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Geocator study reveals that Canarian Plain Swifts *Apus unicolor* winter in equatorial West Africa.

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Summary

The Plain Swift *Apus unicolor* is a range-restricted member of the swift family, breeding only on the Canary Islands and Madeira in the north-east Atlantic. The species is essentially unstudied apart from three investigations on breeding biology in the Canary Islands (Garcia-del-Rey, 2006; Garcia-del-Rey *et al.*, 2008; Garcia-del-Rey *et al.* 2011) and no studies have ever been undertaken into its migratory behaviour.

The populations of these two Macaronesian archipelagos are believed to be partly migratory, with an unknown proportion of the breeding population departing the islands during the winter months (Chantler and Driessens, 1995). Based on infrequent field observations it has been speculated that the wintering grounds of birds leaving the Canary Islands is coastal north-west Africa and the adjacent hinterland (Isenmann *et al.*, 2010). This study aimed to investigate the wintering locations and migratory behaviour of Canarian Plain Swifts using geocator technology.

A total of 16 Plain Swifts were fitted with geolocators at two breeding colonies on the island of Tenerife, Canary Islands in July 2013. Of these birds two were subsequently recovered at one breeding colony the following May. Upon commencement of post-breeding migration, both Plain Swifts in this study flew east then south and spent the majority of the winter months in the forests of eastern Liberia in equatorial West Africa.

The birds departed the Canarian breeding colony in October and November respectively and travelled at least 2,600 kilometres (km) to wintering grounds within eastern Liberia and adjacent areas. Both birds spent the entire wintering period until March/April 2014 in the Upper Guinean forests of Liberia, Guinea and Ivory Coast

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before returning to Tenerife via overland routes through western Africa. Time spent outside the Canary Islands was 195 days and 187 days respectively. One bird made several abortive attempts at return migration, travelling from Liberia to the north-west African coast and back three times between 1 April 2014 and its final return to Tenerife on 2 May.

Our data demonstrate that at least some Canarian Plain Swifts undertake substantial migrations to spend the winter months in the Upper Guinean forests of equatorial West Africa (primarily eastern Liberia) and demonstrate that for some birds this journey can be made in an extremely short timeframe. A new status for Macaronesia as 'migrant breeder' is proposed as a result of this study. The birds' migratory route included passage through several countries with no previous records of the species: this includes Senegal, The Gambia, Guinea-Bissau, Guinea, Sierra Leone and Ivory Coast. The study highlights the importance of the Upper Guinean forest ecosystem for at least some Canarian Plain Swifts, with birds spending more than half their year in this biodiversity hotspot.

Introduction

The Plain Swift is a Macaronesian endemic, confined as a breeding species to the Canary Islands and Madeira, and found in all habitat types. Nest sites are recorded in natural features such as caves and cliff faces, and birds readily utilise man-made features such as buildings (occupied or derelict). Although the Plain Swift is currently listed as 'Least Concern' by Birdlife (Birdlife International, 2018), it is recognised that the species is 'rare' and that whilst 'the population is suspected to be stable in the absence of evidence for any declines or substantial threats', trend data for the decade 1990-2000 were 'not available'. The most recent population estimate data for this species (15,000-40,000 individuals for year 2012) are of 'poor' quality (Birdlife International, 2012) and thus there is clearly a need for further population and trend data for this range-restricted endemic. The populations of the two archipelagos are believed to be partly migratory and there is presumably some inter-island movement although the extent of this is not known.

Most authors concur that the species is a 'partial migrant' in the Canary Islands (Bannerman and Bannerman, 1963; Garcia-del-Rey, 2011) as birds are recorded during the winter period in small numbers (Garcia-del-Rey pers. obs.). According to Martin and Lorenzo (2001) the migrant population leaves the archipelago in September-October and returns back in December-January. However, the breeding season extends from early March to mid-September (Garcia-del-Rey, 2006), hence departure should be best considered from mid-September onwards: this study also demonstrates that departure of some birds occurs between late September and mid-late November and returning birds arrive in the Canary Islands between March and May.

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Prior to this study the wintering grounds for the species were unconfirmed although infrequent sightings in Morocco and Mauritania (Chantler and Boseman, 2018) have suggested that coastal north-west Africa was the likely destination for migrating birds.

In Morocco the status of the species is unclear (i.e. probably an accidental winter visitor since the late 1970s and occasional breeder, either rare resident or breeding migrant, since the late 1980s) with the first reports in the winters 1962/63 and 1963/64. According to Isenmann *et al.* (2010) the species is known to winter on the African coast from Morocco southwards to Mauritania ($n=5$ observations at Nouakchott and Banc d'Arguin), but the wintering grounds of the bulk of the population remain unknown. There is some recent indication that this species may breed in western Morocco (Vernon, 2002; Thévenot *et al.* 2003; Amezian *et al.*, 2006; Aourir *et al.* 2017) although this is not confirmed. The Plain Swift is extremely similar in appearance to both Common Swift *Apus apus* and, to a lesser degree, Pallid Swift *Apus pallidus*, and therefore detailed observations are required to confirm identity. Sightings of small, dark swifts in the Cape Verde islands have been putatively identified as Plain Swift (Hazevoet, 2014).

The Plain Swift is therefore one of the very few migrant species within the European Union for which there is essentially no knowledge of migratory movements, albeit with tantalising anecdotal hints of potential populations at locations on the African mainland. That a proportion of the Macaronesian Plain Swift population may winter in continental Africa is not controversial but was, prior to this study, speculative.

Migratory bird populations can find themselves at risk from various factors and, for a range-restricted endemic species, such factors may have profound impacts. Recent studies of Common Swift migration have shown the importance of regional 'bottlenecks' within continental Africa: if a significant proportion of the global Plain Swift population also utilises such restricted migratory corridors this could render the species vulnerable to anthropogenic environmental or climate change. The often extensive annual movements undertaken by many bird species present significant challenges for conservationists (Runge *et al.*, 2014). The effective conservation of the Plain Swift, and other range-restricted migrants, will necessitate sound knowledge of the species' habitat requirements in both breeding and non-breeding areas. Whilst the species is currently not considered to be threatened, this assessment is acknowledged to be based on poor quality data and takes no account of the species' wintering range (which has until now remained unconfirmed). The description of the species exhibiting 'low' forest dependency (Birdlife, 2018) does not reflect the apparent dependence shown for Afrotropical forest ecosystems as revealed by this study and needs revising.

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Methods

Between the 5 and 12 July 2013 an expedition was made to the Canary island of Tenerife to coincide with the peak Plain Swift breeding season. Two ringing sites were chosen in order to target two apparently-distinct breeding colonies, approximately 50km apart. The first was in the village of El Tablero in the north-east of Tenerife (28.419882, -16.330103), the second in the tourist community of Ten-Bel in the south-west (28.01144, -16.639314). Both sites are well-known and established Plain Swift nesting colonies, having been monitored for many years (Garcia-del-Rey, pers. comm.).

Both ringing sites were within disused and partially-completed buildings, each comprising essentially a bare-concrete shell with open walls and windows (Figure 1) through which adult birds returned to nest holes. The El Tablero building was single-storey whilst the Ten-Bel structure was multi-storey. The swifts were nesting within holes in the ceilings of the buildings, allowing access to the hollow air-blocks used in the buildings' construction. Active nests were identified by piles of fresh droppings below the holes and the repeated visits by adult birds.



Figure 1 Plain Swift breeding colony in uncompleted dwelling, El Tablero, Tenerife

Mist nets were placed within the building interiors, across the most frequently-used entrances and intercepting the flight routes to as many active nest holes as possible. Birds were then caught in small batches at regular intervals and subsequently processed.

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Once caught the birds were metal-ringed and fitted with Intigeo-W65/W55 geolocators, each device of 0.6g equating to c.2 to 3.3% of body mass (adult mass range 18.4g – 30.0g (Garcia-del-Rey *et al.* 2008)). Devices were attached using a thoracic harness which is the standard method used for Common Swifts (Figure 2).

In total, eight birds were fitted with geolocators at each of the two sites, giving a good-sized sample for a geolocator study of 16 individuals. In addition, a total of eight control birds (metal-ringed only) were trapped at the El Tablero site: no additional birds were trapped at Ten-Bel.



Figure 2 Plain Swift H001, El Tablero, Tenerife 9 July 2013

Two birds (geolocators H001 and H006) were subsequently recovered at El Tablero in May 2014 in addition to three control birds (metal ring only). No birds from the Ten-Bel site were recovered as the birds had stopped using the part of the building where the geolocators were fitted. Three trapping sessions at Ten-Bel in May 2014 resulted in a small number of captures of Plain Swifts, each bird showing poor muscle formation and one metal-ringed bird was discovered dead within a nest cavity. This colony was clearly impacted by factors relating to food resources.

The relatively poor recovery rate (12.5%) of tagged birds was disappointing but as the retrap rate was not dissimilar to that of the control birds we do not conclude that the geolocators were having a major effect on the birds. The degree to which geolocators affect survival rates in birds is not well-known and is worthy of further investigation (Bowlin *et al.* 2010; Costantini *et al.* 2013; Matyjasiak *et al.* 2016).

Results

Two Plain Swifts fitted with geolocators were recovered at El Tablero in May 2014.

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Bird H001

This individual was trapped at the El Tablero site on 9 July 2013. It remained in Tenerife and roosted in a cavity each night until the night of 30 September/1 October until leaving its nest cavity for the last time on the morning of 1 October. The data for the period to 18 October are unclear and the bird may have remained within the Canary Islands for this period. From 18/19 October the bird was located in Western Sahara/Mauritania and made its way south to enter Liberia by 23 October (Figure 3).



Figure 3 Position of H001 between 18 October and 26 October 2013

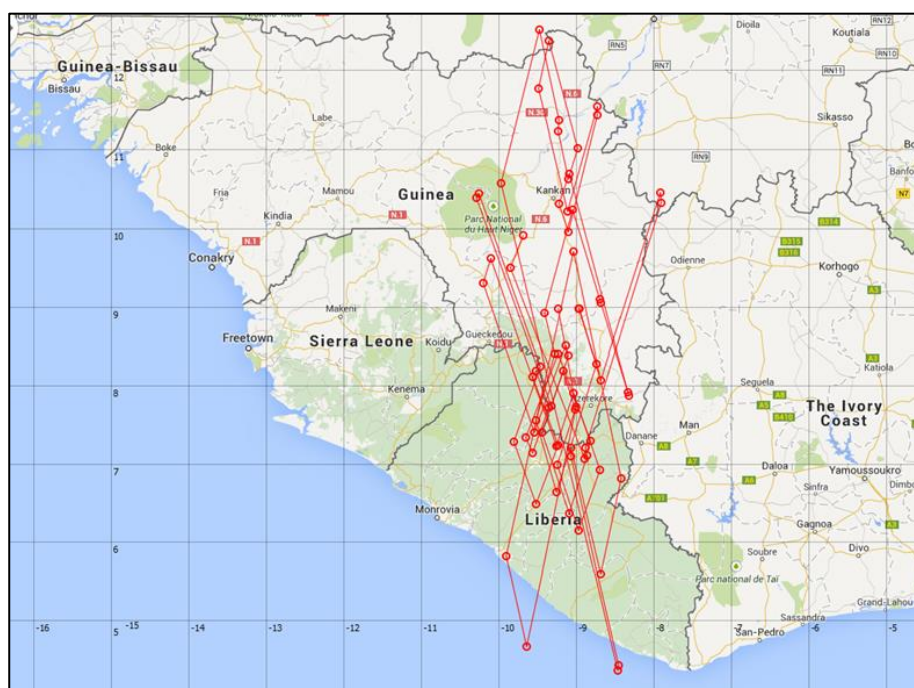


Figure 4 Position of H001 between 25 October and 30 November 2013

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H001 remained within eastern Liberia and south-eastern Guinea throughout November (Figure 4) and until early April.

At the start of its return to the Canary Islands the bird then began a highly unusual series of movements, commencing with a flight to coastal Mauritania between 1 and 5 April (Figure 5). This appears to have been an abortive attempt at return migration, as the bird then heads south again and enters Liberia on 13 April (Figure 6). The bird is again in Mauritania on 16 April (Figure 7) before heading south once more to Liberia until the end of April (Figure 8). On 30 April the bird heads rapidly north, reaching Western Sahara at midday on 1 May and enters a cavity in the Canary Islands on 3 May (Figure 9). This bird therefore made two abortive attempts to reach the Canary Islands, returning from north-west Africa to the Upper Guinean forests for two short periods before finally completing its return migration. It is unclear what caused this unusual behaviour.



Figure 5 Position of H001 between 1 April and 5 April 2014

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Figure 6 Position of H001 between 5 April and 13 April 2014



Figure 7 Position of H001 between 13 April and 16 April 2014

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Figure 8 Position of H001 between 16 April and 27 April 2014



Figure 9 Position of H001 between 27 April and 2 May 2014

Bird H006

This individual was trapped at the El Tablero site on 9 July 2013. It remained in Tenerife and roosted in a cavity each night until the morning of the 22 November when it left its cavity for the last time. The positions for the next week show a rapid

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movement south and east towards Liberia (Figure 10). The week after that shows it to be in Guinea/Liberia.

The following week appears to show the bird situated within Guinea/Liberia and then throughout December and January within eastern Liberia, most likely within and around Sapo National Park, with perhaps some movements eastwards into Ivory Coast. During February the bird appears to have remained in eastern Liberia.

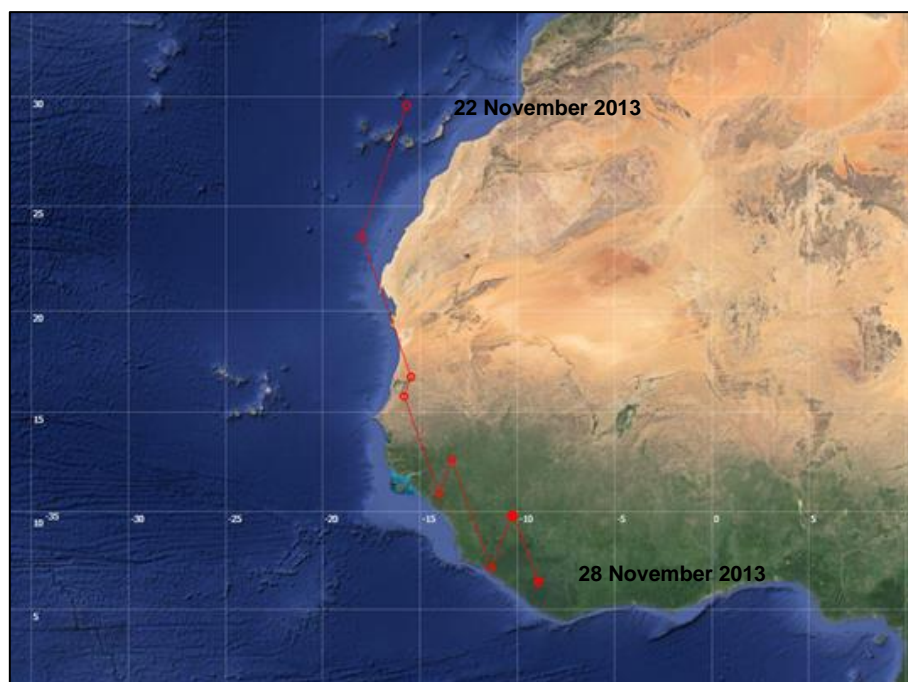


Figure 10 Position of H006 between 22 November and 28 November 2013

H006 remained in equatorial West Africa between late November and late March, and between 28 and 30 March was most likely within Senegal/Gambia/Guinea Bissau. By 12 April the bird had reached the Canary Islands and began roosting within a cavity.

Discussion

The Upper Guinean forest ecosystem of equatorial West Africa is clearly an attractive area for resident and migrant (Palearctic and intra-African) birds including swifts. At least fourteen species of swift are known to occur (either as residents or seasonal migrants) in West Africa: Alpine Swift *Tachymarptis melba*, Mottled Swift *T. aequatorialis*, Plain Swift, Common Swift, Pallid Swift, African Swift *Apus barbatus*, Little Swift *A. affinis*, White-rumped Swift *A. caffer*, Bates's Swift *A. batesi*, Black Spinetail *Telacanthura melanopygia*, Mottled Spinetail *T. ussheri*, Cassin's Spinetail *Neafrapus cassini*, Sabine's Spinetail *Rhaphidura sabini* and African Palm-swift *Cypsiurus parvus*.

The aerial-feeding bird guild of these forests is essentially unstudied and it is not known how these various resident and migrant species interact. There is presumably

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a degree of niche-separation/resource-partitioning within such a diverse aerial-feeding guild, as has been demonstrated within swifts in the Neotropics (Collins, 2015), swiftlets in Asia (Lourie and Tompkins, 2000) and Indo-Australasia and Polynesia (Salomonsen, 1983), as well as amongst aerial-feeders in Europe (Orlowski and Karg, 2013). Similarly-sized species with near-identical foraging behaviour may differentiate themselves from other species in several ways. Species may concentrate on differing prey sizes or types or may occupy different airspace or exploit different habitats. Some studies have investigated gape size and determined that this physiological feature may allow several similar species to utilise the same habitat (Salomonsen, 1983). It seems unlikely that differences in gape size alone between so many similar species would allow full ecological differentiation: rather such diversity may be facilitated by a combination of physiological and ecological adaptations as well as prey diversity, abundance and availability.

Minimal detailed information currently exists on the feeding strategies of Plain Swifts and this aspect of swift ecology has only recently been studied in detail in the more familiar Common Swift (de Margerie *et al.* 2018). In the only study on Plain Swift diet, Garcia-del-Rey *et al.* (2011) found that average prey size was 2.4mm (range 0.5mm – 9.7mm) for birds sampled on Tenerife. This study concluded that, in common with other swift species, Plain Swifts will tend to choose prey items according to size although it is not known with certainty whether Plain Swifts, or any other species, primarily choose prey of a particular size or whether diet simply reflects the availability of prey items in a particular locale at a given time: presumably there will be a degree of seasonality in swift diets and that diet will be affected by foraging habitat. In the Canary Islands intra-specific competition is limited, with only three *Apus* swifts (Plain, Common and Pallid) generally present during the breeding season and therefore the requirement for ecological separation is presumably equally limited. The degree to which Plain Swifts adapt their feeding strategy within an Afrotropical system in the presence of greater intra-specific competition from other resident and migrant swift species is unknown.

It may be that the diversity and extent of suitable habitat (e.g. differing forest types), as well as the diversity and availability of insect prey, allows for such diversity in aerial-feeders in Afrotropical systems. Information on aerial insect diversity and abundance in the Upper Guinean forest ecosystem is non-existent but could be a fruitful area of study for understanding the ecology of the aerial-feeding bird guild and how future land-use changes may impact these species.

That so many swift species appear to inhabit the Upper Guinean forest ecosystems raises the question of whether ongoing threats to these forests may impact swift populations. The relative paucity of information on birds of the Upper Guinean forest ecosystem means that such conclusions are speculative.

The Upper Guinean forest ecosystem is one of the world's great biodiversity hotspots yet is under increasing pressure from anthropogenic land-use change and

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has seen significant alteration in recent decades (Christie *et al.*, 2007; Kofron and Chapman, 1995; Norris *et al.*, 2010; Waltert *et al.*, 2005). For example, each of the eight main forest Important Bird Areas (IBA) within Liberia is considered to be under threat from a range of human activities: logging, agriculture, burning, fragmentation, hunting, mining, infrastructure development, hydroelectricity, warfare and political instability (Birdlife International, 2018) and threat levels are considered to be 'high' in all areas. It is unclear what impacts this activity has on the wider ecosystem but presumably it is generally negative. The extent to which changes in forest cover and type can impact aerial-feeding bird species is unknown.

It is clear from this study that some Canarian Plain Swifts migrate across West Africa and observations of small, dark swift species within e.g. Mauritania, Cape Verde may well relate to migratory Plain Swifts. Records from inland Morocco require confirmation but may well relate to a previously-unknown breeding population.

Conclusion

Two Plain Swifts were tracked from their breeding colonies on the Macaronesian island of Tenerife, Canary Islands. Both birds spent the majority of the winter months within the Upper Guinean forests of eastern Liberia, with movements into adjacent countries. This study confirms for the first time that at least some Canarian Plain Swifts winter in equatorial West Africa and that this Afrotropical system should be considered to be of primary importance for Plain Swift conservation.

Although this study has confirmed the wintering grounds of some Canarian Plain Swifts, and it is reasonable to infer a degree of consistency within the species' migratory movements (Åkesson *et al.* 2012; Jacobsen *et al.* 2017; Wellbrock *et al.* 2017), the sample size of two birds is limited. A larger sample size, ideally comprising birds from varied locations within Macaronesia, is needed in order to investigate whether the Upper Guinean forests do indeed comprise the main wintering grounds for this endemic species. Further study will also allow investigation of any variations in wintering areas as well as any differences between years.

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References and Bibliography

Åkesson, S., Klaassen, R., Holmgren, J., Fox, J.W., and Hedenström, A. (2012). *Migration Routes and Strategies in a Highly Aerial Migrant, the Common Swift Apus apus, Revealed by Light-Level Geolocators*. PlosOne, July 18 2012.

Aourir, M.; Bousadik, H.; El Bekkay, M.; Oubrou, W.; Znari, M. and Qninba, A. 2017. *New breeding sites of the Critically Endangered Northern Bald Ibis Geronticus eremita on the Moroccan Atlantic Coast*. International Journal of Avian & Wildlife Biology 2(3).

Bannerman, D.A. and Bannerman W.M. (1963). *Birds Of The Atlantic Islands, Volume 1*. Oliver & Boyd, Edinburgh.

BirdLife International (2018) *Endemic Bird Areas factsheet: Upper Guinea forests*. Downloaded from <http://www.birdlife.org> on 07/01/2018.

BirdLife International (2018) *Species factsheet: Apus unicolor*. Downloaded from <http://www.birdlife.org> on 07/01/2018.

Bowlin, M.S., Henningsson, P., Muijres, F.T., Vleugels, R.H.E., Liechti, F. and Hedenström, A. (2010). *The effects of geolocator drag and weight on the flight ranges of small migrants*. Methods in Ecology and Evolution 2010 (1): 398-402.

Chantler, P and Driessens, G (1995). *Swifts: a guide to the swifts and treeswifts of the world*. Pica Press, East Sussex.

Chantler, P. and Boesman, P. (2018). *Plain Swift (Apus unicolor)*. In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona.

Christie, T; Steininger, M K; Juhn, D. and Peal, A. (2007). *Fragmentation and clearance of Liberia's forests during 1986-2000*. Oryx 41:4, 539-543.

Collins, C.T. (2015). *Food habits and resource partitioning in a guild of Neotropical swifts*. The Wilson Journal of Ornithology 127:2, 239- 248.

Costantini, D. and Moller, A. (2013). *A meta-analysis of the effects of geolocator application on birds*. Current Zoology 59(6).

Garcia-Del-Rey, E., Gosler, A.G., Gonzalez, J. and Wink, M. (2008) *Sexual size dimorphism and moult in the Plain Swift Apus unicolor*. Ringing & Migration, 24(2): 81-87.

Garcia-del-Rey, E. (2006) *Notes on the breeding biology of Plain Swift Apus unicolor on Gran Canaria, Canary Islands*. African Bird Club Bulletin, 13(1): 56-59.

Geolocator study reveals that Canary Plain Swifts *Apus unicolor* winter in equatorial West Africa.

Garcia-del-Rey E., Collins C.T. and Volpone N.W. 2010. *Food composition of the endemic Plain Swift Apus unicolor in the Canary Islands (Macaronesia)*. *Ardea* 98: 211–215.

Hazevoet, C.J. (2014). *Eighth report on birds from the Cape Verde Islands, including records of nine taxa new to the archipelago*. *Zoologia Caboverdiana* 5 (1): 29-56.

Isenmann, P., Benmergui, M., Browne, P., Ba, A.D., Hamallah Diagana, C., Diawara, Y. and El Abidine ould Sidaty, Z. (2010). *Oiseaux de Mauritanie*. SEOF, Paris. 408 pp

Jacobsen L.B., Jensen NO, Willemoes M, Hansen L, Desholm M, Fox A.D., Tøttrup A.P. and Thorup K. (2017). *Annual spatiotemporal migration schedules in three larger insectivorous birds: European nightjar, Common Swift and common cuckoo*. *Animal Biotelemetry* 5:4.

Kofron, C.P. and Chapman, A. (1995) *Deforestation and bird species composition in Liberia, West Africa*. *Tropical Zoology*, 8:2, 239-256.

Lourie, S. A. and Tompkins, D. M. (2000). *The diets of Malaysian swiftlets*. *Ibis*, 142: 596–602.

de Margerie, A., Pichot, C. and Benhamou, S (2018). *Volume-concentrated searching by an aerial insectivore, the common swift, Apus apus*. *Animal Behaviour* 136, 159-172.

Marin, M. A. and Stiles, F.G. (1993). *Notes on the biology of the spot-fronted swift*. *Condor* 95: 479-483.

Martin, A. and Lorenzo, J.A. (2001). *Aves del Archipiélago Canario*. Lynx Edicions, Barcelona.

Matyjasiak, P., Rubolini, D., Romano, M. and Saino, N. (2016). *No short-term effects of geolocators on flight performance of an aerial insectivorous bird, the Barn Swallow (Hirundo rustica)*. *Journal of Ornithology* 157:653

Norris, K., Asase, A., Collen, B., Gockowksi, J., Mason, J., Phalan, B. and Wade, A. (2010) *Biodiversity in a forest-agriculture mosaic - The changing face of West African rainforests*. *Biological Conservation* 143 (10) pp. 2341-2350.

Orłowski, G. and Karg, J. (2013) *Diet breadth and overlap in three sympatric aerial insectivorous birds at the same location*. *Bird Study*, 60:4, 475-483.

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G. and Fuller, R. A. (2014), *Conserving mobile species*. *Frontiers in Ecology and the Environment*, 12: 395–402.

Geolocator study reveals that Canary Plain Swifts *Apus unicolor* winter in equatorial West Africa.

Salomonsen, F. (1983). *Revision of the Melanesian swiftlets (Apodes, Aves) and their conspecific forms in the Indo-Australasian Polynesian regions*. Biol. Skr. Dan. Vidensk. Selsk. 23 (5): 1-112.

Thévenot, M., Vernon, J.D.R. and Bergier, P. (2003). *The Birds of Morocco*. British Ornithologist Union Checklist Series: 20.

Vernon, R. (2002). *The status of Plain Swift *Apus unicolor* in Morocco*. African Bird Club Bulletin, 9(2): 107-109.

Waltert, M., Bobo, K. S., Sainge, N. M., Fermon, H. and Mühlenberg, M. (2005), *From forest to farmland: habitat effects on Afrotropical forest bird diversity*. Ecological Applications, 15: 1351–1366.

Wellbrock, A. H. J., Bauch, C., Rozman, J. and Witte, K. (2017), ‘*Same procedure as last year?*’ *Repeatedly tracked swifts show individual consistency in migration pattern in successive years*. J Avian Biol, 48: 897–903.