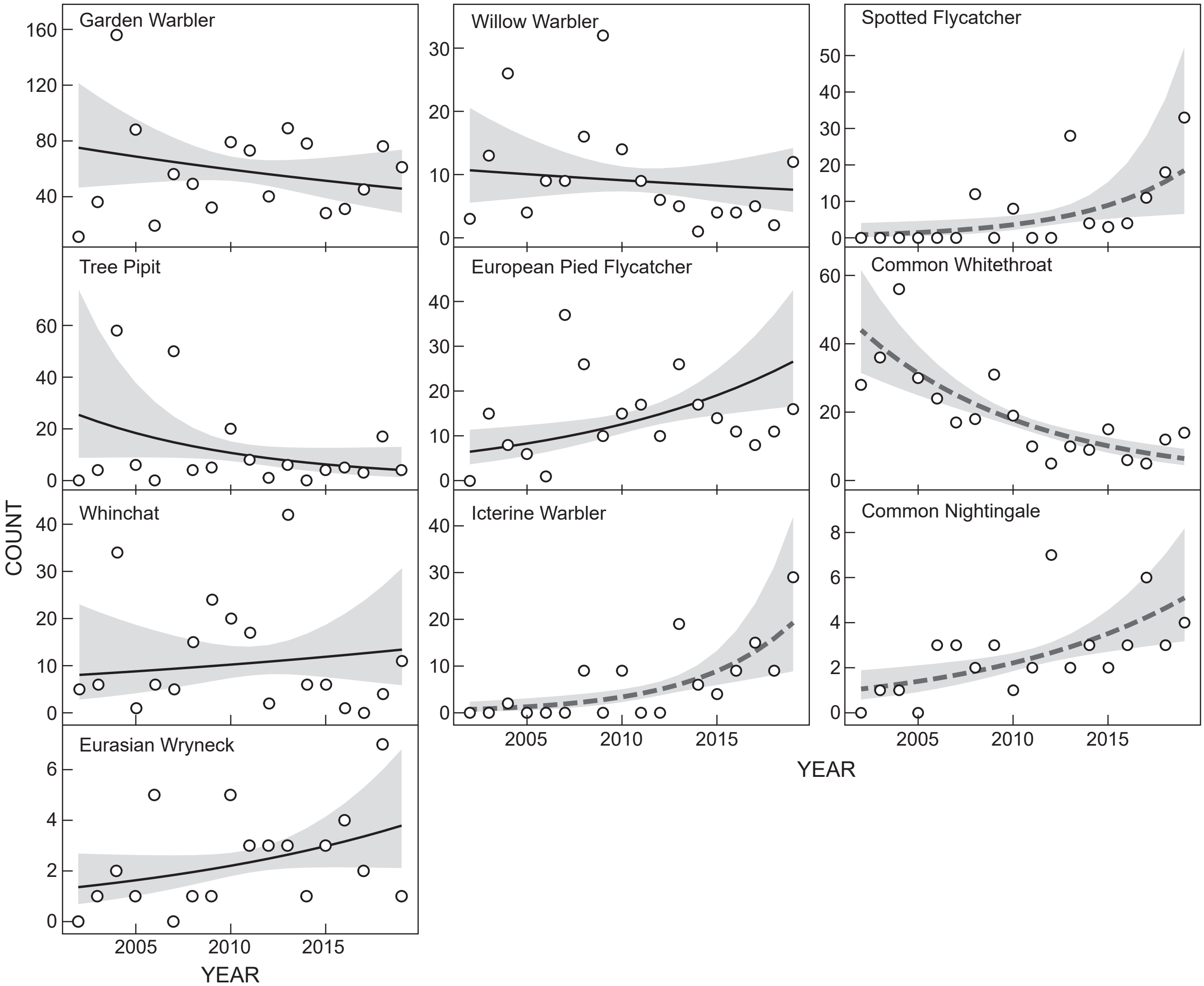

Figure 2: Population trends of Afro-Palearctic bird species at Amurum Forest Reserve, Nigeria, using data for the period 2002–2019; species with significant changes are highlighted with a dashed fitted line on the plot. For an explanation of trend lines, please see Figure 1

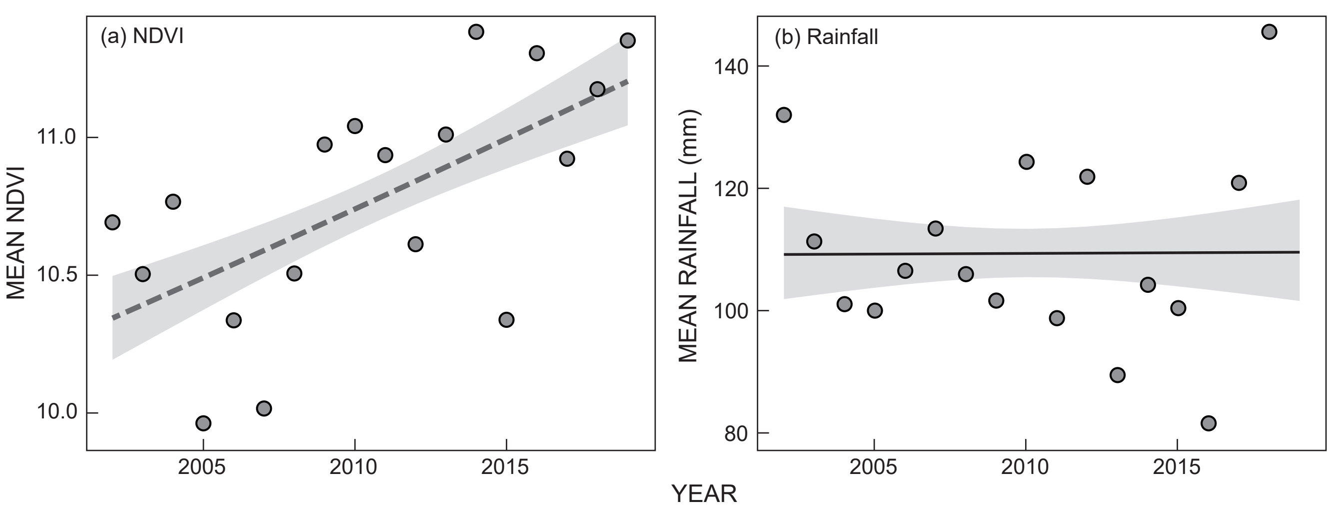

Figure 3: Environmental trend pattern (2002–2019) at Amurum Forest Reserve, Nigeria, with (a) annual mean NDVI data, and (b) annual mean rainfall data (mm)

Table 2: Change in mean annual NDVI (2002 to 2019) and rainfall (2002 to 2018) at Amurum Forest Reserve, Nigeria. Values are in logarithmic form

Parameters	Estimates	Robust SE	*p*-value	Lower CI	Upper CI
			Mean NDVI		
Intercept	2.340	0.014	<0.001	2.309	2.364
Year	0.004	0.001	<0.001	0.002	0.007
			Mean rainfall		
Intercept	4.69	0.024	<0.001	4.570	4.815
Year	0.00	0.009	0.982	−0.017	0.018

Table 3: Population trends explained by mean NDVI and rainfall (mm) for Afro-Palearctic migrant and resident bird species at Amurum Forest Reserve, Nigeria. All models were controlled for ringing effort. Values are in logarithmic form

	Parameters	Estimates	Robust SE	*p*-value	Lower CI	Upper CI
Palearctic species						
Garden Warbler	Intercept	2.64	3.91	0.50	−5.03	10.31
	Mean NDVI	0.18	0.36	0.63	−0.54	0.89
	Mean rainfall	−0.01	0.01	0.58	−0.02	0.01
Willow Warbler	Intercept	−2.49	5.18	0.63	−12.65	7.67
	Mean NDVI	0.74	0.51	0.15	−0.27	1.75
	Mean rainfall	0.00	0.01	0.97	−0.03	0.03
Spotted Flycatcher	Intercept	−8.99	7.09	0.20	−22.88	4.90
	Mean NDVI	0.89	0.61	0.14	−0.31	2.09
	Mean rainfall	−0.02	0.02	0.37	−0.06	0.02
Tree Pipit	Intercept	6.43	9.30	0.49	−11.79	24.65
	Mean NDVI	−0.41	0.97	0.67	−2.30	1.49
	Mean rainfall	0.01	0.02	0.54	−0.02	0.05
Whinchat	Intercept	−6.46	5.74	0.26	−17.72	4.79
	Mean NDVI	1.18	0.49	0.02	0.21	2.14
	Mean rainfall	−0.01	0.02	0.46	−0.05	0.02
European Pied Flycatcher	Intercept	6.17	5.44	0.26	−4.49	16.82
	Mean NDVI	−0.24	0.50	0.63	−1.22	0.73
	Mean rainfall	−0.01	0.01	0.29	−0.03	0.01
Common Whitethroat	Intercept	3.22	2.41	0.18	−1.51	7.94
	Mean NDVI	0.14	0.27	0.61	−0.40	0.68
	Mean rainfall	0.01	0.01	0.25	−0.01	0.02
Icterine Warbler	Intercept	−7.89	5.52	0.15	−18.72	2.93
	Mean NDVI	0.86	0.47	0.07	−0.06	1.77
	Mean rainfall	−0.03	0.01	0.05	−0.06	0.00
Common Nightingale	Intercept	1.61	4.48	0.72	−7.16	10.39
	Mean NDVI	−0.15	0.40	0.70	−0.94	0.63
	Mean rainfall	−0.01	0.01	0.54	−0.03	0.01
Eurasian Wryneck	Intercept	−4.11	5.67	0.47	−15.23	7.01
	Mean NDVI	0.36	0.52	0.49	−0.66	1.38
	Mean rainfall	0.00	0.01	0.92	−0.02	0.02
Resident species						
Gosling's Bunting	Intercept	5.83	6.32	0.36	−6.55	18.22
	Mean NDVI	−0.30	0.57	0.60	−1.42	0.82
	Mean rainfall	0.01	0.02	0.61	−0.02	0.04
Rock Firefinch	Intercept	−2.43	3.39	0.47	−9.07	4.20
	Mean NDVI	0.33	0.31	0.28	−0.27	0.93
	Mean rainfall	0.01	0.01	0.23	−0.01	0.02
Red-billed Firefinch	Intercept	1.15	3.68	0.75	−6.05	8.36
	Mean NDVI	0.02	0.36	0.97	−0.70	0.73
	Mean rainfall	0.02	0.01	0.01	0.00	0.03
Black-bellied Firefinch	Intercept	8.43	4.12	0.04	0.35	16.51
	Mean NDVI	−0.66	0.41	0.11	−1.47	0.14
	Mean rainfall	−0.01	0.01	0.23	−0.04	0.01
Bronze Mannikin	Intercept	−1.51	3.30	0.65	−7.97	4.96
	Mean NDVI	0.46	0.33	0.16	−0.19	1.11
	Mean rainfall	0.00	0.01	0.52	−0.01	0.02
Black-rumped Waxbill	Intercept	0.21	4.30	0.96	−8.21	8.63
	Mean NDVI	0.14	0.40	0.74	−0.65	0.92
	Mean rainfall	−0.01	0.01	0.13	−0.03	0.00

Table 3: (cont.)

	Parameters	Estimates	Robust SE	*p*-value	Lower CI	Upper CI
Resident species						
Lavender Waxbill	Intercept	1.52	1.84	0.41	−2.09	5.12
	Mean NDVI	0.03	0.17	0.85	−0.30	0.36
	Mean rainfall	0.00	0.01	0.43	−0.01	0.02
Red-cheeked Cordon-bleu	Intercept	−2.50	3.25	0.44	−8.87	3.87
	Mean NDVI	0.35	0.32	0.27	−0.27	0.97
	Mean rainfall	0.02	0.01	0.01	0.01	0.04
Quailfinch	Intercept	−1.40	5.04	0.78	−11.28	8.47
	Mean NDVI	0.44	0.59	0.46	−0.71	1.59
	Mean rainfall	0.01	0.02	0.64	−0.03	0.04
Yellow-mantled Widowbird	Intercept	1.12	3.02	0.71	−4.80	7.04
	Mean NDVI	−0.10	0.30	0.72	−0.69	0.48
	Mean rainfall	0.01	0.01	0.53	−0.02	0.03
Northern Red Bishop	Intercept	1.68	7.08	0.81	−12.20	15.55
	Mean NDVI	0.57	0.69	0.41	−0.79	1.93
	Mean rainfall	0.00	0.02	0.79	−0.03	0.03
Black-winged Red Bishop	Intercept	0.37	7.12	0.96	−13.59	14.33
	Mean NDVI	0.03	0.71	0.97	−1.37	1.43
	Mean rainfall	0.03	0.01	0.02	0.01	0.06
Vitelline Masked Weaver	Intercept	1.09	3.37	0.75	−5.51	7.69
	Mean NDVI	−0.14	0.39	0.72	−0.90	0.62
	Mean rainfall	0.03	0.01	0.00	0.01	0.05
Black-necked Weaver	Intercept	−0.09	4.36	0.98	−8.63	8.45
	Mean NDVI	0.19	0.39	0.63	−0.57	0.94
	Mean rainfall	−0.01	0.01	0.66	−0.03	0.02
Village Weaver	Intercept	−2.11	4.51	0.64	−10.94	6.72
	Mean NDVI	0.50	0.40	0.22	−0.29	1.28
	Mean rainfall	−0.01	0.01	0.27	−0.02	0.01
Little Weaver	Intercept	−11.55	4.68	0.01	−20.73	−2.37
	Mean NDVI	1.09	0.43	0.01	0.25	1.92
	Mean rainfall	0.01	0.01	0.15	0.00	0.03
Orange-breasted Bushshrike	Intercept	−10.00	3.46	0.00	−16.77	−3.22
	Mean NDVI	0.96	0.32	0.00	0.34	1.57
	Mean rainfall	0.01	0.01	0.35	−0.01	0.03
Variable Sunbird	Intercept	−4.11	3.21	0.20	−10.39	2.18
	Mean NDVI	0.51	0.30	0.08	−0.07	1.09
	Mean rainfall	0.02	0.01	0.01	0.00	0.03
Scarlet-chested Sunbird	Intercept	3.89	1.85	0.04	0.26	7.51
	Mean NDVI	0.02	0.17	0.89	−0.31	0.35
	Mean rainfall	−0.01	0.00	0.02	−0.02	0.00
Green-headed Sunbird	Intercept	−4.98	3.63	0.17	−12.11	2.14
	Mean NDVI	0.53	0.33	0.11	−0.11	1.18
	Mean rainfall	0.01	0.01	0.21	−0.01	0.03
Northern Yellow White-eye	Intercept	0.63	2.51	0.80	−4.29	5.55
	Mean NDVI	0.18	0.24	0.45	−0.29	0.66
	Mean rainfall	0.00	0.00	0.52	−0.01	0.00
Senegal Batis	Intercept	5.00	3.77	0.18	−2.39	12.40
	Mean NDVI	−0.40	0.34	0.24	−1.07	0.27
	Mean rainfall	0.00	0.01	0.82	−0.02	0.01
Singing Cisticola	Intercept	−0.36	2.62	0.89	−5.50	4.78
	Mean NDVI	0.13	0.23	0.59	−0.33	0.58
	Mean rainfall	−0.02	0.01	0.01	−0.03	0.00
Rock-loving Cisticola	Intercept	−7.83	5.65	0.17	−18.91	3.25
	Mean NDVI	0.84	0.51	0.10	−0.15	1.84
	Mean rainfall	0.00	0.01	0.67	−0.02	0.01
Tawny-flanked Prinia	Intercept	−5.01	3.66	0.17	−12.18	2.16
	Mean NDVI	0.65	0.33	0.04	0.01	1.29
	Mean rainfall	−0.01	0.01	0.02	−0.03	0.00
Northern Crombec	Intercept	0.92	3.02	0.76	−5.00	6.84
	Mean NDVI	−0.01	0.29	0.98	−0.57	0.55
	Mean rainfall	0.00	0.01	0.49	−0.01	0.01
Grey-backed Camaroptera	Intercept	−5.45	3.08	0.08	−11.49	0.59
	Mean NDVI	0.69	0.28	0.02	0.13	1.24
	Mean rainfall	0.00	0.01	0.92	−0.02	0.02

Table 3: (cont.)

	Parameters	Estimates	Robust SE	*p*-value	Lower CI	Upper CI
Resident species						
Moustached Grass Warbler	Intercept	3.98	2.04	0.05	−0.02	7.99
	Mean NDVI	−0.21	0.18	0.26	−0.57	0.15
	Mean rainfall	−0.03	0.01	0.00	−0.04	−0.02
Familiar Chat	Intercept	−2.98	3.53	0.40	−9.90	3.93
	Mean NDVI	0.39	0.35	0.26	−0.29	1.07
	Mean rainfall	0.00	0.01	0.47	−0.01	0.01
Mocking Cliff Chat	Intercept	−0.67	5.10	0.89	−10.66	9.31
	Mean NDVI	−0.08	0.48	0.87	−1.02	0.86
	Mean rainfall	−0.01	0.01	0.46	−0.02	0.01
Snowy-crowned Robin-Chat	Intercept	−1.61	2.50	0.52	−6.51	3.29
	Mean NDVI	0.22	0.22	0.33	−0.22	0.66
	Mean rainfall	0.01	0.01	0.05	0.00	0.02
African Thrush	Intercept	3.57	2.16	0.10	−0.66	7.80
	Mean NDVI	−0.05	0.21	0.82	−0.47	0.37
	Mean rainfall	−0.01	0.01	0.17	−0.02	0.00
Common Bulbul	Intercept	−3.68	3.30	0.26	−10.15	2.78
	Mean NDVI	0.61	0.31	0.04	0.00	1.23
	Mean rainfall	0.01	0.00	0.00	0.00	0.02
Greater Honeyguide	Intercept	−3.30	1.88	0.08	−6.99	0.39
	Mean NDVI	0.45	0.19	0.02	0.08	0.82
	Mean rainfall	0.02	0.00	0.00	0.01	0.03
Vieillot’s Barbet	Intercept	1.19	2.75	0.67	−4.20	6.58
	Mean NDVI	−0.06	0.22	0.77	−0.50	0.37
	Mean rainfall	0.01	0.00	0.00	0.00	0.02
Yellow-fronted Tinkerbird	Intercept	−1.59	1.86	0.39	−5.24	2.06
	Mean NDVI	0.39	0.17	0.03	0.05	0.73
	Mean rainfall	0.00	0.01	0.98	−0.01	0.01
Red-throated Bee-eater	Intercept	−3.44	6.44	0.59	−16.05	9.17
	Mean NDVI	0.24	0.59	0.68	−0.92	1.41
	Mean rainfall	0.02	0.01	0.10	0.00	0.04
Speckled Mousebird	Intercept	1.28	2.78	0.65	−4.17	6.73
	Mean NDVI	0.16	0.26	0.54	−0.35	0.67
	Mean rainfall	0.16	0.26	0.54	−0.35	0.67
Black-billed Wood Dove	Intercept	−2.24	3.86	0.56	−9.81	5.33
	Mean NDVI	0.30	0.36	0.39	−0.39	1.00
	Mean rainfall	0.02	0.01	0.01	0.00	0.03
Laughing Dove	Intercept	1.07	5.19	0.84	−9.10	11.23
	Mean NDVI	0.13	0.47	0.78	−0.79	1.05
	Mean rainfall	−0.01	0.01	0.36	−0.02	0.01
Adamawa Turtle Dove	Intercept	6.64	6.62	0.32	−6.33	19.60
	Mean NDVI	−0.41	0.63	0.51	−1.64	0.82
	Mean rainfall	0.00	0.01	0.81	−0.03	0.02

Discussion

We showed that for both Afro-Palearctic and resident bird species in Amurum, population trends were mostly positive, either increasing or remaining stable. Overall, NDVI increased significantly, suggesting that the habitat of the forest reserve has improved in terms of increased amount of vegetation and primary productivity, as grazing, firewood collection and farming pressures have decreased at the study site. Such changes would have benefitted bird species that use more wooded habitats, such as Icterine Warbler, Spotted Flycatcher and Common Nightingale. All Afro-Palearctic and resident warbler species showed a positive or reasonably stable trend, except for Common Whitethroat, and many of the resident species with decreased trends are granivorous birds (Table 1; Figure 2). Those species that declined were mostly associated with open grassland areas, which will have decreased as the anthropogenic influences were reduced at the study site, beginning at the start of the monitoring period. For example, species that rely on lightly wooded savannah and farmland, such as Common Whitethroat and Red-cheeked Cordon-bleu, have less habitat available. But Rock Firefinches, for example, unlike, other resident finches that declined and utilise open-ground habitats for foraging, utilise bare rock habitats that have not changed over the study period (Brandt and Cresswell 2009).

Ultimately, most of the species’ trends likely reflect changes in local conditions that improve or reduce the availability of resources for a species. The long-term pattern of succession at the site is from degraded agricultural savannah back to wooded savannah and

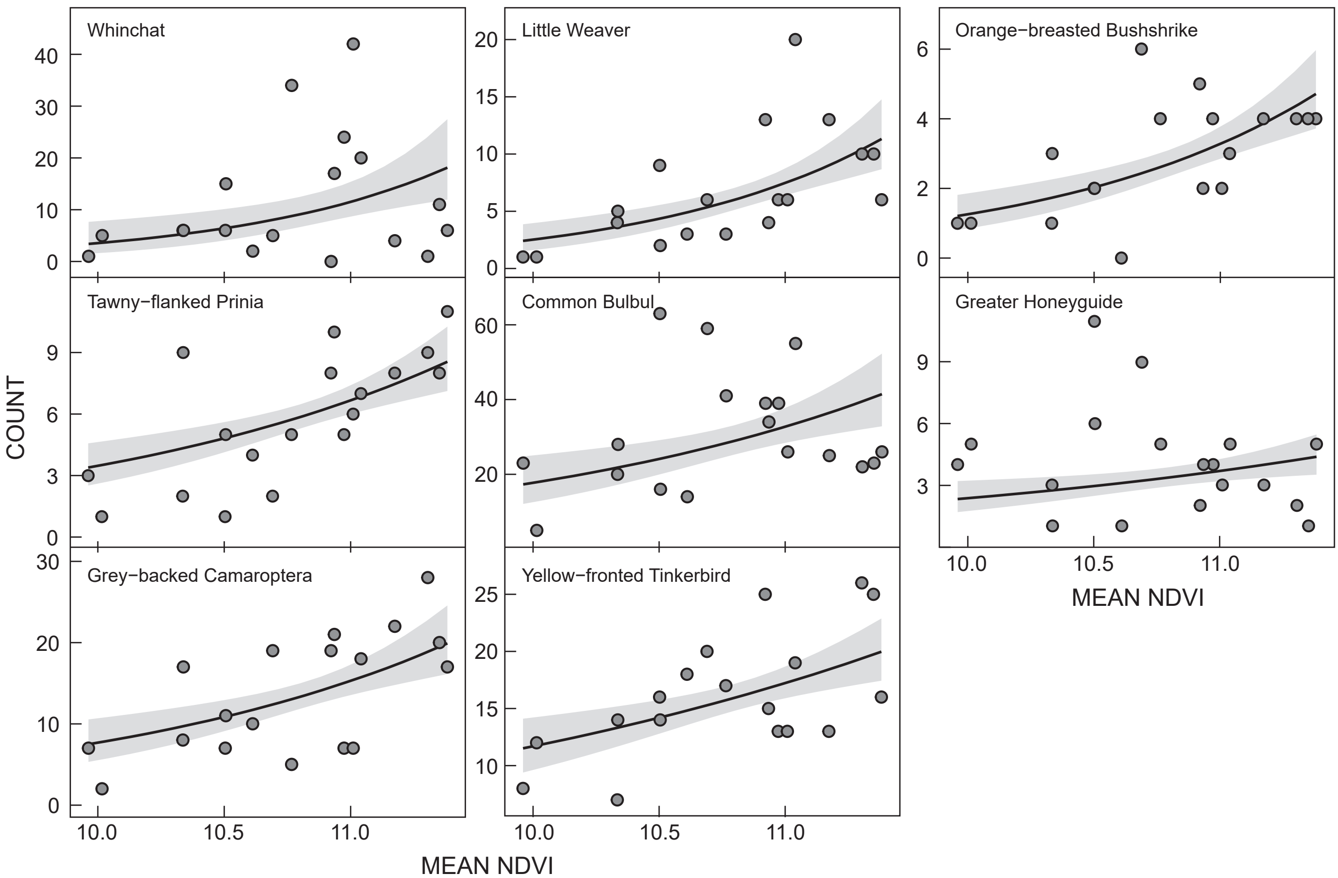

Figure 4: Species-specific population change with annual mean NDVI data (2002–2019) for bird species at Amurum Forest Reserve, Nigeria. Only species with significant changes (see Table 3) are shown

forest. But because of frequent anthropogenic bush fires with variable frequency and intensity, open grassland areas are still common in the study site, although less extensive. Wildfires, as with other ecological disturbances, have both positive and negative effects on bird community dynamics, and species-specific population responses to stochastic events will differ (Rey et al. 2019). Similarly, we found some direct correlations of rainfall and NDVI with population trends of some species: some species will be more sensitive to changes in these ecological conditions (Robson and Barriocanal 2011; Ockendon et al. 2014). It is noteworthy that there was a lack of a negative relationship between declining ‘farmland’ species and increasing NDVI, which would be reasonably expected if the agent of their decline is habitat change, which simultaneously increases NDVI. This highlights that responses to NDVI by species are complicated, because an increase in NDVI can reflect an increase in primary productivity (which might positively benefit a population) while decreasing habitat suitability (which will negatively affect the population).

Overall, population trends for Afro-Palearctic migrants at Amurum were not matched by their global population trends, except for Common Whitethroat (both trends show declines). This disconnect implies that densities in local areas during the non-breeding season can be independent of overall population density. This might arise if Amurum is a relatively ‘good’ area and migrants accumulate there up to the site’s carrying capacity. Other, lower-quality areas would show steep declines as first-year birds can choose the best sites locally to establish their non-breeding territories (Cresswell 2014). This is perhaps obvious, because Palearctic migrant populations have declined to a large degree (Sanderson 2006), and the availability of non-breeding habitat for most species in Africa is large (Newton 2004), thereby creating opportunity for a larger proportion of the population to be concentrated at the best local sites.

The same processes are likely to account for the stability or increase in populations of some of the African species monitored. As local sites degrade, and populations decrease, so the proportion of the population remaining at the best sites increases—but not the density within those areas, which are always at carrying capacity through population process like the ideal free distribution. Again, if we had monitored a relatively poor site, we would expect to see more widespread declines. Alternatively, our results may show that trends were stable because of relatively even resource availability linked to consistent rainfall maintaining primary productivity. This implies that most African bird populations are stable generally, which seems unlikely considering the change in human population in Africa (Cresswell et al. 2020). The majority of our local

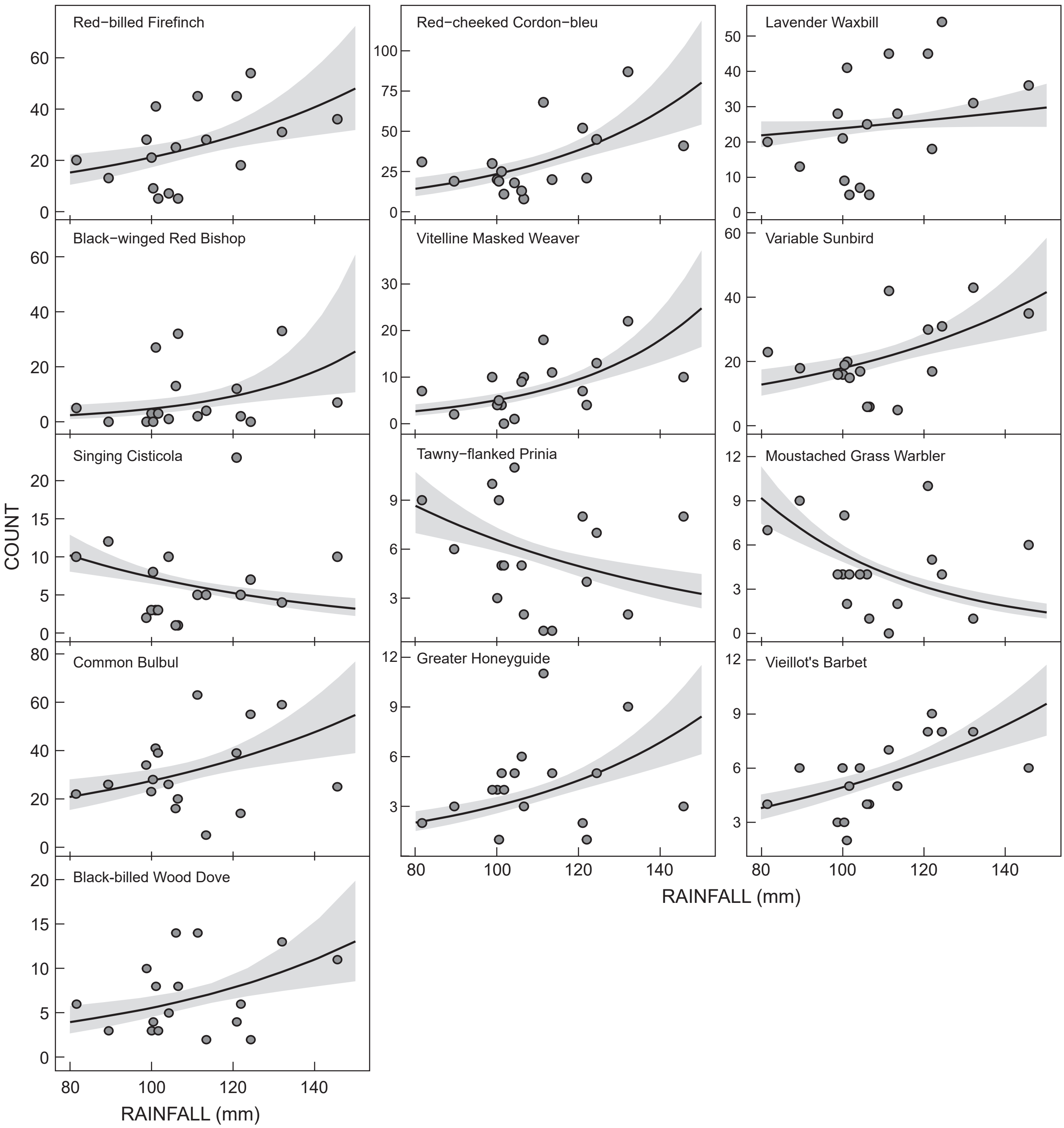

Figure 5: Species-specific population change with annual mean rainfall data (mm) (2002–2019) for bird species at Amurum Forest Reserve, Nigeria. Only species with significant changes (see Table 3) are shown

resident species trend estimates tend to agree with IUCN-reported trends globally (Table 1).

There was no strong evidence for more species of Palearctic migrants declining or increasing compared with resident species, as was initially predicted. Afro-Palearctic migrant populations were expected to be affected by factors operating outside of the study area, and so to show declines in population trends because of adverse conditions operating throughout their lifecycle at a larger spatial scale. As discussed already, this may be simply because we monitored a 'good' site that always attracts whatever bird populations remain locally. But a shortcoming is that we only monitored common species. The nature of constant-effort sites mist-net monitoring of bird populations, like most census techniques, means that rare species do not provide enough data for quantitative analysis, and so they are not featured in the study.

To conclude, we report largely unsurprising and mostly positive population trends for both Palearctic and Afrotropical species monitored in an area undergoing a gradual succession from a lower-quality anthropogenically modified savannah habitat to a higher-quality, more wooded savannah. Amurum is classified as an Important Bird Area for bird species conservation (Ezealor 2002), and our population trend data confirms the quality of the site. But our results cannot be realistically extrapolated to West African population trends generally, particularly because Amurum represents the best local site for birds (and a relatively very small one): since its classification as an IBA, urban sprawl from nearby Jos city has removed nearly all other natural habitat in the local area. Our results, at best, suggest that Amurum remains a "refugium" and "hotspot" for most migratory and resident species. Similar monitoring, given a degree of random sampling across extensive areas and habitats in West Africa, is needed, rather than concentrating on protected areas. Such a network of monitoring is however still a long way in the future, given the extremely low level of ornithological and conservation research capacity in West Africa at present (Cresswell 2018; Pototsky and Cresswell 2020).

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Appendix: Modification of the constant-effort sites (CES) ringing effort from 2002–2019 for bird species at Amurum Forest Reserve, Nigeria. Ringing effort = ringing days x length of mist nets

Period	Length of mist net (m)	Days of ringing	Ringing effort	No. CES per year	No. of nets
2002–2009	270	14	3 780	2	20
2010–2016	324	6	1 944	5	30
2017–2019	408	6	2 448	6	30