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RESEARCH ARTICLE

Geolocator tracking of Great Reed-Warblers (*Acrocephalus arundinaceus*) identifies key regions for migratory wetland specialists in the Middle East and sub-Saharan East Africa

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ABSTRACT
Wetland-dependent migratory songbirds represent one of the most vulnerable groups of birds on the planet, with >67% of wetland-obligate species threatened with extinction. One of the major hurdles for conservation efforts is determining the migration routes, stopover sites, and wintering sites of these species. We describe an annual migration cycle revealed by geolocator tracking of Great Reed-Warblers (*Acrocephalus arundinaceus*) breeding in the Aras River wetlands of eastern Turkey. Because of its relatively large size and breeding ground fidelity, the Great Reed-Warbler is an excellent candidate for geolocator studies and can serve as an indicator species for other wetland songbirds, many of which are particularly threatened in the Middle East. All birds made use of at least 2 wintering grounds in South Sudan, on the Indian Ocean coast and on the western shores of Lake Malawi, as well as several important stopover sites. We also identified a counterclockwise migration path into and out of Africa. Throughout the year, these birds encountered 277 Important Bird Areas, >40% of which had little or no protection. Many species of wetland songbird, particularly threatened species, may be too rare or too small to be the focus of similar studies. Our results not only allow for comparisons with other Great Reed-Warbler populations, but also reveal previously unknown stopover and wintering locations to target conservation efforts that will help wetland-dependent bird species in the Middle East and East Africa.

Keywords: Afro-Palearctic flyway, Afrotropics, avian conservation, Important Bird Areas, migratory species, Turkey, wetland-dependent species, migration bottleneck

Le suivi par géolocalisation d'*Acrocephalus arundinaceus* identifie des régions clés pour les espèces migratrices spécialistes des milieux humides au Moyen-Orient et en Afrique de l'Est subsaharienne

RÉSUMÉ
Les oiseaux chanteurs migrateurs dépendants des milieux humides représentent l'un des groupes d'oiseaux les plus vulnérables sur la planète, avec plus de 67 % des espèces obligées des milieux humides qui sont menacées d'extinction. L'un des plus importants freins aux efforts de conservation est la détermination des routes de migration, des sites de halte migratoire et des sites d'hivernage de ces espèces. Nous décrivons un cycle de vie annuel révélé par le suivi par géolocalisation d'*Acrocephalus arundinaceus* nichant dans les milieux humides de la rivière Araxe, dans l'est de la Turquie. En raison de sa taille relativement grande et de sa fidélité au site de reproduction, cette espèce est une excellente candidate pour les études de géolocalisation et peut servir d'espèce indicatrice pour les autres espèces d'oiseaux chanteurs de milieux humides, dont plusieurs sont particulièrement menacées au Moyen-Orient. Tous les oiseaux ont utilisé au moins deux aires d'hivernage dans le Soudan du Sud, sur la côte de l'océan Indien et sur les rives ouest du lac Malawi, ainsi que plusieurs sites de halte migratoire importants. Nous avons aussi identifié une voie migratoire antihoraire vers et sortant de l'Afrique. Tout au long de l'année, ces oiseaux ont rencontré 277 zones importantes pour la conservation des oiseaux, dont plus de 40 % avaient peu ou pas de protection. Plusieurs espèces d'oiseaux chanteurs des milieux humides, particulièrement des espèces menacées, peuvent être trop rares ou trop petites pour être le point de mire d'études similaires. Nos résultats permettent non seulement la comparaison avec d'autres populations de cette espèce, mais révèlent également la présence de haltes migratoires et de sites d'hivernage ignorés jusqu'à présent afin de cibler les efforts de conservation qui aideront les espèces d'oiseaux dépendantes des milieux humides au Moyen-Orient et en Afrique de l'Est.

Mots-clés: voie migratoire afro-paléarctique, Afrotropiques, conservation aviaire, zones importantes pour la conservation des oiseaux, espèces migratrices, Turquie, espèces dépendantes des milieux humides, couloir migratoire

INTRODUCTION

Every year, between 2 and 5 billion birds migrate between Africa and the Palearctic (Moreau 1972, Hahn et al. 2009). However, populations of many Afro-Palearctic migrants have declined in the last few decades (Vickery et al. 2014). This is particularly true of wetland-dependent species (IUCN 2015). One major conservation challenge is determining critical habitats for these species, not just on their breeding grounds, but also at their wintering and migration stopover sites (Runge et al. 2014). In the past, tracking the migrations of most bird species in detail was impossible, but advances in light-based geolocator technology have helped to reveal migration and wintering sites for ever-smaller songbirds (Bridge et al. 2011, Peterson et al. 2015, Streby et al. 2015). Geolocators have been deployed primarily in North America and Europe (Stutchbury et al. 2009, Delmore et al. 2012, Hahn et al. 2013, Lemke et al. 2013, Salewski et al. 2013, Finch et al. 2015, Briedis et al. 2016); only rarely has the technology been used to track passerines elsewhere (Jahn et al. 2013, Koleček et al. 2016, Yamaura et al. 2016).

Our study species, the Great Reed-Warbler (*Acrocephalus arundinaceus*), is an Afro-Palearctic migratory insectivorous passerine dependent on wetlands for breeding (del Hoyo et al. 2006). The species breeds throughout the Palearctic, from the Iberian Peninsula to the Himalayas, and recent studies have identified wintering regions throughout sub-Saharan Africa (Lemke et al. 2013, Koleček et al. 2016). The Great Reed-Warbler is a good candidate species for geolocator tracking because (1) adults weigh 27 g on average (del Hoyo et al. 2006), thus a 1-g geolocator represents <4% of the bird's overall mass, with expected minimal negative consequences for the bird (Barron et al. 2010), and (2) Great Reed-Warblers exhibit high breeding site fidelity (Bensch et al. 1998, Hansson et al. 2002, Koleček et al. 2015), facilitating recapture and geolocator recovery. As a wetland specialist, the Great Reed-Warbler is of particular interest. Worldwide, wetland specialist species are among the most vulnerable to extinction, with 67% of wetland-obligate species under threat (analysis of IUCN (2015) data). Studying wetland species is essential for identifying the causes of declines in these species and for undertaking the necessary conservation actions. Because of its size, distribution, and relative abundance, the Great Reed-Warbler is an excellent indicator species for threatened wetland passerines across much of Europe, the Middle East, and Africa.

Previous studies using stable isotope analyses or mark–recapture data have suggested that this species exhibits some degree of wintering site fidelity (Nisbet and Medway 1972, Yohannes et al. 2008). Banding studies have suggested that the species typically moves in mid-winter, making use of multiple wintering sites (Hedenström et al. 1993). A previous study tracking the movements of Great Reed-Warblers breeding in Sweden confirmed the use of multiple wintering sites and found pronounced migration speed differences between spring and fall (Lemke et al. 2013). A more recent study tracking the migration of Great Reed-Warblers breeding across Europe and the Middle East reported a moderate degree of migratory connectivity and identified a counterclockwise migration for Great Reed-Warblers breeding in Eastern Europe (Koleček et al. 2016).

Here, we present information on the migration of a population of Great Reed-Warblers breeding in eastern Turkey, including wintering regions in Africa, and the birds' approximate migration routes. We also analyze the number of Important Bird Areas (IBAs) that these birds may have potentially encountered during the course of their migration and the degree of protection that these areas receive. IBAs are a network of ecologically critical sites deemed necessary for bird conservation by BirdLife International (2016). IBAs are designated because of their importance to endangered or range-restricted species, their support of large concentrations of species, or their function as migration bottlenecks (BirdLife International 2016). While IBAs can help to target conservation actions, the sites themselves often do not receive protection. Many IBAs and wetlands in Turkey are not formally protected (Şekercioğlu et al., 2011a,b), including the Aras River wetlands where our study took place, and which are threatened by the proposed Tuzluca Dam (Bilgin et al. 2016).

METHODS

Tagging

All tagging of Great Reed-Warblers with geolocators took place at the Aras River Bird Research and Education Center in northeastern Turkey (40.07°N, 43.35°E). The center is situated at the intersection of the Aras River and Iğdır Plains Globally Important Bird Areas (Bilgin et al. 2016), straddling Iğdır and Kars provinces. These IBAs lie along a major migration corridor and serve as critical breeding, wintering, and migration stopover sites for millions of birds of 284 species recorded to date.

In May of 2013, we attached 1-g geolocators designed by the British Antarctic Survey to 30 Great Reed-Warblers breeding in the Aras wetlands (Geolocator model MK6790 and MK 6740, Biotrack, Wareham, Dorset, UK; stalk length 13 mm at 45°). We caught birds during standard mist-netting sessions and also used playback to attract Great Reed-Warblers with breeding territories around the study site to increase the likelihood of tagging resident breeding birds likely to return the following year. Birds were outfitted with geolocators using rubber catheter tubing arranged in a "leg-loop" harness (Rappole and Tipton 1991), with the device resting on the bird's back and the light sensor extending caudally to minimize light interference from feathers. Geolocators comprised ~3–4% of a bird's body mass, a percentage believed not to have negative impacts (Barron et al. 2010). Geolocators underwent a period of calibration lasting between 2 and 17 days. Unfiltered data from the calibration period showed geolocator recording latitude errors of 39 km (± 115 km SD) and longitude errors of 68 km (± 73 km SD). Unfiltered data from the time of deployment through July 15 showed geolocator recording latitude errors of 60 km (± 62 km SD) and longitude errors of 23 km (± 16 km SD).

In May of 2014, 4 males (hereafter, birds A, B, C, and D) with geolocators were recaptured. In May of 2015, 1 additional bird of unknown sex (hereafter, bird E) that was tagged in the 2013 season and had not been recaptured in 2014 was caught. The 4 birds recaptured in 2014 represented a year-to-year recapture rate of ~13%, higher than the average recapture rate between spring seasons at our site (average = 4%, range = 1–7%). This suggests that geolocators did not reduce survival, although it must be noted that we specifically targeted 2 of the 5 birds with playback.

Data Analysis

After geolocator recovery, data were downloaded and decompressed using BASTrak geolocator software (Fox 2009) and clock drift was accounted for (average drift = 7 min, range = 1–15 min; average and range are based on 4 out of 5 geolocators; see next paragraph). The light file was analyzed in R 3.1.1 (R Core Team 2014) using the GeoLight package (Lisovski and Hahn 2012). Twilight events were identified using a light threshold of 5. Sun elevation angle was calculated using the getElevation function (Lisovski and Hahn 2012). All points from time of capture through July 15 were used in calculating sun elevation, as it was unlikely that any birds would have left the area (all birds were caught in established breeding territories) and thus coordinates could be reliably assigned. The average sun elevation angle was –4.07 (range = –2.31 to –5.30), and values calculated for the breeding grounds were used throughout the year. All twilight transitions were converted to geographic points using the coord function (Lisovski and Hahn 2012), and loessFilter (Lisovski and Hahn 2012) was used to remove extreme outliers by comparing them with 2 interquartile ranges (average percentage of points removed = 20%, range = 9–29%).

A longitudinal adjustment was required for locations calculated for bird D. When locations for this bird were determined following the same protocol that we used for birds A, B, C, and E, the data showed bird D's 2013 and 2014 breeding site to be ~450 km east of its known capture location in eastern Turkey. Other points throughout the course of its migration appeared to be similarly affected. The error was unable to be addressed through clock drift adjustments and likely stemmed from improper time recording during data retrieval. To correct this error, median longitude was calculated for all points from the time of initial capture through July 15, 2013. The difference in longitude (6.28°) between this median and the longitude of the Aras River banding station (where the bird was known to be) was subtracted from all points for bird D.

Probable migration routes and geographic error propagation were inferred using the KFtrack package (Nielsen and Sibert 2004). Each bird's "most probable route" throughout the year (including geographic error; Figure 1) was exported and analyzed in ArcMap 10 (ESRI, Redlands, California, USA). We used BirdLife International data to examine how many Important Bird Areas (IBAs) were included along the migration path of each bird (BirdLife International 2016). IBAs were considered to have been potentially encountered if they fell within the geographic error propagation of a bird's "most probable route" according to KFtrack analysis. In addition to the "most probable route," we analyzed the number of IBAs that fell within each bird's "most efficient route," which was defined as the shortest great-circle route between long-term (>30 days) residency periods. "Most efficient route" points were calculated using the geosphere package for R (Hijmans et al. 2016). The same geographic errors calculated from the "most probable route" were used for the "most efficient route." The number and the geographic area of IBAs that were potentially encountered along each route were compared using 2-sample *t*-tests. We also examined how many of the IBAs along the "most probable routes" had at least some degree of protection as determined by Birdlife International monitoring programs. Only the migration data for 2013–2014 were used (i.e. data from bird E for 2014–2015 were excluded) to analyze potential IBA encounters.

To determine periods of residency and movement, we used the ChangeLight function with a change point probability threshold of 0.03 and a minimum staging period of 3 days (Lisovski and Hahn 2012). Following the protocol of Koleček et al. (2016), we took average latitude

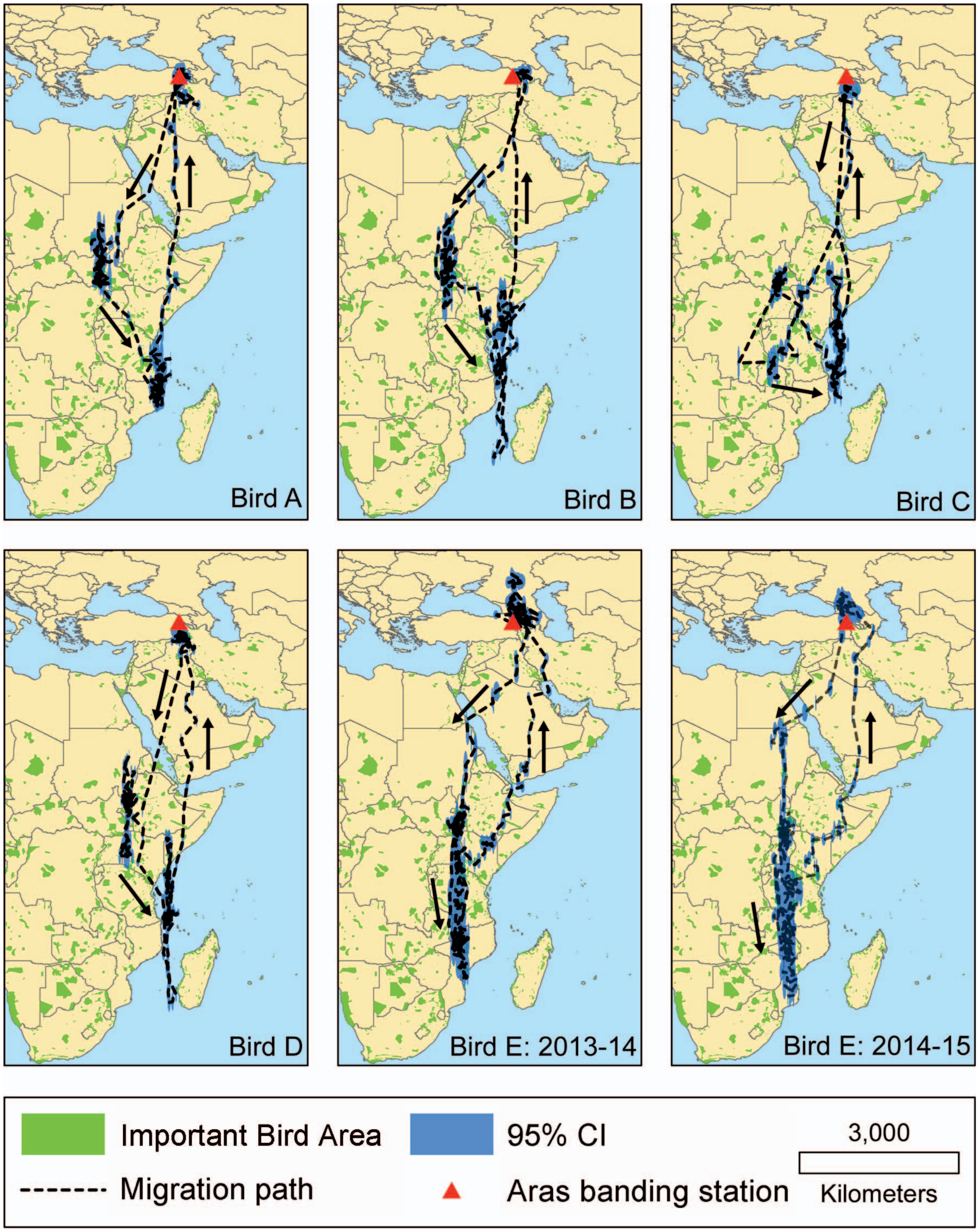

FIGURE 1. "Most probable routes" during migration of Great Reed-Warblers in the Middle East and sub-Saharan East Africa in 2013–2014 (birds A–D) and 2013–2015 (bird E) as identified by KFtrack analysis (Nielsen and Sibert 2004). The red triangle denotes the site of the Aras banding station in Turkey, the dashed black line is the most probable migration route of the individual, and the shaded blue areas represent location error. Green areas are BirdLife International Important Bird Areas (IBAs; Birdlife International 2016). IBAs in Turkey are not shown.

and longitude for each identified stationary period. Subsequent stationary periods with average coordinates <250 km apart were lumped together. Resulting departure and arrival dates were used to calculate the lengths of stay at wintering grounds and stopover sites.

To infer wintering ground locations, we looked at each stationary period delineated by the ChangeLight analysis. Stationary periods of >30 days were considered to indicate probable wintering areas. Points from these periods were converted into kernel density plots with a single 90% contour layer using ArcMap (Figure 2). For stationary periods of <30 days, average latitudes and longitudes of locations were determined and plotted along with latitudinal error (Figure 2). Longitudinal error was too minimal to be evident. These locations were further split based on length of stay.

RESULTS

All 5 birds showed similar movement patterns and wintered in largely the same areas. Birds left eastern Turkey between July 31 and August 12 and spent an average of 29 days (range = 5–61 days) on migration before reaching their first wintering ground. All 5 birds traveled inland across the Arabian Peninsula and crossed over the Red Sea roughly midway between the Sinai Peninsula and the Bab-al-Mandeb Strait (Figure 1). Bird B migrated directly to its first wintering ground in South Sudan, while the other 4 birds made at least 1 stopover during fall migration. Stopover locations included central Sudan, western Ethiopia, central Kenya, and northern Tanzania (Figure 2); the locations of the latter 2 sites may have been influenced by equinox-based geolocator error. Average length of stopover during fall migration was 11 days (range = 5–21 days). All 5 birds spent the first part of the winter in South Sudan or northern Uganda (average length of stay = 91 days, range = 59–119 days). During this time, 2 birds appeared to make small relocations; Bird C moved ~300 km south-southeast on November 17, and Bird E moved ~700 km north on November 3 (Figure 2). These locations may represent additional wintering grounds or may be an artifact of geolocator error. The average distance between breeding grounds and first wintering sites was 3,646 km (range = 3,155–4,123 km).

Between November 25 and January 4, all 5 birds left South Sudan and moved south and east, arriving at a second wintering ground either near Lake Malawi (bird E) or on the shores of the Indian Ocean near the Mozambique–Tanzania border (birds A–D) between December 21 and January 19 (Figures 1, 2). Birds A, C, and D moved directly to their second wintering ground, arriving within 1 day of departure, while birds B and E took 41 and 15 days, respectively, to reach their second wintering ground. Bird B made 2 extended stopovers, 1 in South Sudan from November 26 to December 7, the other in Kenya from December 8 to January 3. Bird E stopped over in northern Mozambique from January 9 to January 18. Bird A relocated ~805 km north on January 29, possibly indicating an additional wintering ground (Figure 2). During the second part of the winter, none of the identified stationary periods for bird E met our criterion for a wintering ground (>30 days) as opposed to an extended stopover (Figure 2). This could have been caused by increased mobility on the part of the bird or geolocator error splitting a stationary period. For birds with an identifiable second wintering period, the length of stay averaged 73 days (range = 33–115 days). The average distance between the first and second wintering grounds was 2,161 km (range = 1,780–2,577 km).

During spring, migration routes were similar for all 5 birds. All birds moved north through the Horn of Africa and crossed into the Arabian Peninsula at the Bab-al-Mandeb Strait (Figure 1). All moved directly north over inland Saudi Arabia rather than tracing the coast (Figure 1). Patterns of movement, however, differed between birds. Bird A and bird D left on April 20 and April 19, respectively, and spent 14 and 12 days, respectively, migrating north. Both stopped over in northern Saudi Arabia–southern Iraq for 9 and 5 days, respectively. Birds B, C, and E left substantially earlier, between February 11 and March 6. All 3 birds made at least 4 stopovers, generally in eastern Kenya–western Somalia and southern Iraq (average length of stopover = 11 days, range = 4–29 days; Figure 2). Birds B and C each showed a stopover between Africa and Madagascar. These locations fell between stationary periods in the Horn of Africa and were likely artifacts of geolocator error. All 3 birds arrived back in eastern Turkey between May 1 and May 28. The average distance between the second wintering ground and the Aras breeding site was 5,533 km (range = 5,351–5,839 km).

During the 2014–2015 season, bird E followed a similar migration pathway as described in the 2013–2014 season (Figure 1). Bird E also exhibited similar patterns of stopover and wintered in similar locations in both years (Figure 2).

Together, the 5 birds potentially encountered 277 IBAs during the course of their migrations (total area = 62,269,453 ha). The majority of these sites (179, 65%) were potentially encountered by only 1 bird. However, 98 (35%) sites were potentially encountered by multiple birds and may be of general importance to migrants in the region (Appendix Table 1). Of all 277 IBAs potentially encountered, BirdLife International (2016) reports 115 (42%) as receiving little or no protection (area = 15,661,258 ha, 25% of total area), 8 (3%) as receiving some protection (7,443,453 ha, 12% of total area), 19 (7%) as mostly protected (area = 8,067,555 ha, 13% of total area), 130

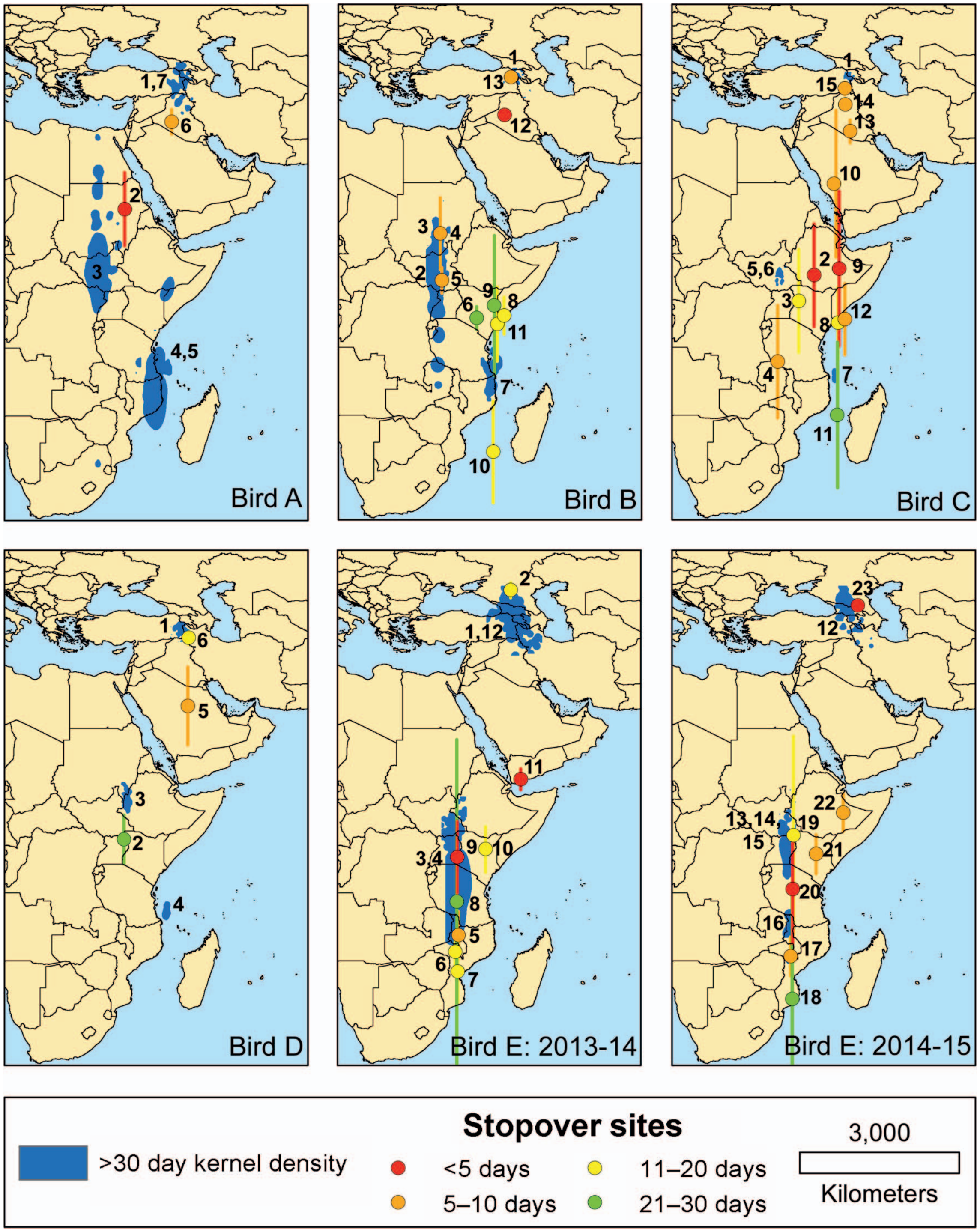

FIGURE 2. Locations of stationary periods throughout the migration of Great Reed-Warblers in the Middle East and sub-Saharan East Africa in 2013–2014 (birds A–D) and 2013–2015 (bird E). All stationary periods of >30 days are represented as blue kernel density plots. Stationary periods of <30 days are represented by average latitude and longitude, with error bars denoting standard deviation in latitude (standard deviation in longitude was too small to be evident). Green points and bars represent areas where birds spent between 20 and 30 days, yellow points and bars between 10 and 20 days, orange points between 5 and 10 days, and red points <5 days. The numbers on each map correspond to the order of visitation. Locations identified off-shore are likely an artifact of geolocator error.

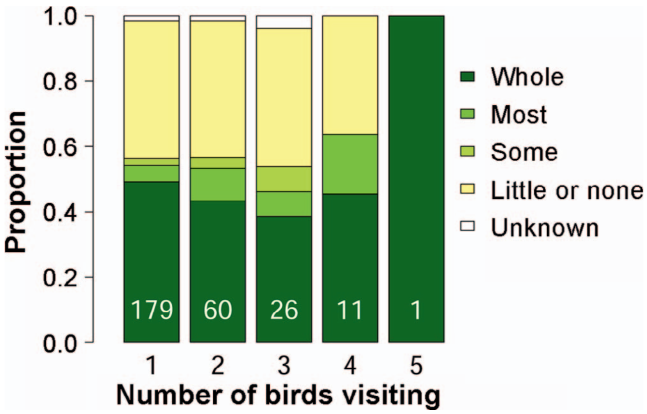

FIGURE 3. All 277 possibly encountered Important Bird Areas (IBAs) in the Middle East and sub-Saharan East Africa with respect to the number of Great Reed-Warblers that potentially made use of them during the 2013–2014 nonbreeding season. The proportions of IBAs within each visitation level receiving different levels of protection are denoted by color. The values within each bar indicate the number of IBAs with that visitation level.

(47%) as receiving complete protection (area = 29,464,187 ha, 47% of total area), and 5 (2%) as receiving an unknown level of protection (area = 1,633,000 ha, 3% of total area; Figure 3). There was no significant difference in the number of IBAs or IBA area encountered between the "most probable route" and the "most efficient route" (2-sample *t*-test, IBA number: $t_{6.925} = -0.63$, $P = 0.55$; IBA area: $t_{9.666} = -0.35$, $P = 0.73$).

DISCUSSION

Wintering Sites

Great Reed-Warblers breeding in Turkey made use of at least 2 wintering grounds in sub-Saharan Africa. This result is consistent with findings from mist-netting studies within Africa (Hedenström et al. 1993) and previous geolocator tracking of Great Reed-Warblers (Lemke et al. 2013, Koleček et al. 2016). South Sudan–northern Uganda, Lake Malawi, and the Indian Ocean coast near the Mozambique–Tanzania border all appear to be well-used wintering sites. The wintering sites in South Sudan and the Mozambique–Tanzania border reaffirm recently identified regions of importance for the Great Reed-Warbler (Koleček et al. 2016), but Lake Malawi appears to be a novel site. Though all 5 birds in our study made large-scale (i.e. >1,000 km) movements in mid-winter, several birds appeared to make smaller relocations as well, possibly indicating the use of more than 2 wintering grounds. As may be expected, these wintering sites are farther east than those used by Great Reed-Warblers that breed in Europe (Lemke et al. 2013), but agree closely with other wintering regions identified for populations of Great Reed-Warbler that breed elsewhere in Turkey (Koleček et al. 2016).

Along with winter site locality, we had occasion to investigate winter site fidelity in 1 individual from which 2 years of data were recovered. There were no obvious year-to-year differences in migration route or winter ground choice, suggesting that Great Reed-Warblers may exhibit winter site fidelity. However, these data come from only 1 individual.

Stopover Sites

We were able to identify many stopover locations, 2 of which were consistently used by several birds (Figure 2). These 2 locations, near the Kenya–Somalia border and in southern Iraq, may be critical stopover sites for birds traveling between Africa and the Middle East because they flank the geographic barrier formed by the deserts of the Arabian Peninsula and the Horn of Africa. Reliable stopover locations are limited in this region (Scott 1995), and Great Reed-Warblers appear to undertake a continuous migration across the Arabian Peninsula, which would explain the extended stopovers before and after crossing. Records of Great Reed-Warblers from either of these stopover sites range from occasional to nonexistent (Scott 1995, Stevenson and Fanshawe 2002, Sullivan et al. 2009). This highlights the importance of geolocator data for identifying regions of importance for bird species that otherwise go largely undetected.

Migration

Migration routes showed that all 5 birds moved in a similar counterclockwise pattern (Figure 1). First, from Turkey they flew southwest across Saudi Arabia and the Red Sea and into Sudan. Next they travelled south and east to either the Indian Ocean coast or the shores of Lake Malawi. Finally, they flew more or less straight north (with the exception of bird E, who first flew northeast to the Indian Ocean coast before continuing in a more northerly direction) across the Bab-al-Mandeb Strait, over inland Saudi Arabia and Iraq (Figure 1). While loop migrations are well documented, they are generally clockwise in both passerines and nonpasserines across the globe (Meyburg et al. 2003, Goodrich and Smith 2008, Klaassen et al. 2010, Schmaljohann et al. 2012, Willemoes et al. 2014). This is thought to be due to the dominant winds running east from ~30°N to 40°N and west from 30°S to 30°N. Some Afro-Palearctic migrants are known to exhibit counterclockwise migration (Bairlein 2001, Berthold 2001), and our study provides more evidence of this phenomenon. Great Reed-Warblers in particular present an interesting model for studying loop migrations, as some populations migrate clockwise while other populations, principally those wintering in east Africa, migrate counterclockwise (Koleček et al. 2016).

We found that birds traveled on average 3,646 km (range = 3,155–4,123 km) from their breeding grounds to their first wintering site, 2,161 km (range = 1,780–2,577 km) from their first wintering site to their second wintering site, and 5,533 km (range = 5,351–5,839 km) from their second wintering site back to their breeding grounds. These lengths parallel recently identified migration distances for another population of Great Reed-Warbler breeding in Turkey, with reported distances of 3,510 km (range = 3,391–3,743 km), 1,813 km (range = 1,251–2,285 km), and 5,123 km (range = 4,479–5,605 km) for 3 similar migration legs (Koleček et al. 2016). These data suggest the potential for Turkish populations of Great Reed-Warbler to migrate more than 12,000 km each year. Except for Great Reed-Warbler populations breeding in Sweden, these distances are the longest yet recorded for the species (Lemke et al. 2013, Koleček et al. 2016).

IBAs and Protection

The birds in this study potentially made use of 277 IBAs throughout the nonbreeding season. Although many of these areas have a substantial degree of protection (on paper, at least), >40% do not. Runge et al. (2015) found that >90% of migratory bird species do not have adequate protection in at least one part of their yearly range (Runge et al. 2015). Loss of habitat at migration bottlenecks in particular can lead to population-level effects (Runge et al. 2014). This study identified the Bab-al-Mandeb Strait as a consistently used migration bottleneck. However, this critical crossing is greatly understudied and the 3 IBAs most immediately associated with this area (Kadda Guéïni, Les Sept Frères, and Bab al-Mandab – Mawza) all receive little to no protection (BirdLife International 2016, Ç. Şekercioğlu personal observation). If human impact in this critical region inhibits the movements of migratory birds or the stopover potential of migration sites, it could result in substantial negative consequences for all birds traveling through this corridor. We found no difference in the number or area of IBAs along the "most probable route" compared with the "most efficient route" of the birds in our study, suggesting that birds are not deviating from the most efficient migration route due to habitat quality.

Conservation Implications

We estimate that each Great Reed-Warbler in our study visited a minimum of 11 different countries on 2 continents, for a total of 17 countries for all individuals. Many of the wetlands and IBAs where these birds spent an extended period of time spanned 2 or more political boundaries. This makes conservation efforts especially difficult in a region where conservation laws and practices vary considerably across borders (Dallimer and Strange 2015), and demonstrates the importance of international collaboration for the conservation of migratory species.

Also of note was the consistent use, during spring migration, of the Bab-al-Mandeb Strait, a substantially understudied part of the world. When migrating animals are funneled into narrow passages (e.g., due to topographic constraints), there is great potential for large population effects to occur if these passages deteriorate in their quality as migration corridors (Runge et al. 2014). Egyptian Vultures (*Neophron percnopterus*) breeding in eastern Turkey (E. Buechley and Ç. Şekercioğlu personal observations) and other Great Reed-Warbler populations breeding in Turkey (Koleček et al. 2016) also appear to favor crossing at the Bab-al-Mandeb Strait, suggesting that this area is critical for many migrants.

Our findings have wide-ranging conservation implications. Because Great Reed-Warblers are larger and more abundant than most wetland passerines, they are an excellent study species and can act as an indicator for other wetland songbirds that are not suitable for a study such as this one. Of the 608 species worldwide that primarily inhabit wetlands, more than a quarter (165 species, 27%) are listed as Near Threatened, Vulnerable, Endangered, Critically Endangered, or Extinct by the International Union for the Conservation of Nature (IUCN 2015). Of the 80 wetland-obligate bird species (i.e. species that reside only in wetlands), 54 species (68%) are threatened with extinction, including the Aquatic Warbler (*Acrocephalus paludicola*) and Basra Reed-Warbler (*Acrocephalus griseldis*). Wetland habitats are rare and increasingly threatened by a number of factors, including draining, reed and peat removal, burning, dam building, pollution, and climate change (Junk et al. 2013). It is important to note that birds may exhibit different habitat preferences during the breeding and nonbreeding seasons (Petit 2000), and thus the use of certain regions by Great Reed-Warblers does not necessarily imply suitability for other wetland breeders. Nevertheless, Great Reed-Warblers are good indicators for migratory wetland birds in the arid part of the world studied herein, and additional similar studies to identify important wetlands are a critical step for ensuring year-round protection for migratory species.

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APPENDIX TABLE 1. A list of all 277 BirdLife International Important Bird Areas (IBAs) in the Middle East and sub-Saharan East Africa potentially encountered by Great Reed-Warblers over the course of the 2013–2014 nonbreeding season. All IBAs include the number of Great Reed-Warblers (GRW) that potentially visited, as well as location, area, and categorical degree of protection according to BirdLife International (2016).

IBA name	Number of GRW that potentially visited	Country	IBA area (ha)	Degree of protection
Lake Uromiyeh	5	Iran	483,000	Whole
Bogol Manyo – Dolo	4	Ethiopia	430,000	Little or none
Baro River	4	Ethiopia	38,400	Little or none
Shur Gol, Yadegarlu, and Dorgeh Sangi lakes	4	Iran	2,500	Whole
Koguta Swamp	4	Kenya	200	Little or none
Masai Mara	4	Kenya	530,000	Whole
Mau Forest complex	4	Kenya	270,000	Most
South Nandi Forest	4	Kenya	13,000	Whole
Laag Dheere	4	Somalia	500,000	Little or none
Bandingilo	4	South Sudan	1,650,000	Whole
Boma	4	South Sudan	4,000,000	Most
Serengeti National Park	4	Tanzania	1,476,300	Whole
Lower Wabi Shebelle River and Warder	3	Ethiopia	1,200,000	Little or none
Gambella National Park	3	Ethiopia	506,100	Whole
Akh Gol	3	Iran	600	Little or none
Kiamaki Wildlife Refuge	3	Iran	95,742	Whole
Benavi and Sararu	3	Iraq	1,809	Little or none
Dure (Dori Serguza)	3	Iraq	2,310	Little or none
Ser Amadiya and Sulav Resort	3	Iraq	60,584	Little or none
Bakhma, Dukan, and Darbandikhan dams	3	Iraq	40,000	Little or none
Huweija Marshes	3	Iraq	30,000	Little or none
Kusa Swamp	3	Kenya	350	Little or none
North Nandi Forest	3	Kenya	10,500	Some
Kakamega Forest	3	Kenya	18,300	Whole
Kiunga Marine National Reserve	3	Kenya	25,000	Whole
Boni and Dodori National Reserves	3	Kenya	249,600	Most
Cherangani Hills	3	Kenya	100,000	Most
Mau Narok – Molo grasslands	3	Kenya	72,000	Little or none
Far Waamo	3	Somalia	140,000	Little or none
Laag Badaana	3	Somalia	334,000	Little or none
Sudd (Bahr-el-Jebel system)	3	South Sudan	5,500,000	Some
Juba	3	South Sudan	20,000	Whole
Imatong Mountains	3	South Sudan	570,000	Whole
Nimule	3	South Sudan	41,000	Whole
Kidepo	3	South Sudan	750,000	Unknown
Budongo Forest Reserve	3	Uganda	81,000	Whole
Murchison Falls National Park	3	Uganda	387,700	Whole
Lake Nakuwa	3	Uganda	16,500	Whole
Kadda Guéïni – Doumêra	2	Djibouti	20,000	Little or none
Eastern Hararghe (Harar-Wabi Shebelle)	2	Ethiopia	1,400,000	Some
Nechisar National Park and surroundings	2	Ethiopia	260,000	Some
Konso – Segen	2	Ethiopia	76,000	Most
Metu – Gore – Tepi forests	2	Ethiopia	383,055	Whole
Omo National Park	2	Ethiopia	430,000	Whole
Gordeh Git and Mamiyand	2	Iran	500	Little or none
Ghara Gheshlaq No-Hunting Area	2	Iran	400	Whole
Lake Kobi	2	Iran	1,200	Whole
Lake Tharthar and Al-Dhebaeji Fields	2	Iraq	340,573	Little or none
Razzaza Lake (Bahr Al Milh)	2	Iraq	156,234	Little or none
Samara Wetlands	2	Iraq	4,470	Little or none
Abu Dalaf and Shari Lake	2	Iraq	128,000	Little or none
Mida Creek, Whale Island, and the Malindi–Watamu Coast	2	Kenya	26,100	Whole
Tana River Delta	2	Kenya	130,000	Little or none
Meru National Park	2	Kenya	87,000	Whole
Lake Baringo	2	Kenya	28,400	Whole
Lake Bogoria National Reserve	2	Kenya	15,000	Whole

APPENDIX TABLE 1. Continued.

IBA name	Number of GRW that potentially visited	Country	IBA area (ha)	Degree of protection
Lake Nakuru National Park	2	Kenya	18,800	Whole
Aberdare Mountains	2	Kenya	190,000	Whole
Kikuyu Escarpment Forest	2	Kenya	37,000	Whole
Kinangop Grasslands	2	Kenya	72,000	Little or none
Mukurweini Valleys	2	Kenya	110,000	Little or none
Ruma National Park	2	Kenya	12,000	Whole
Lake Naivasha	2	Kenya	23,600	Whole
Busia Grasslands	2	Kenya	250	Little or none
Mount Elgon (Kenya)	2	Kenya	110,000	Whole
Lake Ol' Bolossat	2	Kenya	4,600	Little or none
Hells Gate National Park	2	Kenya	68	Little or none
Boja Swamps	2	Somalia	110,000	Little or none
Aangole – Farbiito	2	Somalia	11,000	Unknown
War Harqaan – isha Dolondole	2	Somalia	800,000	Little or none
Gezira	2	Sudan	850,000	Little or none
Dinder	2	Sudan	1,240,000	Most
Mafia Island	2	Tanzania	115,000	Most
Latham Island	2	Tanzania	3	Little or none
Mnazi Bay	2	Tanzania	10,000	Little or none
Bagamoyo District Coastal Forests	2	Tanzania	20,000	Most
Handeni District Coastal Forests	2	Tanzania	12,000	Whole
Muheza District Coastal Forests	2	Tanzania	5,000	Whole
Pangani District Coastal Forests	2	Tanzania	4,600	Most
East Usambara Mountains	2	Tanzania	39,000	Whole
Pemba Island	2	Tanzania	101,400	Little or none
Ruaha National Park	2	Tanzania	1,300,000	Whole
Lake Kitangire	2	Tanzania	12,000	Little or none
Lake Rukwa	2	Tanzania	600,000	Whole
Lake Victoria: Bunda Bay	2	Tanzania	30,000	Little or none
Wembere Steppe	2	Tanzania	160,000	Little or none
Lake Victoria: Mara Bay and Masirori Swamp	2	Tanzania	50,000	Little or none
Mabira Forest Reserve	2	Uganda	30,600	Whole
Ajai Wildlife Reserve	2	Uganda	15,800	Whole
Mount Kei Forest Reserve	2	Uganda	38,400	Whole
Mount Otzi Forest Reserve	2	Uganda	18,800	Whole
Doho Rice Scheme	2	Uganda	3,200	Little or none
Lake Bisina	2	Uganda	25,000	Whole
Lake Opeta	2	Uganda	56,600	Whole
Mount Elgon National Park	2	Uganda	180,000	Most
Mount Moroto Forest Reserve	2	Uganda	48,000	Whole
Ma'rib – Naqil Fardah – Baraqish	2	Yemen	250,000	Little or none
Aden	2	Yemen	10,000	Little or none
Garamba National Park	1	DR Congo	492,000	Whole
Lendu Plateau	1	DR Congo	410,000	Little or none
Marungu Highlands	1	DR Congo	970,000	Little or none
Les Sept Frères	1	Djibouti	4,000	Little or none
Siyal Islands	1	Egypt	200	Whole
Gebel Elba	1	Egypt	500,000	Whole
Danakil Lowlands	1	Eritrea	69,000	Little or none
Western Plain: Barka River	1	Eritrea	490,000	Little or none
Lakes Alemaya and Adele	1	Ethiopia	772	Little or none
Shek Husein	1	Ethiopia	650	Little or none
Boyo Wetland	1	Ethiopia	13,000	Whole
Senkele Sanctuary	1	Ethiopia	3,640	Whole
Sof Omar	1	Ethiopia	18,000	Little or none
Bale Mountains National Park	1	Ethiopia	960,000	Whole
Genale River	1	Ethiopia	93,000	Little or none
Anferara Forests	1	Ethiopia	430,000	Whole
Yabello Sanctuary	1	Ethiopia	249,600	Whole
Lake Chew Bahir	1	Ethiopia	112,500	Whole

APPENDIX TABLE 1. Continued.

IBA name	Number of GRW that potentially visited	Country	IBA area (ha)	Degree of protection
Lake Turkana and Omo Delta	1	Ethiopia	65,000	Little or none
Awi Zone	1	Ethiopia	160,000	Little or none
Mid-Abbay (Blue Nile) River Basin	1	Ethiopia	860,000	Little or none
Finchaa and Chomen swamps	1	Ethiopia	35,000	Little or none
Jibat Forest	1	Ethiopia	38,461	Whole
Tiro Boter – Becho Forest	1	Ethiopia	94,000	Whole
Bonga Forest	1	Ethiopia	160,000	Whole
Divandareh/Zarrineh Owbatu	1	Iran	5,000	Little or none
Hashelan Marsh and Doh Tappeh Plains	1	Iran	10,050	Little or none
Lake Zaribar	1	Iran	1,550	Little or none
Western Zagros north of Nowsud	1	Iran	57,000	Little or none
Arasbaran Protected Area	1	Iran	73,460	Whole
Oshtrankuh Protected Area	1	Iran	99,250	Whole
Dez Dam	1	Iran	1,500	Little or none
Karkheh River Marshes	1	Iran	19,021	Most
Dez River Marshes and Plains	1	Iran	22,834	Most
Karun River Marshes	1	Iran	2,500	Little or none
Horeh Bamdej	1	Iran	12,000	Little or none
Hamidieh (Omidiyeh) Plains	1	Iran	20,000	Little or none
Habbaniya Lake	1	Iraq	45,390	Little or none
Baquba Wetlands	1	Iraq	2,000	Little or none
Attariya Plains	1	Iraq	50,000	Little or none
Haur Al Shubaicha	1	Iraq	75,000	Little or none
Abu Habba	1	Iraq	400	Little or none
Al Jadriyah and Umm Al Khanazeer Island	1	Iraq	310	Little or none
Musayab	1	Iraq	162	Little or none
Hindiya Barrage	1	Iraq	278	Little or none
Ibn Najm	1	Iraq	4,000	Little or none
Arabuko-Sokoke Forest	1	Kenya	41,600	Whole
Kisite Island	1	Kenya	1	Whole
Kisite Island – Marine	1	Kenya	34,285	Little or none
Dakatcha Woodland	1	Kenya	32,000	Little or none
Kaya Gandini	1	Kenya	150	Whole
Kaya Waa	1	Kenya	20	Whole
Sabaki River Mouth	1	Kenya	20	Little or none
Shimba Hills	1	Kenya	21,740	Whole
Lower Tana River Forests	1	Kenya	3,700	Whole
Tsavo East National Park	1	Kenya	1,175,000	Whole
Lake Turkana	1	Kenya	756,000	Little or none
Amboseli National Park	1	Kenya	39,200	Whole
Nairobi National Park	1	Kenya	11,700	Whole
Kianyaga Valleys	1	Kenya	60,000	Little or none
Mount Kenya	1	Kenya	260,000	Whole
Dida Galgalu Desert	1	Kenya	620,000	Little or none
Masinga Reservoir	1	Kenya	100,000	Little or none
Mwea National Reserve	1	Kenya	4,200	Whole
Samburu and Buffalo Springs National Reserves	1	Kenya	29,600	Whole
Shaba National Reserve	1	Kenya	23,900	Whole
Dandora Ponds	1	Kenya	300	Little or none
Yala Swamp complex	1	Kenya	8,000	Little or none
Lake Elmenteita	1	Kenya	7,200	Whole
Sio Port Swamp	1	Kenya	400	Little or none
Misuku Hills Forest Reserves	1	Malawi	2,700	Whole
Nyika National Park (Malawi)	1	Malawi	310,000	Whole
Uzumara Forest Reserve	1	Malawi	610	Whole
Vwaza Marsh Wildlife Reserve	1	Malawi	98,600	Whole
Lake-shore Forest Reserves	1	Malawi	1,500	Most
South Viphya Forest Reserve	1	Malawi	160,000	Whole
Mtangatanga and Perekezi Forest Reserves	1	Malawi	23,000	Whole
Kasungu National Park	1	Malawi	231,600	Whole

APPENDIX TABLE 1. Continued.

IBA name	Number of GRW that potentially visited	Country	IBA area (ha)	Degree of protection
Nkhotakota Wildlife Reserve	1	Malawi	180,000	Whole
Dzalanyama Forest Reserve	1	Malawi	98,934	Whole
Namizimu Forest Reserve	1	Malawi	86,994	Whole
Mangochi Mountain Forest Reserve	1	Malawi	32,553	Whole
Liwonde National Park	1	Malawi	54,800	Whole
Liwonde Hills Forest Reserve	1	Malawi	29,473	Whole
Lake Chilwa and floodplain	1	Malawi	220,000	Whole
Soche Mountain Forest Reserve	1	Malawi	460	Whole
Mount Mulanje Forest Reserve	1	Malawi	60,000	Whole
Thyolo Tea Estates	1	Malawi	450	Little or none
Lengwe National Park	1	Malawi	88,700	Whole
Malawi Hills Forest Reserve	1	Malawi	400	Whole
Ntchisi Mountain Forest Reserve	1	Malawi	9,712	Whole
Netia	1	Mozambique	10,000	Little or none
Bazaruto Archipelago	1	Mozambique	50,000	Whole
Zambezi River Delta	1	Mozambique	500,000	Unknown
Mount Chiperone	1	Mozambique	16,000	Little or none
Furancungo Woodlands	1	Mozambique	10,000	Little or none
Njesi Plateau	1	Mozambique	30,000	Little or none
Gorongosa Mountain and National Park	1	Mozambique	385,000	Whole
Shallal ad-Dahna	1	Saudi Arabia	6,800	Little or none
Raydah Escarpment	1	Saudi Arabia	2,600	Some
Hawtat Bani Tamim	1	Saudi Arabia	236,900	Whole
Jabal Aja and Northern Ha'il	1	Saudi Arabia	400,000	Little or none
Al-Ha'ir	1	Saudi Arabia	2,500	Some
Gulf Coral Islands	1	Saudi Arabia	2,000	Little or none
Boorama Plains	1	Somalia	30,000	Little or none
Jasiira Ceebaad and Jasiira Sacaada Diin	1	Somalia	690	Little or none
Saylac	1	Somalia	370,000	Little or none
Southern National Park	1	South Sudan	2,300,000	Whole
Lake Abiad (South Sudan)	1	South Sudan	250,000	Little or none
En Nahud	1	Sudan	2,500,000	Little or none
Lake Abiad (Sudan)	1	Sudan	250,000	Little or none
Mukawwar Island and Dunganab Bay	1	Sudan	12,000	Little or none
Khor Arba'at	1	Sudan	20,000	Little or none
Mikumi National Park	1	Tanzania	323,000	Whole
Selous Game Reserve	1	Tanzania	5,000,000	Whole
Dar es Salaam Coast	1	Tanzania	61,000	Little or none
Rufiji Delta	1	Tanzania	72,000	Unknown
Zanzibar Island – South Coast	1	Tanzania	4,000	Little or none
Zanzibar Island – East Coast	1	Tanzania	10,000	Little or none
Kisarawe District Coastal Forests	1	Tanzania	42,000	Whole
Rufiji District Coastal Forests	1	Tanzania	15,519	Whole
Pande Game Reserve and Dondwe Coastal Forests	1	Tanzania	1,600	Whole
Kilwa District Coastal Forests	1	Tanzania	213,853	Some
Lindi District Coastal Forests	1	Tanzania	30,000	Most
Mtwara District Coastal Forests	1	Tanzania	1,736	Whole
Jozani Chwaka Bay National Park	1	Tanzania	556	Whole
Rubeho Mountains	1	Tanzania	45,000	Whole
Ukaguru Mountains	1	Tanzania	21,000	Whole
Uluguru Mountains	1	Tanzania	36,000	Whole
Arusha National Park and vicinity	1	Tanzania	42,000	Most
Katavi National Park	1	Tanzania	323,000	Whole
Mount Kilimanjaro	1	Tanzania	190,000	Whole
Ugalla River Game Reserve	1	Tanzania	472,000	Whole
Nyumba ya Mungu Reservoir	1	Tanzania	22,000	Little or none
North Pare Mountains	1	Tanzania	8,000	Whole
West Usambara Mountains	1	Tanzania	38,169	Whole
Longido Game Controlled Area	1	Tanzania	280,000	Most
Loazi-Kalambo Forest Reserves and surrounding area	1	Tanzania	110,000	Most

APPENDIX TABLE 1. Continued.

IBA name	Number of GRW that potentially visited	Country	IBA area (ha)	Degree of protection
Lake Manyara	1	Tanzania	109,699	Whole
Ngorongoro Conservation Area	1	Tanzania	810,000	Whole
Maswa Game Reserve	1	Tanzania	220,000	Whole
Lake Eyasi	1	Tanzania	116,000	Little or none
Kilombero Valley	1	Tanzania	400,000	Whole
Singida Lakes	1	Tanzania	1,100	Little or none
Lake Tlawi	1	Tanzania	300	Little or none
Usangu Flats	1	Tanzania	300,000	Unknown
Livingstone Mountains forests	1	Tanzania	10,802	Whole
Njombe Forests	1	Tanzania	180	Whole
Mount Rungwe	1	Tanzania	45,000	Whole
Umalila Mountains	1	Tanzania	12,000	Whole
Kitulo Plateau	1	Tanzania	65,000	Whole
Sango Bay area	1	Uganda	54,000	Some
Musambwa Islands	1	Uganda	8	Whole
Lutoboka Point (Ssese Islands)	1	Uganda	200	Whole
Nabugabo Wetland	1	Uganda	22,500	Whole
Mabamba Bay	1	Uganda	16,500	Little or none
Nabajjuzi Wetland	1	Uganda	1,763	Whole
Bugoma Central Forest Reserve	1	Uganda	40,100	Whole
Kidepo Valley National Park	1	Uganda	150,000	Whole
Nukhaylah – Ghulayfiqah	1	Yemen	1,800	Little or none
Al-Fazzah	1	Yemen	3,500	Little or none
Al-Mukha – Al-Khawkhah	1	Yemen	7,000	Little or none
Jaza'ir al-Zubayr	1	Yemen	3,300	Little or none
Jabal Sumarah	1	Yemen	37,000	Little or none
High mountains of Ibb	1	Yemen	160,000	Little or none
Bab al-Mandab – Mawza	1	Yemen	5,000	Little or none
Jabal Iraf	1	Yemen	7,700	Little or none
South Luangwa National Park	1	Zambia	905,000	Whole
North Luangwa National Park	1	Zambia	463,600	Whole
Shiwa Ng'andu	1	Zambia	9,000	Whole
Lavushi Manda National Park	1	Zambia	150,000	Whole
Bangweulu Swamps	1	Zambia	1,284,000	Most
Kalungwishi	1	Zambia	15,000	Little or none
Saise River	1	Zambia	4,000	Little or none
Sumbu National Park and Tondwa Game Management Area	1	Zambia	260,300	Whole
Uningi Pans	1	Zambia	1,000	Little or none
Lukususi National Park	1	Zambia	272,000	Whole
Nyika National Park (Zambia)	1	Zambia	27,000	Whole
Mafinga Mountains	1	Zambia	23,000	Most