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A taxonomic review of the genus Zosterops in East Africa, with a revised list of species occurring in Kenya, Uganda and Tanzania

David J. Pearson and Donald A. Turner

Summary

Species limits among East African white-eyes Zosterops are reviewed. Recent molecular studies have revealed that arrangements such as those of Britton (1980), with just three species, and Fry (2000), with four species, are unsatisfactory. Most of the isolated highland forms which have been grouped under Z. poliogaster evolved independently and warrant treatment as full endemic species. Forms hitherto treated as subspecies of Z. senegalensis have been recovered within two divergent African clades. Within a northern clade Z. stuhlmanni appears best split pro tempore from Z. senegalensis (sensu stricto). Within a southern clade, stierlingi and anderssoni may be treated as subspecies of Z. anderssoni. The pale yellow-bellied forms, included until now within Z. abyssinicus, were found in a different lineage from northeast African grey-bellied forms, and must be treated under Z. flavilateralis. With the inclusion of Z. vaughani of Pemba Island this results in a total of eleven East African species. These are listed with details of all constituent subspecies, distributions and synonyms. Occurrence within Kenya, Tanzania and Uganda is summarized in an appendix.

Introduction

The abundance of African white-eye forms, most of them morphologically similar, has long presented problems for taxonomists, in particular the placement of their species limits. Moreau (1957) admitted just three Zosterops species for the African mainland: Z. senegalensis, with yellow-bellied forms widespread in woodland; a duller Z. abyssinicus with grey- or yellow-bellied birds in drier northeastern lowlands; and a rather dull southern Z. pallidus with belly grey, green or buff-and-white. The various isolated forms in the highlands of Ethiopia, eastern Kenya and northeast Tanzania with a rich green back, either a grey or bright yellow belly, and typically a broad eye-ring, he included within Z. senegalensis, as also did White (1963). But Hall & Moreau (1970) treated these together as a separate montane species Z. polioagastrus, and this arrangement of four mainland Zosterops, each with a number of subspecies, was followed by Fry (2000), Dickinson (2003) and von Balen (2008). Following Oatley et al. (2012), Dickinson & Christidis (2014) separated a fifth species, Z. virens from Z. pallidus in South Africa.

Recent molecular genetic studies have brought into question the utility of traditional morphological characters in assessing African white-eye relationships. For example, three Gulf of Guinea species placed in the distinctive-looking genus Speirops have been found to be nested within Zosterops, each aberrant species more closely related to typical Zosterops than they are to each other (Melo et al. 2011). And the wide-ranging Z. senegalensis is clearly polyphyletic, for DNA analyses have recovered
subspecies *stenocricotus* and *stierlingi* in different major African white-eye lineages (Warren et al. 2006, Melo et al., op. cit.).

In East Africa, Britton (1980) admitted three mainland species: *Z. senegalensis*, with three rich green and yellow-plumaged subspecies in Uganda and western Kenya and two more in Tanzania; the paler *Z. abyssinicus*, with two yellow-bellied subspecies in drier northern and eastern Kenya, extending to northeastern Tanzania; and *Z. poliogastrus*, comprising six isolated montane populations (each considered a subspecies), some yellow-bellied, others grey-bellied. The Pemba Island White-eye, treated as *Z. vaughani* by White (1963), was lumped with *Z. senegalensis* by Hall & Moreau (1970) and by Britton (1980), but returned to species status by Zimmerman et al. (1996) and later authors. Based on vocal differences and ecology, some of the highland isolates have recently been considered worthy of full species status, e.g. by Collar et al. (1994) and Borghesio & Laiolo (2004). The latest IOC World List (Gill & Donkster 2016) splits *Z. kikuyuensis* and *Z. sylvanus* (but not other forms) from *Z. poliogaster*.

### The genetic phylogeny of East African white-eyes

DNA investigations of the East African *Zosterops* taxa have recently been published by Habel et al. (2013, 2015), Cox et al. (2014) and Meimberg et al. (2016). Studies using two mtDNA genes revealed extensive non-monophyly in all three mainland species (Cox 2013, Cox et al. 2014). Some endemic montane populations were shown to be more closely related to forms with other habitat and elevation preferences, and dispersal abilities, than to restricted populations in neighbouring forest fragments. Most would thus appear to have arisen independently as a result of niche divergence rather than as relics of an ancestral montane population. Most of the ‘sky island’ forms of Kenya and northern Tanzania were densely sampled, and strong support was found for the monophyly of each one. The forms *mbuluensis*, *sylvanus*, *eurycricotus*, *winifredae* and *kikuyuensis*, all hitherto accommodated within *Z. poliogastrus*, formed independent well-supported clades, polyphyletic with respect to each other and to Ethiopian *poliogastrus*, and so should all now be treated as full endemic species. Northern Kenyan *kulalensis* was recovered close to Ethiopian *poliogastrus*, in a clade sister to *kikuyuensis*, and should be retained pro tempore as a subspecies of a restricted *Z. poliogastrus*. Meimberg et al. (2016) used DNA data from the entire mitogenome but from a restricted number of Kenyan taxa. Their findings were in agreement with those of Cox et al., except that *sylvanus* emerged as basal to other montane populations. They confirmed that *kulalensis* is closely related to *poliogastrus*. But relationships between *sylvanus*, *kikuyuensis*, *kulalensis*, *poliogastrus* and Ethiopian *kaffensis* still require further research.

The various forms hitherto treated as subspecies of *Z. senegalensis* were recovered by Cox et al. (op. cit.) and Cox (2013) within two different major African clades. Within a ‘northern’ clade *senegalensis* and *jacksoni* may still be treated together under a restricted *Z. senegalensis*, but the forms *stierlingi* and *anderssoni* were recovered within a major ‘southern’ clade, as sister to *Z. virens* of South Africa (see also Oatley et al. 2012), and may be treated as subspecies of *Z. anderssoni*. Limited evidence on the east-central African forms (*stuhlmanni*, *toroensis* and *scotti*) indicates that these comprise a group within the northern clade, but polyphyletic with respect to *senegalensis*. We would therefore place them pro tempore within a separate species, *Z. stuhlmanni*. Evidence for placement of the South Sudan form *gerhardi* was conflicting, and requires further research. A specimen from the Imatong Mountains was recovered close to *poliogastrus*, but two more were recovered with *jacksoni*. Although this highland
subspecies is quite distinct from the smaller, paler nominate *senegalensis* of surrounding lowlands (G. Nikolaus, pers. comm.) we prefer to retain it as a subspecies of the northern *senegalensis* clade pending the latter’s further resolution.

Within *Z. abyssinicus* (*sensu lato*), the similar yellow-bellied subspecies *flavilateralis* and *jubaensis* were recovered by Cox (2013) in a different major clade from northeast African grey-bellied subspecies (including *omoensis*), and must therefore be treated under a separate species *Z. flavilateralis*. In genetic studies using nuclear microsatellite DNA (Habel et al. 2013) the Pemba Island form *vaughani* was shown to cluster quite separately from *Z. senegalensis*. With its addition as *Z. vaughani* the number of species occurring in Kenya, Uganda and Tanzania is now expanded to eleven. Details of these follow, and include some suggested new English names. The known distributions of highland and lowland taxa are shown in Figs. 1 and 2.

**Revised list of East African Zosterops species**

Order is based largely on the phylogeny of Cox et al. (2014). Also see Appendix. 1.

**Key to abbreviations**

RB: Breeding Resident. R(B): Resident, but breeding not confirmed
AMNH: American Museum of Natural History; GR: Game Reserve; NP: National Park; MCZ: Museum of Comparative Zoology, Harvard University, USA; NHM: Natural History Museum, Tring, UK; NMNH: National Museum of Natural History, Smithsonian Institute, USA; ZMB: Zoologisches Museum Berlin.

**Zosterops abyssinicus** Guérin-Méneville 1843  **Abyssinian White-eye**

**Nomenclature:** Referred to as the White-breasted White-eye in Mackworth-Praed & Grant (1955). Attributed to Kenya and Tanzania by Hall & Moreau (1970) who at the time treated it as conspecific with *flavilateralis*, a course followed by several subsequent authors.

**Zosterops abyssinicus omoensis** Neumann 1904. Type locality Senti-Tal, a valley between Uba and Gofa, southern Ethiopia.

K Although no records to date, it can be expected to occur in Ethiopian border areas near the southern end of Lake Stephanie.]

**Zosterops mbuluensis** Sclater & Moreau  **Mbulu White-eye**

See Taxonomic comments under the Taita White-eye *Z. silvanus*. Note that the specimens considered in the analyses of Cox et al. (2014) were all from the Chyulu Hills.

Monotypic species. K T RB. Northern Tanzania highlands from Mt Hanang and the Mbulu Highlands north to Oldeani, the Crater Highlands, Ketumbeine, the North Pares, Longido, Namanga Hill and the Chyulu Hills.

**Zosterops virens mbuluensis** Sclater & Moreau 1935. *Bulletin of the British Ornithologists’ Club* 56: 13. Type locality 2100m Oldeani Forest, Crater Highlands, Mbulu District, northern Tanzania, 3°16' S, 35°26' E. Holotype in NHM, collected for Reg Moreau, 6 September 1934. (Includes *chyuluensis*.)

**Zosterops chyuluensis** van Someren 1939. *Journal of the East Africa Natural History Society* 14: 114. Type locality 2070m Chyulu Hills, southern Kenya, c. 2°35' S, 37°50' E. Holotype NHM, van Someren Collection, ex. Chyulu Hills, 26 June 1938.
**Zosterops flavilateralis** Reichenow  
**Pale Scrub White-eye**

**Taxonomic comment:** formerly treated as a subspecies of *Z. abyssinicus*.

**Zosterops flavilateralis flavilateralis.** K T RB. Occurs over much of interior eastern and southern Kenya, and in lowland areas of northern, northeastern and central Tanzania, including much of Masailand, also from the Nairobi suburbs north to Samburu and Laikipia districts, and the central and northern Rift Valley. Birds described as *fricki* from Murang’a District and the Upper Tana north to the Ndotos are smaller and paler, but can hardly be described as intergrades with *jubaensis* (Friedmann 1937). Early specimens from Lotonok, South Turkana, were assigned here, and remain the only records west of the Rift Valley. (Includes *massaicus* and *fricki*.)


[**Zosterops massaica** van Someren 1922. Novitates Zoologicae 29: 192. Type locality Sagala (south of Voi), Taita District, southeastern Kenya, c. 3°30′ S, 38°35′ E. Holotype in AMNH, collected by/for van Someren, 8 August 1918.]

[**Zosterops senegalensis fricki** Mearns 1913. Smithsonian Miscellaneous Collection 61 (20): 6. Type locality Bowlder Hill, Thika River, Fort Hall District, central Kenya, approximately 0°56′ S, 37°21′ E. Holotype in NMNH, collected by Edgar A. Mearns, 28 August 1912.]

**Zosterops flavilateralis jubaensis** Erlanger 1901. Type locality Damasso & Gurra, Somalia. Ornithologische Monatsberichte 9: 182.

**K R(B).** Mt Kulal and the Horr Valley, and birds in northern and northeastern border areas at Moyale, Mandera and El Wak also belong here. Some specimens from Kenya coastal lowlands south to Lamu, Manda, Witu and Ngomeni, and inland along the Lower Tana River to Baomo are reported to be *fricki x jubaensis* intergrades. Records from Wajir and Mombasa are not racially assigned.

**Zosterops silvanus** Peters & Loveridge  
**Taita White-eye**

**Taxonomic comment:** Cox (2013) and Cox et al. (2014) found strong support for *silvanus* as an independent evolutionary unit, quite separate from *mbuluensis* and *winifredae*. No hybrids are known between these forms.


**Zosterops winifredae** Sclater & Moreau  
**South Pare White-eye**

See Taxonomic comments under the Taita White-eye *Z. silvanus*.

Monotypic species. T RB. Confined to the South Pare Mts, northeastern Tanzania.

Zosterops anderssoni Shelley  Southern Yellow White-eye

**Taxonomic comment:** formerly treated as a subspecies of *Z. senegalensis*. The lowland (miombo) *anderssoni* is typically separate from the largely montane forest *stierlingi*, but Irwin (1981) referred to increasing intergradation between the two in areas of contact in Zimbabwe. There are also marked morphological differences: one pale yellowish-green above and bright yellow below with a narrow eye-ring (*anderssoni*), the other darker green above with a broader eye-ring (*stierlingi*). Here we treat *stierlingi* as a subspecies of *Z. anderssoni*. Meanwhile, molecular evidence in Oatley et al. (2012), Habel et al. (2013) and Cox et al. (2014) suggests that there may be a case for placing both *anderssoni* and *stierlingi* within the southern African *Zosterops virens* group. Further studies of both forms are warranted.


*Zosterops anderssoni anderssoni* T RB. Southern and southwestern savannas and woodlands. Birds in miombo in the Mpenda–Katavi–Rukwa region appear to belong here, as do others in Ruaha NP, the Selous GR, Songea District, the Rondo Plateau and some southeastern coastal forests, despite reported intergrades with *stierlingi* in several areas. (Includes *niassae*.)

[Zosterops niassae Reichenow 1904. *Journal für Ornithologie* 52: 133. Type locality Songea, Ruvuma Region, southern Tanzania, 10°41′ S, 35°39′ E. Type material in ZMB, collected by Dr N. Stierling, 28 July 1900.]

*Zosterops anderssoni stierlingi* T RB. Southern Tanzanian highlands from Mt Rungwe, the Poroto and Livingstone Mts, Matengo Highlands and Songea north to the Iringa Highlands and the Eastern Arc Mountains including the Udzungwas, Rubehos, Ulugurus, Ukagurus, Ngurus and the Usambaras. [Birds at Mahale Mountains NP (not satisfactorily assigned) require evaluation.]

*Zosterops stierlingi* Reichenow 1899. *Journal für Ornithologie* 47: 418. Type locality Iringa, Uhehe country, southern Tanzania, 7°47′ S, 35°42′ E. Type material in ZMB, collected by Dr N. Stierling, 1 May 1897. (Includes *sarmenticius* and *usambarae*.)


[Zosterops usambarae Reichenow 1909. *Ornithologische Monatsberichte* 17: 42. Type locality Mlalo, near Wilhelmstal, West Usambaras, northeastern Tanzania, 4°34′ S, 38°19′ E. Type material in ZMB, collected by Pastor K. Roehl.]

*Zosterops vaughani* Bannerman  Pemba White-eye

**Taxonomic comment:** Formerly treated by many authors as a subspecies of *Z. senegalensis* despite differing vocalizations, but proves to be genetically distinct (Habel et al. 2013). A molecular comparison is needed with *stierlingi* and *anderssoni*. Monotypic species. T RB. Common throughout Pemba Island including off-shore islets.

Zosterops eurycricotus Fischer & Reichenow  
**Tanzania Broad-ringed White-eye**


*Zosterops eurycricotus* Fischer & Reichenow 1884. *Journal für Ornithologie* 32: 55. Type locality base of Mt Meru (= Arusha NP), northern Tanzania, c. 3°14’S, 36°45’E. Holotype in Hamburg Museum, collected by G. Fischer, 17 July 1883. (Includes *perspicillatus* and *meruensis*.)

[**Zosterops perspicillata** Shelley 1889. *Proceedings of the Zoological Society* p. 366. Type locality 1520 m on Mt Kilimanjaro (east side), northern Tanzania, c.3°04’S, 37°35’E. Syntypes (2) in NHM, collected by H.C.V. Hunter, 11 August 1888.


Zosterops stuhlmanni Reichenow  
**Green White-eye**

**Taxonomic comment:** Cox (2013) found that *stuhlmanni*, *toroensis* and *reichenowi* were recovered as a distinct evolutionary lineage, which we treat as *Z. stuhlmanni*. Included are birds which have been known as *Z. virens stuhlmanni* or *Z. senegalensis stuhlmanni*. Placement of the Albertine Rift montane form *scotti* remains tentative.

*Zosterops stuhlmanni stuhlmanni* **T U RB.** Ngara, Biharamulo, Mwanza and Bukoba Districts of northwestern Tanzania north to western and southern Uganda below 1700 m, including most Lake Victoria off-shore islands. **K.** Intergrades with *Z. senegalensis jacksoni* reported from Nyanza and Kakamega districts.

*Zosterops stuhlmanni* Reichenow 1892. *Journal für Ornithologie* 40: 54. Type localities Bukoba (1°19’S, 31°49’E) and Sesse Islands (0°20’S, 32°20’E), Lake Victoria. Syntypes ZMB, collected by Emin (Bukoba) November 1890, and F. Stuhlmann (Sesse Islands), December 1890.

*Zosterops stuhlmanni toroensis* Reichenow 1904. *Journal für Ornithologie* 52: 133. Type locality Kitamba, Semliki, DR Congo.

**U R(B).** Lowland areas of western and southwestern Uganda, notably the Bwamba lowlands and Semliki NP.

*Zosterops stuhlmanni scotti* **U RB.** 1850–3000 m in the Rwenzoris, also in the Bwindi-Impenetrable NP and above 3000 m in the Virunga Volcanos.

*Zosterops scotti* Neumann 1899. *Ornithologische Monatsberichte* 7: 24. Type locality 2440 m Yerua (= Yeriya Forest), east Rwenzori Mts, western Uganda, 0°31’N, 30°06’E. Holotype in NHM, collected by G.F. Scott-Elliott (mid-1890s).

Zosterops kikuyuensis Sharpe  
**Kikuyu White-eye**

Monotypic species. **K RB.** Central Kenya highlands from Meru and Embu Districts, Mt Kenya, and the Aberdares south to Nairobi.

*Zosterops kikuyuensis* Sharpe 1891. *Ibis* (6) 3: 444. Type locality Kikuyu forest, central Kenya, c.1°00’S, 36°40’E. Holotype in NHM, collected by Sir F. Jackson, 15 August 1889. (Includes *somereni.*)
Zosterops virens somereni Hartert 1928. Novitates Zoologicae 34: 207. Type locality Mt Kenya, above Chuka, Embu District, 0°20′S, 37°39′E. Holotype AMNH, collected by Noel van Someren, 15 January 1921.

Zosterops poliogastrus Heuglin  Heuglin’s Montane White-eye

**Taxonomic comment:** Cox (2013) found that most of the former Z. poliogastrus subspecies formed independent clades polyphyletic with respect to each other. But kulalensis proved to be associated with Ethiopian montane forms, and is retained here within Z. poliogastrus. It was genetically close to kikuyuensis but more distant from the southern forms mbuluensis, sylvanus and winifredae.

Zosterops poliogastra Heuglin 1861. Type locality northern Ethiopia. Species name change from poliogastra to poliogastrus follows David & Gosselin (2002).

Zosterops poliogastrus kulalensis. K RB. Confined to Mt Kulal, northern Kenya, where it seasonally favours areas of evergreen bush as well as forest.


Zosterops senegalensis Bonaparte  Northern Yellow White-eye

**Taxonomic comment:** Cox (2013) found that with the exception of jacksoni (Kenya highlands), all former East African senegalensis subspecies were recovered in clades independent from the nominate form.

Zosterops senegalensis Bonaparte 1850. Type locality Senegal.

Zosterops senegalensis senegalensis U RB. Northern Uganda south to lakes Albert and Kyoga. Savanna birds at Kidepo NP and elsewhere in Karamoja District may also belong here. (Includes superciliosus.)

[Zosterops superciliosa Reichenow 1892. Journal für Ornithologie 40: 193. [See also Chapin 1954: 180.] Type locality “Wadelai” but specimens came from Kiri (South Sudan) and Fadjulle (= Pajule, Acholi country, northern Uganda), 2°58′N, 32°57′E. Syntype from Pajule in AMNH, collected by Emin Pasha, 1881.]

Zosterops senegalensis jacksoni K RB. 1525–3050 m in the northern and western Kenya highlands from the Loima Hills, Mt Elgon, Cheranganis, southern Kerio Valley, Tugen Hills, Ndotos, Mathews Range and Mt Marsabit south to Laikipia, Mt Garguess and the lower slopes of Mt Kenya. In the west it occurs in Kakamega and Nandi districts, also the Gwassi Hills, and from Trans-Mara, Lolgorien and Mara GR east to the Loitas and the Ngurumans, the Mau, Gilgil, Naivasha and some western Nairobi suburbs. Meanwhile, birds in some western border areas appear to be intergrades with stuhlmanni. T RB. Known only from the Loliondo area of the northern Serengeti. Birds of the Mara Region and on Ukwerere Island (not racially assigned here) may be closer to Z. stuhlmanni. U RB. Birds in the south Elgon foothills around Mbale and Tororo appear to belong here, as do birds that reach 3400 m on the Mt Elgon moorlands. [A specimen collected from mist-forest at 2600 m on Mt Moroto (May 1963), and treated at the time as Z. senegalensis flavilateralis requires re-evaluation.]

Zosterops jacksoni Neumann 1899. Ornithologische Monatsberichte 7: 23. Type localities: the Mau, Guasso Massai, Nandi country and Mt Elgon. Syntypes ZMB, collected by
Neumann (November 1894) and Jackson (February 1890). (Includes garguensis, bayeri, elgonensis and yalensis.)

[Zosterops virens garguensis Mearns 1913. Smithsonian Miscellaneous Collections 61 (20): 7. Type locality 2165 m Mt Gargues (Uraguess), northern Kenya, 0°56’ N, 37°24’ E. Holotype in NMNH, collected by Edmund Heller, 25 August 1911.]

[Zosterops bayeri Lönnberg 1917. Arkiv för zoologi 11(5): 3. Type locality Londiani Forest, central Kenya, c. 0°10’ S, 35°36’ E. Holotype in RMCA, Tervuren, collected by Dr Leo Bayer, 29 March 1914.]

[Zosterops elgonensis van Someren 1922. Novitates Zoologicae 29: 191. Type locality Bukedi (= Bugwere), near Mbaile, western side of Mt Elgon, eastern Uganda, c. 1°00’ N, 34°00’ E. Holotype in AMNH, collected by / for van Someren, 13 January 1916.]

[Zosterops yalensis van Someren 1922. Novitates Zoologicae 29: 191. Type locality Kaimosi, Kakamega District, western Kenya, 0°11’ N, 34°47’ E. Lectotype in AMNH, collected by Allen Turner (pp. Col. R Meinertzhagen) 22 January 1917.]


Discussion

In mainland East Africa, the treatment of some 16 recognized taxa within three white-eye species (Hall & Moreau 1970, Zimmerman et al. 1996, Fry 2000) has long seemed unsatisfactory. Species limits have partly been based on phenotypic characters such as the intensity of yellows and greens in the plumage and width of the eye-ring, yet grey-bellied forms have been lumped as sub-species with yellow-bellied ones. Habitat and altitude preferences have also been considered important in defining species. Thus, the grouping of the isolated eastern montane populations under a single species Z. poliogastus has assumed that all were derived from a forest ancestor which diverged into distinctive populations following retreat into isolated highland refugia during cool and arid climatic periods of the Plio-Pleistocene (Hall & Moreau op. cit., Diamond & Hamilton 2009). The continued placement of other highland taxa such as jacksoni, stierlingi and scotti with lowland Z. senegalensis has therefore seemed far from logical.

Molecular genetics, which provided answers concerning the evolution of white-eyes in the western Indian Ocean (Warren et al. 2006) and the Gulf of Guinea (Melo et al. 2011), is now revealing relationships among mainland African forms, especially in East Africa. The traditional taxonomy no longer proves acceptable. Thus, most of the eastern ‘sky island’ forms have been found to represent independent species; the morphologically very similar forms inhabiting lowlands in southern Tanzania and northern Uganda have been recovered in quite separate lineages; and the paler yellow birds of the drier eastern Kenyan and northeast Tanzanian lowlands prove not to be allied to grey-bellied Ethiopian forms. In East Africa we must thus recognize at least five additional highland species, Z. sylvanus, Z. winifredae, Z. kikuyuensis, Z. eurycricotus and Z. mbuluensis, and at least one new lowland species Z. anderssoni (and preferably a second, Z. stuhlmanni), while our former Abyssinian White-eye becomes Z. flavilateralis.
Our understanding of the distribution of some white-eye taxa in East Africa has been obscured by difficulties of separation and correct identification in the field. Specimens are lacking from some areas where forms potentially come into contact or overlap. Thus the range of *anderssoni* in Tanzanian lowlands, and the extent of its contact, if any, with *stuhlmanni* and *flavilateralis*, remain to be clarified. The absence of white-eyes from wide areas of arid northern and eastern Kenya needs to be confirmed. And the limits of *senegalensis* and *toroensis* in Uganda require further definition. The restricted ranges of the highland taxa are better known, but questions remain regarding birds that occupy the Mahali and Gombe Stream National Parks in western Tanzania, and highlands near the northeast Uganda/northwest Kenya border. Good photographs from some of these lesser explored areas are likely to be essential to answer pending questions.
Figure 1. East African distribution of highland taxa: 1–*mbuluensis*, 2–*sylvanus*, 3–*winifredae*, 4–*stierlingi*, 5–*eurycricotus*, 6–*scotti*, 7–*kikuyuensis*, 8–*kulalensis*, 9–*jacksoni*, 10–*gerhardi*, ?–taxon undetermined.
Figure 2. East African distribution of lowland taxa: 1–*flavilateralis*, 2–*jubaensis*, 3–*anderssoni*, 4–*vaughani*, 5–*stuhlmanni*, 6–*toroensis*, 7–*senegalensis*, x–reportedly *flavilateralis/jubaensis* intergrades, ?–undetermined.
Acknowledgements

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References


Appendix 1. East African Zosterops taxa

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<td>Z. s. gerhardi</td>
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Number of taxa 9 7 9 6
The increasingly urban status of the Cattle Egret *Bubulcus ibis* in Uganda, with some observations on its variable breeding seasons and associated species

Esther Toloa, Micheal Kibuule, Daniel Blasberg and Derek Pomeroy

**Summary**

Cattle Egrets *Bubulcus ibis*, long known for their expanding geographical range, have in recent years also become increasingly urbanized in Kampala, a city with over 1.5 million people, and elsewhere. First recorded roosting in Kampala over 15 years ago, their numbers now exceed 16 000, spread across several sites, at most of which they have also been breeding for several years. However, the numbers nesting are far lower than might be expected from those that come nightly to roost. Breeding in Kampala shows bimodal peaks, perhaps because some birds breed twice a year—which would partly explain their rapid increase in numbers. Timing of breeding is linked to rainfall, but shows more variation between sites and between years than might be expected. Some birds may always have fed in the area that is now Kampala. Today, some feed at the city’s main land-fill site, but most go to the countryside where their consumption of bush-cricket, grasshoppers and other insects is presumably beneficial to farmers. Overall, for breeding and roosting, and to some extent feeding, Cattle Egrets can now be considered as urbanized in this near-equatorial city.

**Introduction**

The process of urbanization in birds is generating increasing interest around the world. There are even books on urban bird-watching (e.g. Milne 2006, which includes Kampala, mentioning Cattle Egrets *Bubulcus ibis* and many other species). The process can involve remarkable changes of behaviour as seen, for example, in Marabou Storks *Leptoptilus crumeniferus* in Kampala (Pomeroy 1978), whilst the Australian White Ibis *Threskiornis moluccus* has not only colonized urban areas, but has become a pest (Martin *et al.* 2012). In Britain, Evans *et al.* (2010), using the Blackbird *Turdus merula* as an example, propose a model in which urbanization proceeds in three stages—arrival, adjustment and spread. As we shall see, Cattle Egrets may have skipped the first of these stages.

In the city of Kampala an increasing number of bird species is well established within the most urban parts (Chamberlain *et al.* in press), and this includes the Cattle Egret. This species is also spreading globally, to become one of the most cosmopolitan of birds (del Hoyo *et al.* 1992). From having long been widespread in Africa they have, in the past 40 years or so, been spreading northwards from the western Mediterranean basin, first breeding in France in 1989 (Snow & Perrins 1998) and in England in 2008, where their spread is continuing (Balmer *et al.* 2013). Although Brown *et al.*
Increasingly urbanized Cattle Egrets in Uganda (1982) does not mention that the species was spreading in Africa at that time, there have been many subsequent reports of it doing so, and of increases within its traditional range (e.g. Kushlan & Hafner 2000). This could imply a high reproductive rate, and Brown et al. (1982) states that although they mostly start breeding at the age of two, some start earlier. Also significant, perhaps, is that they may breed more than once a year, as suggested below.

In both East and West Africa, Cattle Egrets are a common sight in urban areas, including Dakar, Nairobi and Dar es Salaam (C. Barlow, D.A. Turner, pers. comm.), although they often continue to roost outside of urban centres. Urban nesting is known from Nairobi (where Cattle Egrets have recently begun nesting together with Sacred Ibis *Threskiornis aethiopicus*, D.A. Turner pers. comm.) and several places in Uganda, including Busolwe and Mbale (Nachuha 2007) as well as Kampala.

In this paper, we describe how the number of roosting sites, and the number of roosting birds, have continued to rise and so too have the numbers nesting, sometimes in mixed colonies, and almost throughout the year. We also compare nesting success in mixed and single-species colonies.

**Methods**

The locations of the various roosts and nesting colonies in Kampala are shown in Fig. 1. They were found by personal observation, supplemented in one case by a helpful informant. Although it is hard to be certain, we believe that all sites have been found; birds flying into roost were probably all seen since they tended to follow the main valleys.

![Figure 1](image_url) Map of the central parts of Kampala, showing the positions of all known nesting and roosting sites in 2016 (NFA = National Forest Authority, Bugoloobi). The total area of Kampala City is 190 km², so it extends well beyond the area shown.
Cattle Egrets lend themselves to total counts. Nest and roost counts were made in the months from mid-2012 to early 2013, and then monthly at Makerere during 2013, and at all sites throughout 2014 and 2015, usually around the middle of the month. At Kabaka’s Lake, where the largest numbers of both nesting and roosting birds were found, some of the nests were in two acacia trees beside the lake, and others on two small islands within the lake, which we accessed by boat. In 2015, additional observations were made to assess breeding success, which was deduced from weekly counts at two colonies, at Makerere and NFA Bugalobi. The number of young fledged was assumed to be the number of grown young present in the nests at the last count. The nests at Makerere were in trees that also had Marabou Stork nests, whilst trees at Bugolobi were only used by Cattle Egrets. Marabou nests were located in the crown of the tree, above those of the egrets.

Roost counts were also made monthly. Beginning at least an hour before sunset, flocks of birds were counted as they arrived. Counting continued so long as birds continued to arrive, by which time it was often completely dark apart from light from the sky and local electric lights (which may have helped the birds to come so late to roost). Most incoming flocks were quite small, the majority consisting of fewer than 25 birds, and hence easily counted.

Observations of feeding behaviour were mainly opportunistic, except at the city’s land-fill site where monthly counts were made from 2013 to 2016.

Results

Kampala roosts

By the 1980s Cattle Egrets were common in Kampala City, feeding on grassed verges and roundabouts. However, there was no record of them roosting or nesting in the city at that time (Carswell 1986). The first documented record was in 2000, when an average count of 4669 was recorded for birds roosting on acacia trees and shrubs on islands within the 3-ha Kabaka’s Lake at Mengo, about 3 km southwest of the city centre (Banage & Pomeroy 2000). The size of this roost suggested that it must already have existed for some years before 2000—and it has been in continuous use since then; it is now also the site of the biggest nesting colony. Subsequently, a number of other roosting sites have been found in various parts of the city.

Fig. 1 shows all known roosting and nesting sites in Kampala; all except that at the Aga Khan School (where the roosting trees were cut down) were still in use in 2016. Fig. 2 shows combined monthly counts of all known roosts from January 2014 to the end of 2015, together with data from shorter periods in 2012 and 2013. As can be seen, numbers fluctuated between successive months, but with no strong seasonal pattern. The general increase over these four years is clear. Monthly variations were probably due in part at least, to difficulties in counting, but could also be attributable to some birds changing roosts, and the possibility that there were nearby roosts that were still unknown to us. For example, local people told us that the one on Gayaza Road had been there for some time before it was first counted in November 2015. This is in a valley along which many birds fly towards dusk, but is unusual in that whereas some stop to roost there most continue on towards the more central sites. Numbers at roosts should be considered as minimum counts since some birds continue to arrive until it is too dark to see them clearly. Because of this, the highest recorded number shown in Fig. 2 of 15789 birds in January 2015 might imply a total of well over 16 000.
Figure 2. Roost counts (combined totals for all roosts) in 2014 and 2015, with data for some months of the two previous years.

Nest counts

Table 1 summarizes the months of peak nest counts each year for all six known nesting colonies in Kampala and Fig. 3 shows monthly counts for four years at the largest colony, Makerere East. Several points are worth noting. First, the Aga Khan School in Old Kampala where nesting trees were cut down but other apparently suitable ones were left, has been abandoned. Secondly, in 2014 and 2015 there was a bimodal pattern to nest numbers which was not seen in 2013 (no counts were made in the middle months of 2012). The bimodal peaks approximate the peaks in rainfall, and to some extent to the pattern recorded by Brown & Britton (1980) who were recording egg-laying dates. Since the total period of nesting, from egg-laying to fledging, is about 55 days (Brown et al. 1982), it would be perfectly possible for the same individuals to breed twice a year, although we have no evidence that this is in fact the case. Thirdly, there was a very big increase in the number of nests in November 2015, a particularly wet month (the average rainfall data in Fig. 3 are more than 50 years old, but more limited recent data show a similar pattern). But while rainfall is clearly a factor in determining the timing of nesting, it may not be the only one since there are clear differences in timing between the different colonies, yet presumably they all received similar amounts of rain. Thus peak months for the first nesting period in 2014 varied from April to June, while peaks for the second period ranged from September to December in 2014—but were all around November to December in 2015. Altogether, peak counts in Table 1 occurred among the various sites in every month except March and July. Looking at the nest count data for one of the two largest sites, Makerere East, in more detail (Fig. 3), we see that peak numbers were during May to June in 2014, but around the turn of the year in the other three years. And while the peak in 2013 was below 200 nests, in other years it was above 400.
By 2014, the total numbers of Cattle Egret nests found in Kampala had reached just over 1500, presumably representing some 3000 breeding birds. Similar numbers were recorded in 2015 (Table 1).
Table 1. Peak nesting months for first and second nesting periods at the six known nesting colonies in Kampala from 2012 to 2015. A dash (–) indicates no count. See Fig. 2 for more details. Mak = Makerere University; Aga Khan = Aga Khan Schools.

<table>
<thead>
<tr>
<th>Month of first count</th>
<th>Mak E</th>
<th>Mak W</th>
<th>Bugoloobi</th>
<th>Kabaka’s Lake</th>
<th>Mulago</th>
<th>Aga Khan</th>
<th>Totals b</th>
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<tr>
<td>2012</td>
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<td>Dec</td>
<td>545</td>
<td>15</td>
<td>69</td>
<td>–</td>
<td>–</td>
<td>Oct</td>
<td>39</td>
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<tr>
<td>Jan c</td>
<td>193</td>
<td>103</td>
<td>266</td>
<td>–</td>
<td>–</td>
<td>Jan</td>
<td>5</td>
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<tr>
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<tr>
<td>Dec</td>
<td>165</td>
<td>5</td>
<td>0</td>
<td>Nov</td>
<td>–</td>
<td>0</td>
<td>1527</td>
</tr>
<tr>
<td>June</td>
<td>524</td>
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<td>Nov</td>
<td>452</td>
<td>272</td>
<td>295</td>
<td>Nov</td>
<td>397</td>
<td>81</td>
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</tbody>
</table>

a No count from March to June 2013
b Only for periods when all colonies were counted
c These are presumably from the same breeding period as in December 2012

Nesting associations

Throughout Africa, Cattle Egrets often nest with other species in mixed colonies (e.g. Brown et al. 1982, Ewbank 2014). The main example of this in Kampala is at Kabaka’s Lake, where Little Egrets *Egretta garzetta* and a few Black-headed Herons *Ardea melanopcephala*, Sacred Ibis, Open-billed Storks *Anastomus lamelligerus* and Reed Cormorants *Phalacrocorax africanus* share the site, although the ibises nest rather later than the others. In neighbouring Kenya, Cattle Egret nests have been found positioned below those of various species, including Black-headed Heron and Sacred Ibis (D.A. Turner in litt.).

At Makerere East all 18 trees used by Cattle Egrets in 2015 were also occupied by nests of the Marabou Stork, although the Marabous, which had over 800 nests altogether on the Makerere campus, also had many trees to themselves. Both species had used most of the same trees in previous years, the egrets nesting lower down than the storks. There were various interactions between Cattle Egrets and other bird species. Cattle Egret nests were occasionally attacked by Marabous, Pied Crows *Corvus albus* and, once, an African Harrier Hawk *Polyboroides typus*, but the Cattle Egrets usually defended their nest contents successfully. At least twice Marabous were observed feeding on young egrets that had apparently fallen from their nests (and were already dead). Both species also fed on insects and other items on the ground below the nests, which became rich in organic refuse.

As mentioned above, all the trees used by Cattle Egrets at Makerere East also contained nests of Marabou Storks, whereas at the National Forest Authority (NFA) grounds at Bugolobi some trees were occupied by both species while others held only
Cattle Egret nests. This provided an opportunity to compare the nesting success of the egrets at the two colonies between trees that were used by both species and those that were not. Since there are many trees at Makerere in which neither species nests, there appears to be no compelling reason for egrets to nest in the same trees as Marabous. It is possible therefore that sharing nesting trees confers some benefit. But, as can be seen in Fig. 4, the mean number of young egrets fledged per nest was almost identical at the two colonies \((t=0.058, P=0.954)\), and although the proportion of nests that failed was slightly higher at Makerere, those that did fledge young produced rather more. Thus there appears to be no overall benefit, or disadvantage, in nesting in the same trees as Marabous.

**Urban feeding**

Most Ugandan data on Cattle Egret population growth are for the Kampala area where some feed in the city itself, but most of those that roost and nest in the city are thought to fly considerable distances to feed. Elsewhere they are known to travel up to 60 km according to Cramp et al (1977). In some parts of their range Cattle Egrets are commensal with large mammals, particularly the larger herbivores, especially grazers (Brown et al. 1982, Kioko et al. 2016). However, in the Kampala area where cows and other large herbivores are relatively few they search solitarily for bush-crickets, grasshoppers and other large insects on all types of open ground, swamps, shallow waters and also in trees. This last is particularly noticeable when the migratory bush-cricket *Ruspolia differens* (known locally as *nsenene*) is present in its millions and many spend the day roosting in trees, forming an easy prey. A particular year-round feeding ground, about 12 km from the city centre, is the main land-fill site at Kiteezi, where up to about 600 can be counted together with Grey Crowned Cranes *Balearica regulorum*, Marabou Storks, Yellow-billed Kites *Milvus migrans parasitus*, Pied Crows and other species.
Discussion

It is clear that Cattle Egrets are only one of a number of species that have adapted to urban environments in Africa, many of these being large-bodied non-passerines such as Marabou Storks and Black Kites *Milvus migrans* (Ssemmanda & Pomeroy 2010, Chamberlain *et al.* in press), perhaps because they associate such places with reduced risks of predation. Although urban Cattle Egrets are not mentioned by Mackworth-Praed & Grant (1952) it seems likely that they were present in the Kampala area long before the city expanded (which it is still doing). The original natural vegetation of the area included some savanna vegetation on hilltops, where soils are shallow (Langdale-Brown *et al.* 1964), and although cutting down of forests to allow for cultivation had begun about a thousand years ago (Hamilton 1984) the hilltops were less affected. Thus, although not documented (see below), the egrets may have adapted slowly while becoming increasingly confined to those areas that remained open, such as parks. In this way they missed the first stage in urbanization as proposed by Martin *et al.* (2012), namely arrival. Nevertheless, adapting to an urban environment must involve a change in behaviour, something not generally considered in books on bird behaviour (e.g. Stutchbury & Morton 2001).

Feeding by Cattle Egrets in villages is mentioned in *Birds of Africa* (Brown *et al.* 1982), but neither that work nor *Birds of the Western Palaearctic* (Cramp 1977) describe urban roosting or nesting by Cattle Egrets, implying that these habits are relatively recent. However, we know that feeding in urban areas is not new (Pomeroy 1975, Dean 1978, and various correspondents—all of these referring to birds feeding on refuse, or fly maggots and other insects).

Urban nesting has been recorded in Madagascar’s capital, Antananarivo (Safford & Hawkins 2013) as well as more recently in The Gambia in West Africa and in Nairobi (C. Barlow, D.A. Turner *in litt.*). It is apparent that urban roosting preceded nesting by a number of years in Kampala; both occur in places where many people pass by the trees on which most nests are placed. Although the numbers of Cattle Egrets nesting in Kampala are high for an urban area, the largest recorded count of breeding birds in East Africa was of about 10,000 pairs in the Wembere heronry in Tanzania in the 1960s (D.A. Turner pers. comm., who considers that the total East African population of Cattle Egrets exceeds one million birds).

The highest recorded number of Cattle Egret nests in Kampala was about 1500 in the first half of 2014, but over 13,000 birds were recorded roosting then (including those on nests). Evidently there was a large and unexplained number of non-breeding birds in all years, only some of which are likely to have been immatures (which cannot be easily distinguished when they come into roost at dusk). And whereas Car- swell (1986) reported “an increase in most years from September to February” our data for the numbers roosting showed considerable variation between years, but no clear seasonality. In part, this may have been because birds show less fidelity to roosts, and consequently some roosts may have been missed.

A noteworthy feature of the data on numbers of nests is the bimodal seasonal pattern, which implies either that there are two sub-populations or that there is a single population which breeds twice a year, or some combination of the two. Such bimodal patterns of breeding in tropical birds have long been known and are fairly common in East Africa (Brown & Britton 1980) and elsewhere in the tropics (e.g. in the Rufous-collared (Andean) Sparrow *Zonotrichia capensis*, Miller 1962). To clarify the pattern it would be helpful if an opportunity arose to mark some birds. Although
second, and possibly third, broods in Cattle Egrets are known, as are replacement broods (Cramp et al. 1977), none of these would produce the bimodal pattern seen in Fig. 3, since the gap between the two modes is about three times as long as a nesting cycle. Considering both Table 1 and Fig. 3 it is clear that peak nesting occurs after the peak in rainfall, when adult grasshoppers may be most abundant, or more easily seen as grasses dry out.

The seasonal abundance of bush-crickets, attracted to Kampala by the bright lights, may have been the original reason for Cattle Egrets coming to Kampala in such large numbers. But when the bush-crickets are not present (which is most of the year) many of the egrets have to fly considerable distances out to their feeding sites. We believe that the more than 15 000 Cattle Egrets in Kampala is the largest urban roost anywhere in Africa, but Kushlan & Hafner (2000) reported a roost of a quarter of a million at Walado Debo in the inland Niger delta in Mali in December 1995. Such high numbers may well be of economic importance given that bush-crickets and grasshoppers are an important part of their diet, and that these insects presumably compete for grass with livestock. Furthermore, grasshoppers may also feed on cereal crops (L. Fishpool pers. comm.). Thus Cattle Egrets can be seen as farmers’ friends—an aspect in need of proper study.

Acknowledgements

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References

Notes on the increasing use of urban nesting and roosting sites in Kenya: a nesting site for Yellow-billed Storks *Mycteria ibis* and Pink-backed Pelicans *Pelecanus rufescens* in Naivasha

Introduction
Historically, birds have been known to thrive in urban areas and close to human habitation where various species seem at home, feeding and nesting calmly without feeling threatened by the presence of man. Some species have even acquired names that relate to these sites. Common examples of urban nesters include the House Sparrow *Passer domesticus* and Little Swift *Apus affinis*. Many members of the pigeon family have long used buildings for nesting, and various weaver and sparrow species such as the Village Weaver *Ploceus cucullatus* and the Kenya Rufous Sparrow *Passer rufocinctus* nest close to human residences. Some species have actually taken to nesting inside the roof gutters of houses.

Urban nesting in Kenya
Nesting in urban areas has become more common in Kenya in recent decades, and there are now many examples. One of the best known is a Marabou Stork *Leptoptilos crumeniferus* nesting site along Mombasa Road, Nairobi, next to Nyayo Stadium, which was recently publicized widely on audio-visual and social media platforms. Over 48 Angola Swallows *Hirundo angolensis* nested inside classrooms in Ol Bolossat Primary School and further individuals of this species utilized the Abasuba Cultural Museum buildings on Mfangano Island. Great Sparrowhawks *Accipiter melanoleucus* and Ayres’s Hawk Eagles *Hieraaetus ayresii* have frequently nested very close to urban centres, houses or hotels in various parts of the country. A pair of Wahlberg’s Eagles *Aquila wahlbergi* have often nested on a tree in a residential area of Thika, while Lanner Falcons *Falco biarmicus* and Great Sparrowhawks alternately use a nest site inside the National Museums of Kenya headquarters compound. Lanner Falcons have even nested on the eighteenth floor of the famous KICC building in the middle of Nairobi City, and it is well known that a pair of Peregrine Falcons *Falco peregrinus* has for many years nested on the Law Courts Building next door to the KICC. Lanner Falcons also often nest around buildings in different areas of Westlands, a suburb of Nairobi. Large predators like the Crowned Eagle *Stephanoaetus coronatus* often nest in very small forest blocks in urban areas, at times close to hotels, and some of the large raptors such as Martial Eagle *Polemaetus bellicosus* and Tawny Eagle *Aquila rapax* may nest on electricity pylons. During the 2013/2014 wet season a pair of Augur Buzzards *Buteo augur* nested on trees beside Thika Road, Muthaiga, and White-backed Vultures *Gyps africanus* have attempted to nest in Nairobi on a tree beside Langata Road, near the Galleria Mall. Black Kites *Milvus migrans* have been observed nesting inside the Nairobi Arboretum and Kenyatta University main campus among other urban locations.

In Murungaru Town, North Kinangop, one *Eucalyptus* tree is currently being used...
as a communal nesting site by Black-headed Herons *Ardea melanocephala*, Reed Cormorants *Phalacrocorax africanus* and Cattle Egrets *Bubulcus ibis*. An interesting feature here is that this tree is a rejuvenated shoot from trees used by the same species in the 1990s, which were cut down, displacing the birds, but to which they returned after the new shoots had matured. A similar colony of Black-headed Herons exists at the edge of Nyadorera Town in Nyanza. Pied Crows *Corvus albus* have for long been associated with nesting on human infrastructure such as power lines, telecommunication boosters and chimney pillars. However, in the last five years, some active nests have been built on tall leafless trees in urban centres, e.g. in Githurai market (Nairobi), Kabati market (Naivasha) and outside Kenyatta University main campus Administration Block. Silvery-cheeked Hornbills *Bycanistes brevis* have been reported nesting near Westlands, Nairobi. More recently, the rare Somali Sparrow *Passer castanopterus* has been found nesting at Archer’s Gate, Samburu National Reserve, and this species (or a hybrid with House Sparrow) has been recorded doing a similar thing at Sala Gate, Tsavo East National Park.

Thus urban nesting seems to be a developing behavioural trait in Kenya among a range of bird species. It will undoubtedly be recorded in many more species in the coming years as habitat changes continue to occur.

### Naivasha nesting site

One very interesting recent urban nesting site in Kenya involved a mixed colony of Yellow-billed Storks *Mycteria ibis* and Pink-backed Pelicans *Pelecanus rufescens* at Naivasha. This site was first recorded on 16 April 2013, but it is possibly older. There was a mix of the two species nesting on *Acacia xanthophloea* trees around the Banda-Kihoto area, with a dominance of Yellow-billed Storks. On 16 August 2013 the same site was visited and nesting activity recorded, with a good abundance of Pink-backed Pelicans. Over the following years, the same nesting pattern was observed at the same time of year. In February 2016, the birds were observed congregating at the nesting site, which had now extended to Moi Avenue in Naivasha Town, and in mid-April both Yellow-billed Storks and Pink-backed Pelicans were reported nesting again. Currently, the nest site extends from the Banda Fish Landing Beach to Naivasha Town (Moi Avenue). The stick nests are built on *Acacia xanthophloea* trees, positioned among the top branches. Yellow-billed Storks continue to dominate the nesting site over Pink-backed Pelicans. Broken egg shells are common underneath the nesting trees.

![Figure 1. Yellow-billed Storks and Pink-backed Pelicans nesting in a single colony in Naivasha. Photos: W. Wachira.](image-url)
The Yellow-billed Stork has been observed to nest when food is available (Hancock et al. 1992), but del Hoyo et al. (1992) note that breeding can occur either after the rains or during the dry season. Brown (1982) states that it often nests together with other species in small groups of 10 to 20 pairs, but Hancock et al. (op. cit.) note that as many as 50 pairs have been recorded. The nests are made of sticks and may be placed on small trees over water or high up in large trees on dry land (Hancock et al. 1992, del Hoyo et al. 1992), and spaced 1–3 m apart (Anderson 2005).

The Pink-backed Pelican is stated to nest in small groups or larger colonies of 20–500 pairs, often among other species. Stick nests can be in trees, reeds or low bushes along water fronts or more rarely on the ground on sandy islands or even in mangroves (Brown 1982, del Hoyo et al., op. cit., Langrand 1990, Ogilvie 1997, Nelson 2005). Nests are built close to each other and may often touch neighbouring nests (Ogilvie 1997). They are re-used and refurbished over many years until they collapse (Nelson 2005).

Discussion, and urban roosting

Urban nesting sites are very important in an ever-changing human world. Many habitat conversion activities are pushing species out of their breeding sites, forcing them to seek alternatives. Urban nesting may also improve species fitness, if proved to improve breeding success. Human presence may serve as a predator deterrence strategy, increasing chick fledging rates. Some species that have adapted to feeding strategies that are aided by human activities, such as dumpsite feeding, may also become more successful with urban nesting. Nests that are close to feeding sites are favourable as they reduce parent absence and increase chick survival through parental protection and sustainable food provision.

Apart from nesting, some species have taken to roosting in urban areas, a trait that may also become more common over the next few decades, as more wild areas become inhabited by man. A good example is a huge roosting flock of some 200 to 500 Pied Crows inside Kenyatta University main campus, gathering at around 17:00–19:00 and leaving around 06:00–08:00. At Crane’s Haven Camp in the Sibanga area of Trans Nzoia, a flock of about 10–20 Eastern Grey Plantain-eaters *Crinifer zonurus* roosts in one tree just outside the camp, and are often joined by a pair of wintering Pallid Harriers *Circus macrourus*. Marabou Storks have taken to roosting in Nairobi on roadside trees along Thika Road, in the Ruaraka area, in the Central Business District (Kenyatta Avenue), in Upper Hill, and along Mombasa Road. Black Kites also roost in huge numbers to the south of Nairobi City, with congregating flocks easily seen around the Central Business District and the Ngara area around 17:00–19:30, flocks depart south again at 06:00–08:00, while a smaller flock occasionally roosts in the Ngara area, along Murang’a Road. This small flock is seen every morning sunning communally (with all birds perched on the eastern edge of the tree — facing the rising sun) at a mango tree located along Murang’a Road. Cattle Egrets and Sacred Ibises *Threskiornis aethiopicus* are common communal roosting species around urban areas.

However, not all these urban flocks are doing so well. In the 1950s, Hooded Vultures *Necrosyrtes monachus* nested in the *Eucalyptus* trees close to the then Ainsworth Hotel, just across the road from the Nairobi Museum. This was a good urban population of this currently Critically Endangered species. Today, it is virtually extirpated in Nairobi and its urban populations seem to be confined to western Kenya, where it is still seen in towns like Busia and Eldoret. In other countries, it is doing better in urban
areas, for example in Kampala, Uganda. Urban sites may provide refuge for many species in the future in the light of the fast decline of natural habitats, and they should perhaps be better protected.

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References


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Hobbies (Falco cuvieri and F. subbuteo) versus bats over Kampala skies

The African Hobby Falco cuvieri is widely distributed in the sub-Saharan part of the continent (Ferguson-Lees & Christie 2001). However, it is unaccountably rare in much of the range (Brown et al. 1982), making specific observations challenging. One major exception is the area of Kampala, Uganda’s capital, where the African Hobby has been regularly recorded for decades (Steyn 1965, Pitman 1966, Carswell et al. 2005).

In the course of a wider study of the ecology of the entire ‘hobby group’ (sensu Fuchs et al. 2015), we visited Uganda from 29 December 2015 to 7 January 2016. Most of the time we spent in Kampala. However, we also visited Bwindi Impenetrable Forest and Queen Elizabeth National parks in the southwest of the country.

In the Kampala area we observed a minimum of nine African Hobbies and four Eurasian Hobbies Falco subbuteo. Five of the African Hobbies could be identified as adults, but four could not be aged due to our distance from the birds. For the Eurasian Hobby, there were two each of adults and first-winter birds.

Both hobby species are said to feed on insects, birds and bats (Brown et al. 1982). As far as we could establish, both species spent most of the daytime sitting in the shade
or hunting insects (mostly dragonflies emerging from nearby Lake Victoria), largely out of sight. We only once saw an African Hobby trying to catch birds, on the early morning of 7 January, flying low and at high speed over the houses and gardens of the Kampala suburbs.

The situation changed dramatically during dusk and dawn, when hobbies became noticeable, trying to catch bats. In a short period of about 30 minutes of each twilight time, both species appeared in the skies over Kampala. Bats apparently flew at dusk towards Lake Victoria for feeding and back at dawn to their resting places, making them vulnerable to attacking predators on their comparatively long flights. Altogether, we observed 13 bat kills, nine by the African Hobby and one by the Eurasian Hobby, while in three cases the hobby species could not be identified. Catches were observed between 06:30 and 06:40 in the morning, and between 19:07 and 19:19 in the evening. Hobbies only attacked small to medium-sized bats, whereas they ignored completely the likewise numerous, but obviously too heavy Straw-coloured Fruit-Bat *Eidolon helvum*, which weighs from 230 to 350 g.

Although the sample size is small, hobbies seemed to be very successful in catching this rewarding prey type. Fourteen African Hobby hunts at fairly close ranges resulted in five kills, while the falcons had no success on seven occasions and in two cases the outcome was unclear. This amounts to a hunting success rate of about 35–50%, much higher than that reached by Eurasian Hobbies on similar sized birds (<20%; Probst *et al.*, 2011, Probst 2013). However, African Hobbies were also reported to be successful predating roosting Barn Swallows *Hirundo rustica* in Nigeria (Bijlsma & van den Brink 2005). Furthermore, Kampala’s hobbies often did not drive home an attack, but simply switched to another target if they could not catch a bat immediately. Therefore, hunting success could have been even higher when purposefully chasing an individual target, and approaching the 50% capture success for Eurasian Hobbies on emerging bats in Africa reported by Fenton *et al.* (1994).

Bats may be an important prey for African and Eurasian Hobbies (cf. Haensel & Sömmer 2002, Stanton 2016) and their congeners and ecological counterparts within the tropical zone (Oriental Hobby *Falco severus*; Bat Falcon *F. rufigularis*). Uganda is enormously rich in micro-chiropteran species (Kityo & Kerbis 1996), making them in some regions a profitable prey base. For example, we saw a Bat Hawk *Macheiramphus alcinus* killing three small bats within a few minutes on the evening of 7 January. However, one should be careful about generalization on a larger regional scale as we could not observe hobby–bat interactions at Lake Bunyonyi (evening of 2 January and morning of 3 January), or the Kazinga Channel between Lakes George and Edward (evening of 3 January).

At Kampala we noticed some differences between hunting at dusk and dawn. At dusk, masses—hundreds, if not thousands—of small bats were visible flying in mid-air, while at dawn only a few were seen, typically flying low over the houses and canopies. Probably many of them had already reached their roosts during the hours of darkness. Therefore, bats were much more readily caught in the evening than in the morning. As a result, we estimated individual hobbies to kill two bats per day on a rough average, zero to one in the morning and one to two in the evening. Given a necessary daily intake of an estimated (low) 30 g in the African Hobby (Brown *et al.* 1982), falcons could easily cover their prey needs by catching bats and dragonflies. However, this is not the case when supplying juveniles, as bats are only available for a short time during the day. We can predict that birds might become a major prey component then.
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Observation of Grey Kestrel *Falco ardosiaceus* raiding the nest of Dickinson’s Kestrel *F. dickinsoni* in the Selous Game Reserve, Tanzania

On 31 January 2014, along the shoreline of Lake Manze in the Selous Game Reserve, Tanzania, we heard loud and incessant screeching coming from the crown of a dead Borassus palm *Borassus aethiopum* where we had been watching a pair of Dickinson’s Kestrels *Falco dickinsoni* nesting for the past month, being in full view of the verandah of PSB’s house. The shore around this stretch of Lake Manze is edged with palm forest,
the dominant species being *Hyphaene compressa*, *Borassus aethiopum* and *Combretum constrictum*. Moving inland from this thin strip, it starts to open up to *Acacia* and *Terminalia* woodland.

As we watched, a Grey Kestrel *Falco ardosiaceus* flew from the top of the *B. aethiopum* clutching something in its talons, closely pursued by one of the pair of *F. dickinsoni*, screeching its protests as it flew. The *ardosiaceus* alighted in the fronds of another *B. aethiopum* and proceeded to consume what we could now see was a chick. During this time the *dickinsoni* sat on a nearby frond continuing to voice its distress.

No record of *F. ardosiaceus* displaying nest-raiding behaviour could be found. In fact, Sinclair & Ryan (2003) suggest that interactions with *F. dickinsoni* may result in hybridization where the two species’ ranges overlap in southern DR Congo. Jenkins (2005) describes their diet as consisting mainly of insects and lizards, but also rodents and small birds, sometimes supplemented with husks of *Hyphaene petersiana*. They further note that *ardosiaceus* may occasionally pursue birds and bats in aerial chases. We would therefore assume that our observation was simply an opportunistic event. However, on consuming its meal, the *ardosiaceus* proceeded to thoroughly search the crown of the same *B. aethiopum*, where we strongly suspected a pair of Red-necked Falcons *F. chicquera* had nested a few months previously. This suggests to us that this individual was actively searching for nests to raid.

*F. ardosiaceus* and *F. dickinsoni* are thought to be largely allopatric, but having a contiguous range (Ferguson-Lees & Christie, 2001). In the Selous, we encounter *dickinsoni* very regularly and they are present in large numbers. Although we have found no confirmed nests of *ardosiaceus*, there are numerous old Hamerkop *Scopus umbretta* nests in the area, and these are known to be commonly utilized by breeding *F. ardosiaceus* (Tarboton, 2011). Despite the lack of confirmed breeding in the area, our observation of *ardosiaceus* on three other occasions at different times of year (two sightings in June 2013 and one in September 2013) would suggest that they are resident, if only in small numbers, and that the Selous is one area where the two species’ ranges overlap. All these sightings have been in similar habitats — riverine palm forest or the ecotone between this and open *Acacia*/*Terminalia* woodland.

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Wood-hoopoes: are *Phoeniculus purpureus niloticus* (Neumann 1903) and *Phoeniculus damararensis granti* (Neumann 1903) conspecific?

The Green Wood-hoopoe *Phoeniculus purpureus* (Miller 1784) is represented in all savanna regions of Africa, and has long been the subject of debate (Turner 2014). In addition, birds referred to as the Violet Wood-hoopoe (*damarensis* and *granti*) and Black-billed Wood-hoopoe (*somaliensis*) appear very closely related to *purpureus*, and have been variably treated as either separate species or subspecies, while much needed DNA data remains scant. In East and northeastern Africa several forms are currently recognized: *Phoeniculus purpureus marwitzi* Reichenow 1906, *Phoeniculus purpureus niloticus* Neumann 1903, *Phoeniculus damarensis granti* Neumann 1903, *Phoeniculus somaliensis somaliensis* Ogilvie-Grant 1901, *Phoeniculus somaliensis abyssinicus* Neumann 1903 and *Phoeniculus somaliensis neglectus* Neumann 1905 (Ligon 2001, Dickinson & Remsen 2013, del Hoyo & Collar 2014).

All are slim, small-bodied birds with long, slender, graduated tails, broad rounded wings, narrow decurved bills and short tarsi. The plumage is largely iridescent black with green, violet or blue sheens, and individual forms differ only in the degree and colour of gloss. Bill colour is normally red or black, often varying with age. Sexes are alike in all forms.

In all wood-hoopoes the degree of phenotypic divergence among currently recognized taxa is poorly characterized, while mantle plumage varies among individual wood-hoopoes and between age classes (Cooper et al. 2001). At the same time there appear to be only minor discernible vocal differences between any of the above named forms. In southern Africa, some authors treat the Violet Wood-hoopoe *P. damarensis* as an endemic, but others believe that it might simply be a plumage variant and junior synonym of *P. purpureus* (Cooper et al., op. cit).

In Kenya, *P. purpureus marwitzi* is largely blackish, glossed with green on the head, upperparts and breast, while *P. p. niloticus* has the head, mantle, breast and tail appearing more steel-blue than green, thus appearing very similar to the Violet Wood-hoopoe (*P. damarensis granti*) of eastern Kenya. The continuum between green and purple is well known to all who study iridescent plumage, with colours shifting from one to the other as the light source and angle vary. Thus, plumage colours in *purpureus* may appear to change from greenish to blue or violet to almost blue-black depending on whether the bird is seen in bright sunlight, deep shade or dappled light, often leading to identification difficulties. Perceived colour may also differ between early morning and late afternoon viewing conditions. The Black-billed Wood-hoopoe *Phoeniculus somaliensis*, long considered a race of the Green Wood-hoopoe, was deemed worthy of separate species status by Davidson (1976) on the grounds that the largely all-black bill is typically more slender and decurved than in either *purpureus* or *damarensis*, and indeed that longer bill does serve to distinguish it from the other two (Turner 2014). Meanwhile, its status in northern Kenya border areas vis-à-vis any sympathy with either *niloticus* or *granti* remains unclear.

Dowsett & Dowsett-Lemaire (2015) recently discussed in some detail birds they observed in the Omo Valley of southwestern Ethiopia, believed to be the Violet Wood-hoopoe *Phoeniculus damarensis*. They commented on birds collected by Zaphiro from the Zoula River, Uba, in July 1905, which were also considered to have been
*Phoeniculus damarensis granti*. No mention was made, however, of the possibility that the Omo Valley birds may have represented what in northwestern Kenya border areas are referred to as *P. purpureus niloticus*, also known from the Gambela region of southwestern Ethiopia, South Sudan, and from Lake Stephanie (to the east of the Omo Delta). Neumann visited southern and southwestern Ethiopia in 1901–1902, later describing in *Orvnithologische Monatsberichte* (1903) the forms *niloticus*, *abyssinicus* and *damararensis granti*, with only very minor plumage differences separating them.

*P. damarensis granti* is endemic to the palm-fringed river systems of eastern Kenya, with as yet no proven cases of intergrades with *purpureus*. Elsewhere in southern Kenya, birds reported as *granti* may be nothing more than individual *purpureus* with distinctive violet tail and mantle feathering appearing more prominent due to light conditions at the time. Records in arid country from Kapedo northwards probably refer to *P. p. niloticus*, a form largely impossible to separate from *granti*. Adult *granti* possess varying densities of green-, blue- or violet-glossed feathers, and in the field juveniles cannot safely be distinguished from juvenile *purpureus*. In addition, any observed differences in plumage colour between Green and Violet Wood-hoopoes may well be clinal or habitat-related, with perhaps a more pronounced violet colouration in birds in arid areas. Dowsett & Dowsett-Lemaire (2015) commented that the voice of their Omo Valley birds sounded drier than that of *P. purpureus*. Do *niloticus*-type birds in northwest Kenya sound similar, as they are often referred to as Violet Wood-hoopoes?

There is no disputing that *niloticus* and *granti* both tend to show more blue and violet on the mantle, breast and head than *P. purpureus marwitzi*, but one cannot rule out the possibility that all three may, in fact, be conspecific, with *niloticus/granti* representing a dry country form of *P. purpureus* which extends from the palm-fringed river systems of eastern Kenya north through Samburu and Baringo districts to southern and southwestern Ethiopia. Both *marwitzi* and *granti* are reported to have been collected at Archer’s Post (Samburu District) on the same day (Oberholser 1945), which may underline the difficulty in distinguishing between these two. Comprehensive molecular analysis of all forms would now appear warranted, and the nomenclature of birds known as the Violet Wood-hoopoe may also require attention since both *niloticus* and *granti* were named and described in the same publication (Neumann 1903).

Current known localities for *niloticus* and *granti* are:

Kenya: Kapedo, Upper Turkwell, Ndotos, Mathews Range, Lodwar, Lokichogio.
Ethiopia: Lake Stephanie, Gambela.

*P. (d.) granti*: Kenya: Kibwezi, the Tsavo, Galana, Northern Uaso Nyiro, Upper Tana and other river systems in the Tsavo NPs, Meru NP, Shaba and Samburu GRs.
Ethiopia: Omo Valley, Zoula River.

From the above it is clear that there is an almost contiguous range of *granti* and *niloticus* stretching from the eastern Kenya riverine areas northwest through the Northern Uaso Nyiro to the Mathews Range, the Ndotos, the Upper Turkwell, Lodwar and Lokichogio. Both forms then re-appear in Ethiopia, with *niloticus* in western border areas and the Gambela region, and with *granti* in the Omo Valley and along the Zoula River. In reality there may not even be a break in distribution from the Tsavo River
all the way to the Omo Valley and Gambela on the Ethiopia–South Sudan border. The type locality of *niloticus* was on the Nile in southern Sudan, while that of *granti* was in the Tsavo region of southeast Kenya. As these two forms cannot be irrefutably separated, which name would take priority? Regarding possible intergradation, some has been suggested between *niloticus* and *marwitzi* (Friedmann 1936, Oberholser 1945), and the report of *marwitzi* and *granti* being collected on the same day at Archer’s Post, Samburu District, may also reflect the same. This would add to the case for suggesting that all are members of one species *P. purpureus*. Also, since *granti* has often been allied with southern African *damarensis*, this would question again the status of the latter with regard to *P. purpureus*.

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**References**


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