Flight feather moult patterns and stable isotope analysis in the Woodland Kingfisher (*Halcyon senegalensis*)

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Declaration

This thesis reports original research that I conducted under the auspices of the FitzPatrick Institute of African Ornithology, University of Cape Town. All assistance received has been fully acknowledged. This work has not been submitted in any form for a degree at another university.

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Abigail Ramudzuli

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Abstract

The Woodland Kingfisher *Halcyon senegalensis* is an intra-African migrant that is widely distributed south of the Sahara. Migrating populations have to undergo an annual cycle that includes two migrations between the breeding and non-breeding grounds, the renewal of feathers and reproduction. All the mentioned processes are energetically expensive and they need special physiological adaptations. I investigated the timing of moult by actively catching Woodland Kingfishers in the field and scoring them for moult. This showed that migrating Woodland Kingfishers that breed in South Africa do not moult their flight feathers while they are on their breeding grounds. Resident populations in Ghana and Uganda sampled between June and August, during their breeding season, were also not in moult, but some individuals were growing feathers that they had lost through mechanical damage. Moult data from the SAFRING database also showed no evidence of active moult for all adult birds in the southern Africa region, suggesting that they moult on the non-breeding grounds. This knowledge of moult allows us to use natural markers that are fixed in feathers to potentially infer where migrant birds spend their non-breeding period.

To infer non-breeding grounds of the Woodland Kingfisher, I measured stable isotope ratios of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and hydrogen ($\delta^{2}H$) in primary (P1), secondary (S1) and tail (R1) feathers from birds caught in Ghana, South Africa and Uganda between 2015 and 2018 during the respective breeding seasons. Feather $\delta^{13}C$ of Woodland Kingfishers caught in Ghana suggest that these birds grow their feathers in areas dominated by C3 plants, whereas feathers from Woodland Kingfishers caught in Uganda and South Africa indicated that they moulted in areas dominated by C4 plants. This enables us to assign birds to different feeding areas. The $\delta^{2}H$ values were

highest in South African feathers but not significantly different from the Ghanaian feathers, while the Ugandan $\delta^{2}H$ feather values were the lowest. The similar $\delta^{13}C$ and $\delta^{2}H$ values of feathers of birds from Uganda and South Africa suggests that the non-breeding grounds of the migrant South African population lies within the same isoscape band as that of Ugandan birds. $\delta^{15}N$ values, which indicate trophic levels, were similar for all the birds, suggesting that Woodland Kingfishers in Ghana, South Africa and Uganda forage on similar prey. The observations of colour-ringed Woodland Kingfishers in Uganda outside the breeding seasons confirm the Ugandan population to be sedentary and this enabled us to infer that the birds that were caught in this area were sedentary. While yet-unpublished telemetry data indicates Woodland Kingfishers that breed in South African spend their non-breeding period in areas around Chad, Sudan and Central African Republic. This region is within the same $\delta^{13}C$ isoscape as Uganda. The use of stable isotopes, especially when combined with other techniques, shows a lot potential as means of inferring the non-breeding grounds of migrating Woodland Kingfishers. The approach of exploring moult patterns and analysing SI signals should be expanded for use on other intra-African migratory bird species because the migratory behaviour of most intra-African migrants still remains unknown.

Chapter 1: General Introduction

The Woodland Kingfisher is a partial intra-African migrant; some populations are migratory and some are sedentary. This individual trapped in South Africa is fitted with a miniature geolocator to track its migratory movement

(Photo: Dr Samuel T. Osinubi)

Introduction

The seasonal and cyclical movement of individuals between two distinct geographical locations, referred to as migration, has long been a source of fascination to people (Bauer & Hoye 2014). Migration forms an important aspect or aspect of natural history in a number of animal species and has great implications for survival and individual fitness (Drent et al. 2006, Beatty et al. 2013). This behaviour allows mobile species to take advantage of temporally predictable changes in productivity or other resources required to complete their life history. Some of the factors that drive migration include accessing food resources, or avoiding or reducing competition and diseases (Newton & Rothery 2005). However, these benefits need to be balanced against the risks of moving between locations. Therefore, energy optimisation and nutrient acquisition during migration is an important consideration because of the energy expenditure over the distances being covered and the stochastic availability of food at sites along the migratory routes (Anteau & Afton 2006, 2009). Different taxonomic groups show some form of migration, including some mammals (Fryxell & Sinclair 1988, Beatty et al. 2013), amphibians and reptiles (Semlitsch 2010), insects (Woiwod et al. 2003), fish (Hodgson et al. 2006), and birds (Martin et al. 2007, Yamaguchi et al. 2008). Much of what is known about bird migration comes from studies of birds that move between continents, termed inter-continental migrants (Robinson 2015). There have also been studies of intra-continental migrants within Europe and North America, but less is known about such regional movements on other continents (Berruti et al. 1994).

Palearctic and intra-African migrants

Avian migration across the African continent generally involves two groups of birds, the Palearctic migrants that move between Africa and Eurasia, and the species that

migrate within the continent of Africa, referred to as intra-African migrants (Hubbard 1973). Most bird migration is latitudinal (north-south), but this is neither absolute nor without variation. Some intra-African migrant bird species like Abdim's Storks *Ciconia abdimii* and Rosy Bee-eaters *Merops malimbicus* undertake longitudinal (west-east) movements (Bacon et al. 2019). Some species are only known as partial migrants (Fandos & Tellería 2020) where populations of the same species may include both sedentary and migratory individuals (Chapman et al. 2011). Studying intra-African migrants (or intra-continental migrants as a whole) is crucial to our understanding of the where, when and how these species move (Bensch et al. 2018) across the African landscape, therefore aiding in developing efficient conservation measures for intra-African migrants. There have been many studies on Palearctic migrants, but much less is known about intra-African migrant species.

Seasonality influencing migration in Africa

The total area of the African continent is about 30.3 million km^2 (Moreau 1952). However, about 9.2 million km^2 is occupied by the Sahara. This great desert area, larger than Australia and almost as large as the United States of America, is a prominent feature on the African continent and constitutes a major obstacle to many terrestrial avian migrants (Newton & Dale 1996). To put this in perspective, the Sahara is the largest hot desert, and third largest desert overall, after the ice deserts of Antarctica and the Arctic. The Sahara runs across the African continent from 15 to 30 ºN and many migrant species need to either avoid or navigate this expanse. Seasonality in rainfall and productivity (Figure 1.1) is the main driver of many of breeding migrant birds in local avian assemblages, with migrants that are coming into these areas benefiting from the extra resources and energy that is available in areas

of high seasonal differences (Elmberg et al. 2014, Somveille et al. 2015). This may also be true because of the absence of some of the local migrants. In terms of temperature, low temperature has seemed to be the main contributing factor of winter harshness that most birds experience, probably as a result of a direct effect of low temperatures on bird metabolism (Somveille et al. 2015) or through an indirect effect of temperature on resource availability (Graber & Graber 1979, Somveille et al. 2015) or as there is a reduction in insect activity (Williams 1961). Seasonality also influences diseases like avian malaria which can in turn also be a migration driver (Altizer et al. 2006, Wills 2017). Thus, seasonality influences productivity, temperature, competition, disease, all of which collectively drive both the timing and direction of migration. This suggests that migration is largely based on extrinsic factors (Brenner 1965, Graber & Graber 1979, Saleweski et al. 2019)

The most common form of migratory movement among intra-Africa migrant birds is to move to temperate areas for breeding, usually in accord with the beginning of the rainy seasons and summer in the breeding grounds (Moreau 1952, Hockey et al. 2003). They are generally assumed to winter in more tropical regions. However, few intra-African migrants travel north across the Tropic of Cancer, probably because of the Sahara. Most birds travel south across the Tropic of Capricorn to breed in the austral or southern summer (Brenner 1965, Graber & Graber 1979, Koleček et al. 2016).

Determining birds movements between areas of breeding and non-breeding is important to our understanding of their ecology (Wassenaar & Hobson 2000, Pain et al. 2004, Ali 2012). Establishing migration routes and stopover sites between areas

used by intra-African migrant birds throughout their yearly cycles is crucial to the conservation of intra-African migratory birds (Wassenaar & Hobson 2000). For many years, studies of bird migration relied on trapping and catching birds to use extrinsic markers (e.g. rings or other tags) physically attached to animals. This was done with the hope that some of the marked animals will be recaptured at different location (Bauer & Hoye 2014, Viljoen et al. 2016, Jelle Loonstra et al. 2019). The chances of recapturing the bird is highly dependent on the number of observers available for the work, the habitats and regions, and behaviour of the bird species, all of which results in the chances of re-sighting or recapture typically being low (Viljoen et al. 2016).

Moult in birds

Feathers need to be renewed regularly as their functional life span is shorter than the potential life span of the bird due to damage to feathers from mechanical abrasion, photochemical processes and parasites (Barta et al. 2008, Rohwer & Wang 2010, Kiat & Sapir 2017, Rohwer & Rohwer 2018). This renewal of feathers, termed moult, includes performance, time and important energetic costs that are combined into the yearly cycle (Rohwer & Wang 2010, Zuberogoitia et al. 2016). Indeed, moult forms one of the three energy-demanding processes that migrant birds need to go through in their yearly cycle, together with breeding and migration (Newton & Rothery 2005). These demanding processes in the yearly cycle are energy- and time- consuming, and the extent of investment in these processes can compromise each other (Hedenström 2008, Rohwer & Rohwer 2018). Moult investment and migration investments are selected so that lifetime fitness is maximized, while maintaining the ultimate goal of breeding (Åkesson & Hedenström 2007, Rohwer & Wang 2010). The timing of these events differs according to their ecological conditions under which certain populations

or species are found (Salewski et al. 2004). In most species, flight feather moult rarely overlap with other yearly processes of migrant birds (i.e. breeding and migration) (Barta et al. 2008). However, the timing and to some extent sequence of moult is flexible both at the species and the individual levels, and its phenology is typically more variable than other life history events (Neto et al. 2006). For example, some of the migratory birds grow new feathers while in their breeding areas just after breeding is over, others moult at a staging area or migration stopover, while others moult on their non-breeding grounds (Zuberogoitia et al. 2018). Yet others suspend moult completely during migration, replacing part of their plumage in one place and completing moult in another (Zuberogoitia et al. 2018). Different variants on these patterns can occur in different populations of the same species (Salewski et al. 2005, Pyle 2013, Pillar et al. 2016, Zuberogoitia et al. 2018). Some species of birds have an overlap in breeding and moulting, while some have an overlap in moulting and migration, more especially body moult, which can potentially occur without reducing flight efficiency of birds. However, feather growth can be reduced to compensate for the nutritional demands of other activities. Typically, resident adult passerines have an annual complete moult shortly just after their breeding time (post-breeding moult) (Neto et al. 2006). However, this is not always the case for many migratory birds, which evidently shows a great variety of wing-moult strategies or patterns (Jenni & Winkler 1994, Neto et al. 2006). An understanding of moult is important in enabling us to interpret bird life-history strategies, but is also crucial if one wishes to use stable isotopes to infer movement patterns among birds (Svensson and Hedenström, 1999; Figuerola and Domènech, 2003).

The evolution of winter moult in northern temperate species migrating into Africa has been characterised by two main circumstances: firstly, the increased migration distance may encourage and initiate the early start of post summer migration, which may reduce the time available for moult right after breeding (Hall & Fransson, 2001); secondly, the high availability and easy accessibility of resources for moulting birds in African habitats may favour the evolution of winter moult (Barta et al. 2008). Although there is an intense debate surrounding the factors that affect moult pattern variation in passerines, the determinants of these diversification are still not well understood (Salewski et al. 2005, De La Hera et al. 2010). Besides bird ringing or banding, mentioned above, an alternative approach to understanding bird migrations uses intrinsic markers to study animal or bird migration, one of these intrinsic methods being the use of stable isotopes (Haché et al. 2012).

Using stable isotopes to infer avian migration

Isotopes are varying weights of particular chemical elements that are known to have the same number of protons but different numbers of neutrons. Some isotopes are unstable, breaking down over time, whereas others are more stable and can be used as natural tracers. Elements such as hydrogen, nitrogen, carbon, sulphur and oxygen and sulphur have scarce heavier isotopes, each with one additional neutron, resulting in them being heavier than the lighter and more common isotopes (Norris et al. 2007, Alexander & Downs 2016). The increased mass slows the rate of chemical reactions that results in varying ratios of the heavier to lighter isotopes in materials, depending on their origin and history (Alexander & Downs 2016). This process is known as isotopic fractionation and it is the comparable separation of the lighter and heavier isotopes between two phases that coexist in a natural system (Hobson, 2005). The

extent of isotopic fractionation depends on temperature and on the mass difference between isotopes in relation to their individual isotopic mass (and thus is more pronounced for elements with relatively few protons and neutrons; (Michener & Lajtha 2008) . The expression of isotope ratios is in delta-value notation (δ) which reflects the ratio of light to heavy isotopes in relation to a known standard (Alexander & Downs 2016). The "δ" values calculated are represented as parts per thousand (‰) using the equation:

"δ sample (‰) = [(Rsample/Rstandard) - 1] x 1000

where R = isotopic ratio of heavy to lighter isotopes for sample and standard, e.g.$^{13}C/^{12}C$ (Hobson 2005b, Hoefs & Hoefs 2009)".

Carbon

The carbon stable isotope (δ ^{13}C) values found in organisms' tissues have always been used to determine dietary composition and geographic origins of living organisms (Ehleringer & Dawson 1992). Carbon isotope may be different because of different physiological and biological factors that different animals go through. The differences can be used to determine the geographic origins of organisms. The geographical makeup of a given area has an influence on the δ ^{13}C values of animals and plants, be it differences in altitude, distance from the coast or latitude (Figure 1.2, Symes 2009). A number of different researches have depicted that δ ^{13}C of bird feathers are directly correlated with latitude; feathers grown at higher latitudes have more negative δ ^{13}C values because organisms at high latitudes dependently rely on CO_2 as an inorganic source of carbon while low latitude plants make use of HCO_3 directly (Symes 2009, Alexander et al. 2018). Feather samples that show δ ^{13}C signature above –

30 ‰ suggest that the plants found in the area where the feather was grown take up HCO_3 directly (Hofmann & Heesch 2018). However, $\delta^{13}C$ values also increase with altitude (Symes 2009) so that $\delta^{13}C$ values at low altitudes in high latitudes may be similar to $\delta^{13}C$ values at high altitudes in low latitudes (Kelly et al. 2002). Additionally, values of $\delta^{13}C$ become more negative with increasing distance from marine ecosystems because terrestrial environments generally have more negative isotopic signatures than marine environments (Hobson 1999b, 2005).

Carbon stable isotope ratios in organic compounds also depend on the photosynthetic pathway used to fix the carbon. Terrestrial plants use two main photosynthetic pathways namely C3 and C4 (Peneycad 2018). The first photosynthesized organic compound in the C3 group has three carbon atoms while C4 plants have four (Viljoen et al. 2016). Most plant species (85%) are C3 and have low values of $\delta^{13}C$, between −22‰ and −30‰. C4 plants, which include tropical herbs and most grasses, have higher values of $\delta^{13}C$, between −10‰ and −14‰. Xeric regions typically have more C4 and Crassulacean Acid Metabolism (CAM) plants and thus generally have more positive $\delta^{13}C$ values than areas that are mesic with a greater dominance of C3 plants (Alexander et al. 2018). In regions that have greater tree cover, $\delta^{13}C$ values may appear more negative than areas with less vegetation cover (Cherel & Hobson 2007, Alexander et al. 2018). Stable carbon isotope analysis can help determine the environment in which a bird grew its feathers, as its diet reflects the vegetation types that form the base of the food chain and that are influenced by geography, climate, and anthropogenic factors (Alexander et al. 2018).

Nitrogen

Plants make use of both atmospheric- and soil-nitrogen, which is passed on from one trophic level to another (Peterson & Fry 1987, Symes 2009, Alexander et al. 2018). Values of $\delta^{15}N$ are also used to describe the diet of animals and give estimation of where particular tissues are grown (Hall-Martin et al. 1993) Fractionation of $\delta^{15}N$ happens because of different given factors, including environmental (Peterson & Fry 1987, Evans et al. 2012, Alexander et al. 2018) and anthropogenic influences (Hobson, 2005), trophic level shifts (Symes 2009, Boecklen et al. 2011, Alexander et al. 2018) as well as physiological factors (Kelly 2000, Veen et al. 2014).

Values of $\delta^{15}N$ typically enrich c. 3–5‰ per trophic level (Deniro & Epstein 1981, Gannes et al. 1997, Hobson et al. 2017) because the heavier ^{15}N molecules are favoured less than the lighter ^{14}N molecules in dietary absorption and thus the ^{15}N:^{14}N ratio decreases with each trophic level (Gannes and Martinez del Rio, 1997; Kelly, 2000). Differences in ^{15}N enrichment may also occur within species because larger individuals feed on different prey depending on availability, or there being easy access to different food types, but this pattern is seldom found among birds as they have determinate growth once fledged (Pain et al. 2004, Procházka et al. 2008, Symes 2009). It is therefore crucial to understand the ecology of the organism that is in question, so that there is an initial understanding or idea of the expected $\delta^{15}N$ values in relation to the food base (Kelly 2000, Pain et al. 2004, Podlesak et al. 2005, Chen et al. 2008, Symes 2009, Evans et al. 2012). It is also important to understand the state of the organism; nutritional and water stress, moult, and reproductive status as they may all have an effect on the fractionation and assimilation of $\delta^{15}N$ within the body (Hobson & Welch 1992, Kelly et al. 2002, Katzenberg 2007, Symes 2009, Veen

et al. 2014). During moult, migration and reproduction, or even in times where there are bouts of poor health, metabolic rate may increase. This may generally then lead to an increased assimilation of biochemical components or even altered assimilation so that higher energy can be acquired (Coiffait et al. 2009). To add to that, there could be an alter to the isotopic values caused by organisms sourcing nutrients from their reserves in their bodies. Although this is of advantage during the times of these bouts of increased metabolic activity, it could result in results that are not true or good enough to give credible answers (Hobson & Welch 1992, Cherel et al. 2000, Rocque et al. 2006).

Deuterium/Hydrogen

Hydrogen (H) that is found in water is taken up into plants' tissues from rain and/or ground water (Cherel et al. 2000, Symes 2009, Topalov et al. 2012, Alexander et al. 2018). Analysis of deuterium (^{2}H) is used to determine the geographic origins of organisms in relation to global patterns of $\delta\ ^{2}H$ in precipitation (Wassenaar & Hobson 2000, Kelly et al. 2002, Rubenstein & Hobson 2004, Bowen et al. 2005, Hobson 2005a, Hobson et al. 2012). The change of latitudinal mean-annual temperature, decreasing with distance from the Equator or with increasing altitude, has a direct influence on the amount, frequency, and the type of precipitation that occurs (Bowen et al. 2005a). When there is latitudinal or latitudinal decrease in temperature, deuterium values tend to be less positive (Dansgaard 1964, Wassenaar & Hobson 2000, 2003, Kelly et al. 2002, Bowen et al. 2005, Hobson et al. 2012, Arizaga et al. 2016). Generally, areas that are cooler receive more rain or precipitation, or they would usually experience less evaporation than areas that are warmer, and this would then

result in increased temperatures in such environment, thus have more positive δ ^{2}H values in precipitation (Dansgaard 1964; Wassenaar and Hobson 2000; McKechnie 2004; Cherel and Hobson 2007; Hobson et al. 2012). Fractionation through evaporation also results in δ ^{2}H values decreasing as one moves further and further away from the sea (Lloyd-Evans 1966, Hobson 1999, Kelly et al. 2002, Cherel & Hobson 2007, Dolan et al. 2018). Values of δ^{2}H in the ocean relatively remain the same at a constant of around 0‰ (Lloyd-Evans 1966). However, fractionation occurs during evaporation and the water vapour removed from the ocean is depleted in δ ^{2}H (Lloyd-Evans 1966, Symes 2009). As the water get deposited as rainfall and it is re-evaporated farther inland, it becomes even more negative in δ ^{2}H which results in the most depleted waters being found even further away from the sea. Africa does not have distinct changes in δ ^{2}H with increasing latitude as Europe and North America, but there is a decrease in δ ^{2}H values when moving east-west decrease (Bowen et al. 2005, Hobson 2005b, Symes 2009, Veen et al. 2014, Arizaga et al. 2016).

Fractionation of δ ^{2}H also occurs within plants and animals. Water vapour diffuses out of plants when stomata are open, and this results in the remaining water being more positive in δ ^{2}H values, increasing the δ ^{2}H values of plant tissues. Similarly, animals that use the process of evaporative-cooling to manage well with heat stress caused by the water vapour loss, and have more positive δ ^{2}H values in their tissues (Hobson et al. 2006). However, there is no fractionation between trophic levels (Wassenaar & Hobson 2003). The physiological influence on δ ^{2}H values in plants is passed on to their consumers. Although this may not be a physiological process for the consumer, it occurs indirectly because of the plant's physiological processes. However, after ingestion, δ ^{2}H can still experience physiological

fractionation. The δ ^{2}H obtained through drinking water or different sources of food is exchangeable with food molecules that is typically found in the form of carbohydrates and proteins (Rocque et al. 2006), resulting in differences between the δ ^{2}H values of consumer tissue and that of the environmental δ ^{2}H values.

Stable isotopes in feathers

Feathers are the most commonly used tissue used to infer bird movements using stable isotopes because they record the stable isotope signal to which the bird is exposed at the time of moult (Carravieri 2014). Thus for birds caught outside the moulting period, they provide a way to link migrants to their moulting grounds because feathers are inert tissues that keep isotopic information based on the geographical areas of where the bird was during the time of feather growth (Yohannes et al. 2005b, 2007, Alexander et al. 2018). This allows the place of origin of where the feathers were grown to be determined more easily than metabolically active tissues, like muscles, because feathers fix the stable isotopic signals of resources used to grow the feathers. Typically, this is the isotopic signature of the area where moult occurs, although some feather growth might be fuelled by stored reserves rather than food obtained in the area (Hobson 2005b). New feathers, thus typically would show isotopic signatures of the geographical of growth, which may possibly be different from the region where the bird is trapped and where the sample was taken (Pain et al. 2004, Bond & Jones 2009, Alexander et al. 2018). Among migrant birds, different feathers may grow in different regions, and this is dependent of the growth rate and moult pattern of the bird. The presence of lipids in the birds food intake or diet also has the ability not influence isotopic signatures of feathers as much as they can influence other tissues simply because feathers are primarily formed from proteins (Hobson 1999, 2005). This then

may suggests that the δ ^{13}C and δ ^{15}N values of feathers are little influenced by dietary lipids, but δ ^{2}H values of feathers can be influenced by ambient water vapour (McKechnie 2004, Cherel et al. 2009, Wakelin et al. 2019). Because diet between different age classes and different species may differ between, this can ultimately alter δ ^{2}H, δ ^{13}C or δ ^{15}N values (Smith et al. 2008, Hobson et al. 2012).

Most intra-African migrant species are widely distributed across Africa, south of the Sahara (Allan et al. 2000). Many intra-African migrant species have both migrant and resident populations, with individuals of populations that breed close to the Equator tending to be sedentary, whereas those that breed at higher latitudes migrate between breeding and non-breeding grounds. I studied the Woodland Kingfisher *Halcyon senegalensis* as one of the good examples of intra-African migrants.

Study species

The Woodland Kingfisher is an intra-African migratory species, widely distributed across sub-Saharan Africa (see Figure 1.3). There are three subspecies described with different yet overlapping ranges, the forest race known as the *H. s. fuscopileus* is sedentary, but the northern savanna race *H. s. senegalensis* is known to move north with the intertropical convergence to breed in the boreal summer (Figure 1.3, Greig-Smith 1978). In the south, it is replaced by *H. s. cyanoleuca*, which migrates to southern Africa to breed during the austral summer. *H. s. cyanoleuca* can be told from the other two subspecies by the black stripe that runs through the eye. It was generally assumed that *H. s. cyanoleuca* winters in central Africa after breeding, but a recent study found that the few adults tracked migrated across the Equator to spend the non-

breeding season during the boreal summer in South Sudan and the Central African Republic (Tarboton & Tarboton 2014).

Overview and outline of this thesis

This study aims to explore the migratory behaviour of the Woodland Kingfisher in southern, eastern and west Africa through the analysis moult patterns and stable carbon, nitrogen and deuterium in their flight feathers. In **Chapter 2**, I determine the timing of moult in Woodland Kingfishers by scoring moult patterns in primary feathers. This could give an indication of possible differences in where and when these birds grow their flight feathers. I combine moult data from adult Woodland Kingfishers captured on their breeding grounds (Ghana for west Africa, Uganda for east Africa and South Africa for southern Africa) with moult data from the South African Bird Ringing Unit (SAFRING).

In **Chapter 3**, I compare the stable isotope values ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) of different flight feathers between individual Woodland Kingfishers from Ghana, South Africa and Uganda. I also look at stable isotope values ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) of primary wing feathers from museum samples of Woodland Kingfishers in Uganda to determine whether stable isotope analysis within individuals provides additional and relevant information for changes in isotopic signatures over time.

Finally, in **Chapter 4**, I synthesise the results from the preceding chapters, and make deductions of where the migrating Woodland Kingfisher may be going to winter after breeding in South Africa. Also, I elaborate more on the timing of moult in the Woodland Kingfisher. I also suggest related topics for future research.

Figures (Chapter 1)

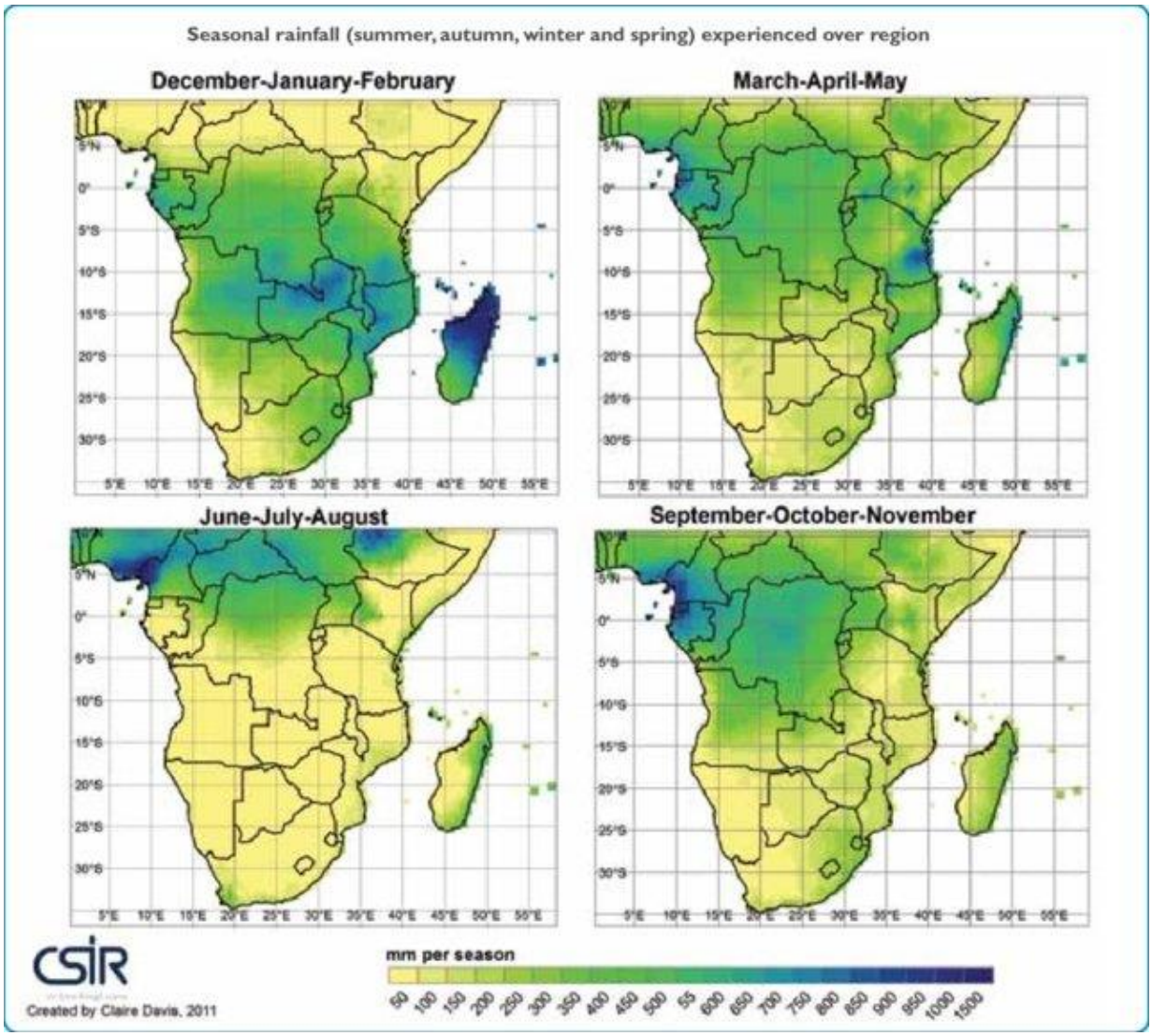

Figure 1.1: Average seasonal rainfall totals (mm per season) across sub-Saharan Africa (from Davis et al. 2011).

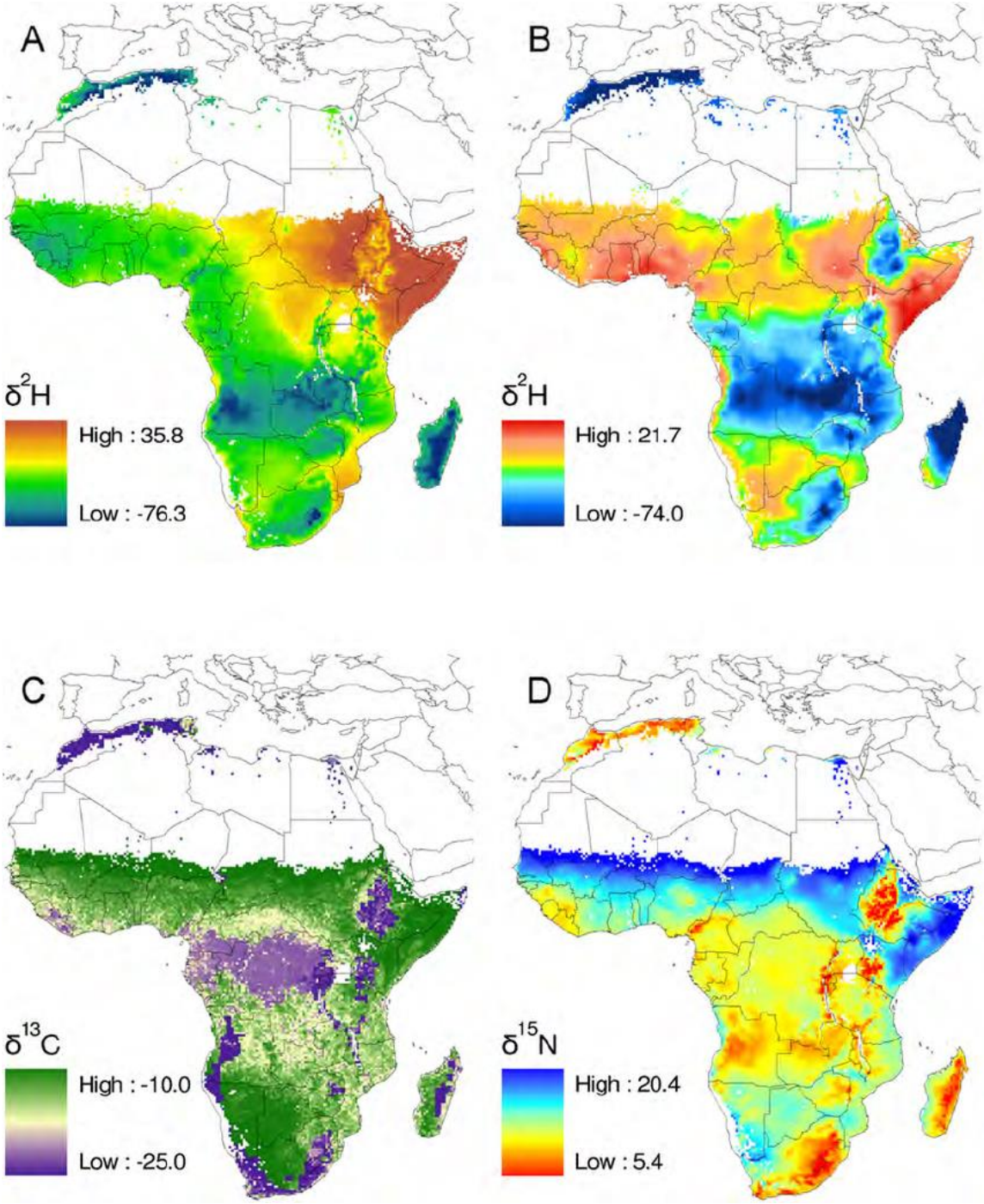

Figure 1.2: Annual sub-Saharan deuterium (A and B), carbon (C) and nitrogen (D) isotope ratios in precipitation. Isotope values are indicated in the bars bottom left each map (from Bowen et al. 2005).

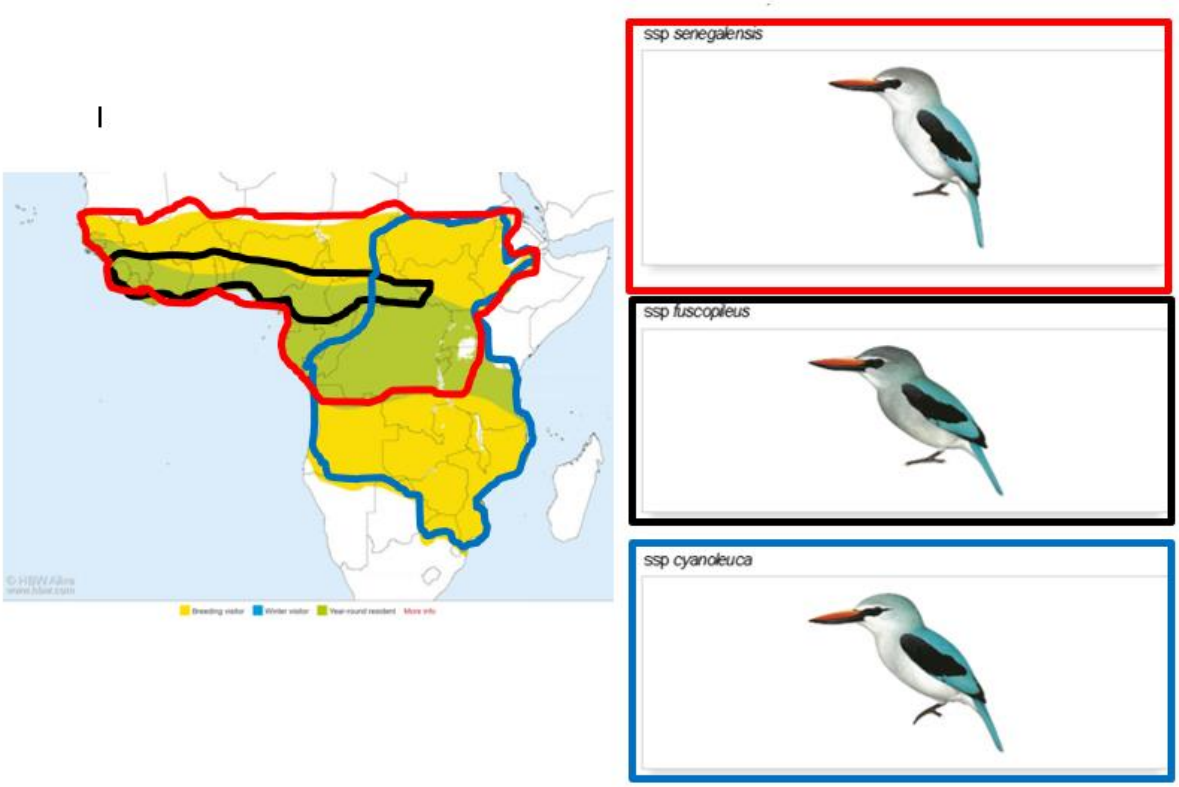

Figure 1.3: Map showing the distributions of *H. s. senegalensis*, *H. s. fuscopileus* and *H. s. cyanoleuca*. The yellow shaded areas indicate where Woodland Kingfishers are seasonal migrants; the green shaded area is where they are found throughout the year (although both migratory and resident populations may occur in this area).

Chapter 2: Patterns and Timing of Moult in the Woodland Kingfisher

The wing of an adult Woodland Kingfisher being assessed for primary feather moult in the field (Photo: Abigail Ramudzuli)

Introduction

For a bird to maintain good flight, waterproofing and heat insulation, feathers that are old and worn out need to be replaced through the process of moulting. As a rule, each feather needs to be replaced at least once a year, although in some large birds like albatrosses (Diomedeidae) and Bearded Vultures (*Gypaetus barbatus*), individual flight feathers are only moulted every second or even third year (Pillar et al. 2016). Moulting may be induced by changes in photo-period, temperature, food availability, rainfall, or mechanical damage. As stated in Chapter 1, the typically shortened breeding season of birds that migrate allows for time and energetic trade-offs between reproductive efforts, migration and feather moult (Stutchbury et al. 2011). Reproductive success in some species has been shown to be reduced by the simultaneous moulting and breeding (Gargallo 1994, Hall & Fransson 2001, Raess 2005, Barta et al. 2008, Okahisa et al. 2013) but rushing post-nuptial moult can potentially lower the quality of flight feather (Dawson 2004). In some species, there are individuals that undergo and complete feather moult just after the breeding season. These individuals tend to reserve more fat than those in which moult and the post-breeding migration overlap (Okahisa et al. 2013). Knowledge about moult relative to breeding and migration is important in developing conservation strategies for migrant birds, especially as they pass through different countries which often have a wide range of conservation policies (Jenni & Winkler 1994, Warnock 2010, Franzoi 2016). Little is known about moulting patterns of intra-African migrants, because so far, relatively little attention has been focused on these migrants. Understanding and describing the moult patterns of intra-African migrant birds is a challenge because, at best, this requires the collection of moult data from across the continent. However, at

the barest minimum, it requires some insight into when moult takes place in the annual cycle (Leu & Thompson 2002).

The main objective of this chapter is to explore the flight feather moult pattern of an intra-African migratory species, the Woodland Kingfisher, which is a partial migrant (Chapter 1). Beyond the inherent interest in how migratory and sedentary populations of this species might vary in moult strategies, an understanding of the timing of moult in relation to migratory movements is crucial if we are to use chemical signals in the Woodland Kingfisher's feathers to infer where they spend the non-breeding season (Chapter 3). Based on observations in southern Malawi, Hanmer (1980) inferred that migratory Woodland Kingfishers only moult on the non-breeding grounds. Among related species, the Mangrove Kingfisher (*Halcyon senegaloides*), which forms a super-species with the Woodland Kingfisher, has a complete post-breeding moult from February to June (Clancey 1992). The Brown-hooded (*Halcyon albiventris*) and Striped Kingfishers (*Halcyon chelicuti*) both have complete post-breeding moults in Zambia (RJ Dowsett unpublished data) but in Malawi, the Striped Kingfisher seemingly can suspend moult to breed, replacing inner primaries before breeding, and outer primaries afterwards (Pyle 2013). The Grey-headed Kingfisher also has complete post-breeding moult in Malawi (Hanmer 1980), with the first primary replaced being p1, followed by scattered feathers of the crown and forehead and some belly feathers and flanks from primary moult. Although I cannot conclusively say when and what type of moulting pattern the Woodland Kingfisher undergoes, it is possible that most kingfishers, if not all, follow the same moulting pattern.

In this chapter I use moult data collected from birds in the field, combined with ringing data from the South African Bird Ringing Unit (SAFRING) database to determine the timing and moult pattern of primary feathers in the Woodland Kingfisher.

Methods

Adult Woodland Kingfishers were caught during the breeding season in Accra (Ghana), Entebbe (Uganda) and Limpopo Province (South Africa) from 2015 to 2019. Ghanaian birds were sampled in June – July, Ugandan birds in July – August and South African birds in November – January. All birds mist-netted or spring-trapped were ringed and the extent of primary moult was checked according to the method described by Ginn & Melville (1983), where old feathers scored 0, growing feathers from 1 to 4 and new feathers 5. The Woodland Kingfisher has 10 primary feathers, and the standard numbering of primary feathers is from the innermost p1 outwards to p10 (Kiat et al. 2016) (Figure 2.1 and 2.2). Secondary and tail feathers were not inspected for moult scoring. Additional data were obtained from the SAFRING database (Bonnevie et al. 2003), which included location and date of capture as well as primary moult scores. Woodland Kingfisher records were obtained from January 1970 to December 2017.

Results

A total of 68 Woodland Kingfishers were sampled in the three study regions: South Africa, Ghana and Uganda, with most records from South Africa (Table 2.1). None of the 49 South African breeding birds were found in active moult (Appendix 1). The SAFRING database included a further 406 ringing records of adult Woodland Kingfishers from southern Africa (Botswana, Namibia, Malawi, South Africa,

Swaziland and Zimbabwe). All of these birds were caught during the breeding season. Field data for South African breeding population showed that birds caught during the early breeding season (Nov – Jan) had fairly new primary feathers, suggesting that primary moult was completed not too long before the onset of the breeding. However, Woodland Kingfishers in the SAFRING database that were caught in southern Africa in March – April were often scored as having old feathers (Appendix 7). Two out of the eight Woodland Kingfishers caught in Ghana appeared to be in moult. One bird (caught in 2018/06/27) apparently was a sub-adult that was moulting feathers on both wings and the tail (Appendix 2 and Appendix 3). The other bird (caught in 2018/06/28) appeared to be a result of mechanical damage because only one feather on the right wing was being replaced (Appendix 4). Two of four caught in Uganda on 2018/08/09 also were in moult, with one feather still in the feather tubular sheath (stage 1) and the adjacent feather half grown (stage 3-4), with similar growth on both wings (Appendices 5 and 6).

Discussion

Of the three subspecies, *H. s. cyanoleuca* appears to be the longest distance migrant, breeding in southern African in the austral summer then making a trans-Equatorial migration (Berruti et al. 1994). This is consistent with their wing length and weight. The South African breeding birds (*H. s. cyanoleuca*) were heavier than the Uganda and Ghanaian breeding birds and this has been observed to be case with migrating birds (Lee & Kang 2019). These long-distance migrants arrive in southern Africa from early October, at the onset of its breeding period (Harrison et al. 1997). Because birds arrive to breed in South Africa with fully grown primary feathers (Hanmer 1980, this chapter), these feathers are grown prior to their southward migration. There are no data on the

duration of primary moult in adult Woodland Kingfishers, but in Malawi juveniles commence moult when they are 8-9 months old, and take an estimated 124 days (4 months) to replace all their primaries (Hanmer 1980). Looking at the arrival time (first bird caught in December 2018) of Woodland Kingfishers in South Africa and when the early birds were caught on their breeding grounds (Figure 2.1 and 2.2; Table 2.1), there is not enough time for a single bird to grow an entire set of its primary feathers, suggesting that the South African breeding birds moult their flight feathers elsewhere, presumably before undertaking their southwards migration from their non-breeding grounds (Hanmer 1980).

From the results I found, there were some individuals from the Ghanaian and Ugandan breeding populations that were in active moult during the breeding season (Ghana: June – July and Uganda: July – August). These two populations are described as sedentary with individuals found all year round in the same areas they breed in. Both Ghana and Uganda have tropical climate, generally with rainy and dry season (Nwaogu et al. 2019). The timing of moult may be due to the reason that moult is dependent on rainfall and it is influenced environmental productivity, such as vegetation regeneration and increased invertebrate abundance (Nwaogu et al. 2019). The moult pattern of Woodland Kingfishers in Ghana, and those found in Uganda, suggest that the onset of moult is variable within populations which could be a result of low variation in seasonality (Chapter 1; Ward 1969). The Ugandan sample sizes were too small for me to make any positive assumptions about whether they moult all year round or not.

Tables and Figures (Chapter 2)

Table 2.1: The total number of birds sampled in Limpopo (South Africa), Accra and Cape Coast (Ghana) and Entebbe (Uganda), showing the months when they were caught.

Study area	**Number of birds sampled per month**												**Total**
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
South Africa	3	-	-	-	-	-	-	-	-	-	4	42	49
Ghana	-	-	-	-	-	8	2		-	-	-	-	10
Uganda	-	-	-	-	-	-	4	5	-	-	-	-	9

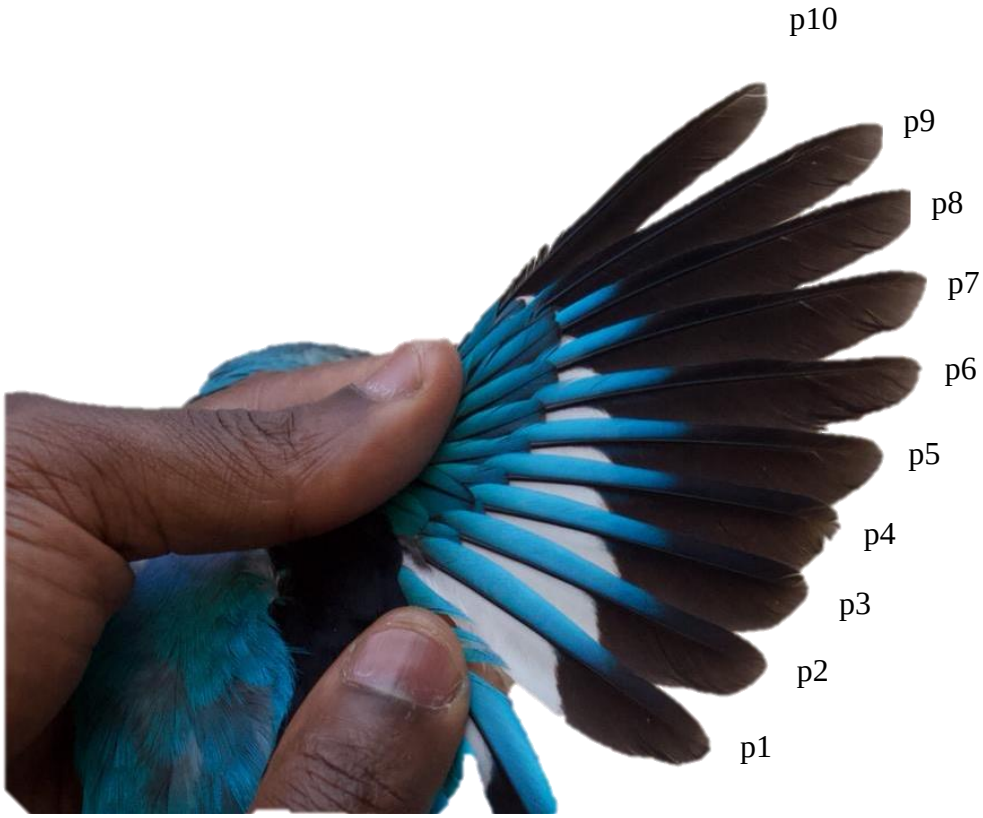

Figure 2.1: Photograph of an adult Woodland Kingfisher wing showing the ten primary feathers (p1–10) fully grown with no sign of significant wear (moult score 50). Photographed at Mogalakwena, Limpopo Province, South Africa. 05/12/2018 (Photo: Abigail Ramudzuli).

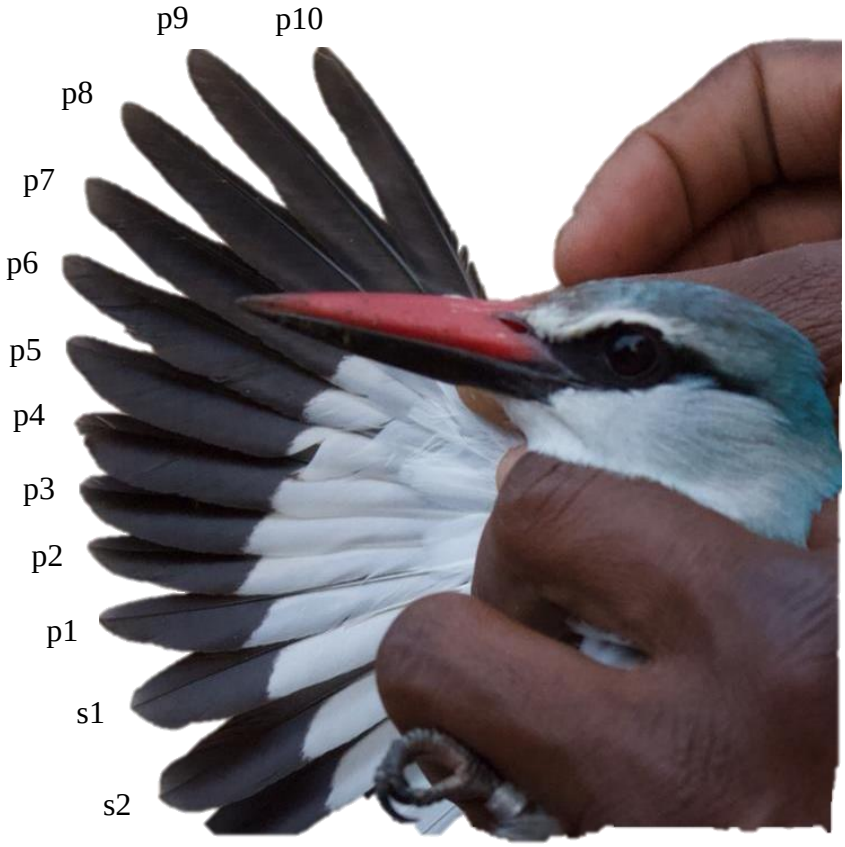

Figure 2.2: Photograph of an adult Woodland Kingfisher wing showing all ten primary feathers (p1–10) fully grown with no sign of intensive wear (moult score 50). Photographed at Mogalakwena, Limpopo Province, South Africa on 05/12/2018 (Photo: Abigail Ramudzuli).

Chapter 3: Using Stable Isotope Analyses of Flight Feathers to Identify Non-breeding Grounds of Woodland Kingfishers

Woodland Kingfisher (Photo: Abigail Ramudzuli)

Introduction

To conserve migrant birds we need to identify their breeding and non-breeding areas, as well as their migratory routes (Vickery et al. 2014). Various methods are used to study migratory behaviours of different birds, each with their advantages and shortcomings (Hall & Fransson 2001). For many decades, much of our understanding of bird movement patterns was through direct observations and the tagging of birds with rings and other markers (Smith et al. 2015). However, the proportion of birds re-trapped and rings recovered is generally low, requiring intensive marking effort to obtain even a few recoveries (Webster et al. 2002). More recently, tracking techniques using transmitters detected by satellite arrays or tags that use the Global Positioning System (GPS) have revolutionised our understanding of bird movements at a global scale, but there remain challenges to using these techniques on small birds (Mazerolle et al. 2005). Another approach that is rapidly being used is the use of intrinsic markers, such as trace elements, genetic markers and stable isotope ratios (Ambrosini et al. 2014). These intrinsic markers can complement ringing schemes and enhance our ability to answer key questions that concern avian migration. Stable isotope analyses are also used for other applications such as determining food choice in ecosystems (Polis & Strong 1996, Pain et al. 2004, O'Brien et al. 2005, Inger et al. 2006).

Inferring breeding and non-breeding grounds of birds using stable isotopes is strongly based on the reason that the isotope signatures of bird tissues show isotope signatures of those of local food webs that they feed on (Mizutani et al. 1990, Neto et al. 2006, Yohannes et al. 2007), this in turn varies spatially as a result of different numerous biogeochemical processes. Past feeding isotopic information is retained by animals that move between food webs that are isotopically-distinct and this depends

fully on the elemental turnover rates in the tissues of interest (Yohannes et al. 2005a, Neto et al. 2006). Stable isotope analyses have been used to determine provenance of feeding and diet in the aim to trace the origin of migration, and this can also be used to link winter and summer events (Hobson 1999). In migratory birds it can be used to distinguish feathers that are moulted on the breeding grounds from those that are grown on the non-breeding grounds (Cherel et al. 2000).

In bird studies, feathers are the most commonly used tissues because they are easy to sampled, without posing any significant negative effect on the birds and they give indications and interpretation for the moulting period (Hobson & Clark 1992, Mizutani et al. 1992, Cherel et al. 2000, Bearhop et al. 2002, Symes 2009). Migration studies mostly use tissues that can retain their isotopic signatures forever, whereas studies that are focused on diet make use of tissues which retain their signatures for some years, depending on the research question that needs to be answered (Hobson & Clark 1992, Thompson & Furness 1995). When one is looking at the possible migratory connectivity, feather samples are an important source of information because they fix the stable isotope conditions to which the bird was exposed at the time the feather was in the process of growing (Hobson & Clark 1992). Using the stable isotope signal in feathers to infer bird migration patterns also requires a clear understanding of patterns of feather moult and hopefully he duration of moult for the bird species on interest (Chapter 2; Symes 2009, Alexander et al. 2018).

The reasons for regional isotopic differences, discussed in Chapter 1, include physiological influences that affect tissues with different growth rates. The geographical areas and prevalent season of tissue growth influences tissue isotope

values (Mizutani et al. 1992, Bearhop et al. 2002, Alexander et al. 2018). Isotope values of $\delta^{2}H$ in primary producers vary temporally across seasons (Tieszen et al. 1983, Webster et al. 2002) and spatially with geographic localities (Chamberlain et al. 1997, Hobson 1999, Kelly 2000, Hobson et al. 2004c), whereas $\delta^{13}C$ and $\delta^{15}N$ tend to mainly vary spatially and seasonally if there are changes in primary production (Chamberlain et al. 1997, Kexlly 2000, Evans et al. 2012). These differences are generally reflected in a consumer's tissues.

This chapter infers where Woodland Kingfishers spend their non-breeding season and hence their migratory status by comparing the stable isotope signal in Woodland Kingfisher feathers among breeding populations in South Africa, Uganda and Ghana. I approached this using the analyses of stable isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) in their flight feathers. Chapter 2 shows that at least the southern African migratory population of Woodland Kingfishers moult their primary feathers in their non-breeding grounds. If this population of Woodland Kingfishers move between isotopically different regions, I can infer where they winter by examining the stable isotope signal in the flight feathers moulted on their non-breeding grounds.

Methods and materials

Primary (P1), secondary (S1) and tail (R6) feathers were collected from Woodland Kingfishers caught in mist-nets and spring traps between 2015 and 2018 (Chapter 2). Birds were sampled from three breeding populations: Accra and Cape Coast in Ghana (west Africa); Entebbe in Uganda (eastern Africa); and the Limpopo Province in South Africa (southern Africa). Where possible, museum specimen were sought to explore historical differences and augment sample sizes. Although I wanted to make use of

feathers of Woodland Kingfishers from museum specimens, this was not possible. All feathers sampled during the study were fully grown, yet with no extensive wear. About 1.5 cm was cut from the tip of each feather sampled using scissors and stored in paper envelopes at room temperature for later analysis. The sequence of flight feather moult in adult Woodland Kingfishers is not known, but based on the pattern of replacement in a bird approaching 1-year old (Hanmer 1980) it appears to follow the typical Daceloninae pattern (Cramp & Brooks 1992). P6 thus represents the start of primary feather moult. Any consistent stable isotope difference between these feathers may thus reflect either seasonal changes in stable isotope signal at the moult location, or movement between locations during moult.

Sample preparation and analysis

Feathers were cleaned in a 2:1 chloroform:methanol solution to remove surface oils and contaminants and then air-dried for at least 24 h in a fume hood. Once dry, the feathers were finely cut up using clean stainless steel scissors. For $\delta^{13}C$ and $\delta^{15}N$ analyses, 0.4–0.6 mg feather samples were placed in tin capsules and then combusted at 1,020 ˚C in an Elemental Analyser (Flash HT Plus; Thermo Fisher Scientific, Bremen, Germany). The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios were then determined using a Thermo Delta V Plus continuous-flow isotope ratio mass spectrometer (CFIRMS; Thermo Fisher Scientific) interfaced with the elemental analyser using a Con-Flo IV gas controller (Thermo Fisher Scientific). Laboratory working standards (C and N: Merck Gel and a Urea Working Standard) were included at intervals (on average, after every 24 unknown samples) to correct for analytical drift.

Measurement precision, based on repeated measurements of laboratory working standards, were ±0.44% and ±0.11% for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Analyses of $\delta^{2}H$ in animal tissues are complicated by the exchangeable hydrogen fraction that equilibrates with water vapour in the environment in which the tissues are stored (Wassenaar & Hobson 2000, 2003). To correct for the exchangeable hydrogen fraction, I used the comparative equilibration approach where samples are equilibrated with the same ambient water vapour as keratin working standards with known non-exchangeable $\delta^{2}H$ values (Hobson et al. 2003). Woodland Kingfisher feather samples (0.2–0.3 mg) and two keratin working standards (Kudu horn (KHS) = -108 ± 4% Vienna Standard Mean Ocean Water (VSMOW), Caribou hoof (CBS) = -187 ± 2%) were weighed into silver capsules and then stored for > 48 hours in a room prior to analysis. I analysed the samples through pyrolysis using a Thermo DeltaV Advantage mass spectrometer which was coupled to a Flash HT Plus elemental analyser. Based on repeated measurements of laboratory working standards, measurement precision was ± 0.56% for $\delta^{2}H$.

Statistical analyses

I used a Shapiro-Wilk test to determine normality the data (Shapiro & Wilk 1965). I calculated the mean (± SD) for each isotope and feather type. I also tested differences between feather types using ANOVA for normally distributed data, and Kruskal-Wallis for non-normally distributed data. I then carried out a pairwise comparison among different feather types using Tukey HSD for normal data and Wilcoxon Signed-Rank test for non-normal data, which were Bonferroni adjusted. Isotope differences between

Ghana and Uganda, Ghana and South Africa, and South Africa and Uganda were tested. I also ran a Principal Component Analysis (PCA) to visualise similarities among the three study sites (Ghana, Uganda and South Africa) and three feather groups (primary, secondary and tail) from South African breeding birds.

Results

I sampled 76 birds from the three breeding grounds (Table 3.1). I first tested for differences among feathers of each breeding population. $\delta^{12}C$, $\delta^{15}N$ and $\delta^{2}H$ of primary, secondary and tail feathers of South African breeding birds were not distributed normally, and as such, I used non-parametric tests to test for differences (Table 3.2). $\delta^{15}N$ and $\delta^{2}H$ of the Ghanaian flight feathers were normally distributed and the ANOVA tests showed that there are significant differences among flight feathers (Table 3.3). $\delta^{12}C$ samples were not normally distributed, and the Kruskal-Wallis for the $\delta^{12}C$ showed that flight feathers are not significantly different (Table 3.3). For the Ugandan birds, $\delta^{12}C$ and $\delta^{15}N$ showed non-normal distribution but the differences among the flight feathers were not significant. The $\delta^{2}H$ samples were normally distributed, and the differences among feathers was also not significant (Table 3.4).

Differences among flight feathers of South African birds

For $\delta^{13}C$, secondary feathers were more negative than primary tail feathers but not significantly different. Primary feathers were also more negative than tail feathers, suggesting an overall enrichment from wing feathers (both primaries and secondaries) through to tail feathers. However, secondary feathers were more positive for $\delta^{15}N$ than

primary and tail feathers (Appendix 8). Primary feathers were more positive than secondary and tail feathers for $\delta^{2}H$. Secondary feathers were also more positive than tail feathers for $\delta^{2}H$. For $\delta^{13}C$ (Figure 2.2) and $\delta^{15}N$ there is an increase from wing feathers (primaries and secondaries) to tail feathers. For $\delta^{2}H$, there seem to be a reduction in isotope values from wing feathers to tail feathers (Appendix 8).

Differences among flight feathers of birds caught in Ghana

For $\delta^{13}C$, tail feathers were more negative than secondary and primary feathers and but stable isotope signatures were not significantly different. Secondary feathers were also 0.34$^{o}/_{oo}$ more negative than primary feathers, suggesting an overall enrichment from wing feathers (both primaries and secondaries) through to tail feathers. However, secondary feathers were more positive for $\delta^{15}N$ than primary and tail feathers, respectively (Table 3.2). Primary feathers were also more positive than tail feathers for $\delta^{15}N$ (Table 3.4). I also found that secondary feathers were more positive than tail and primary feathers for $\delta^{2}H$. Tail feathers were also more positive than primary for $\delta^{2}H$. For $\delta^{13}C$ there is an increase from wing (primary and secondary) to tail feather enrichment, and for $\delta^{15}N$ there is a decrease from wing feathers to tail feathers. For $\delta^{2}H$, there seem to be a reduction in isotope values from wing feathers to tail feathers.

Differences among flight feathers of birds caught in Uganda

For $\delta^{13}C$, I found that tail feathers were also more negative than primary feathers and secondary feathers but not significantly different. Secondary feathers were also more negative than primary feathers but still not significant, suggesting an overall

enrichment from wing feathers (both primaries and secondaries) through to tail feathers. Secondary feathers were more positive than primary and tail feathers. Although there were these differences among feathers, the differences were still not significant.

Regional differences in feather stable isotopes

When I analysed the data for different regions (i.e. Ghana, South Africa and Uganda), only $\delta^{12}C$ samples were normally distributed for flight feathers, and as such parametric tests were used to test for degree of variance (reported as *F* values), while the non-parametric chi-square was used for $\delta^{15}N$ and $\delta^{2}H$ (Table 3.5). The analyses revealed significant differences between sub-regions for all isotopes. For $\delta^{13}C$, Ghanaian breeding birds were more negative for all the flight feathers than South African birds and Ugandan birds (Table 3.5). South African birds averaged 0.63‰ more negatively than the Ugandan birds for $\delta^{13}C$ (Table 3.5, Figure 3.1), but this difference was not statistically significant (Appendix 9). For $\delta^{15}N$, Ghanaian birds were more positive than the South African (Table 3.5, Figure 3.2). Flight feathers from the Ugandan birds were 1.95‰ more positive than the South African birds (Table 3.5). Feathers from the South African birds were 6.81‰ and 20.76‰ more positive than birds from Ghana and Uganda respectively for $\delta^{2}H$ (Table 3.5). However, birds from Ghana yielded more positive $\delta^{2}H$ values than birds from Uganda (Table 3.5, Figure 3.3).

Relationships among different study sites and feather groups

The carbon and nitrogen stable isotope ratios of each study area were plotted on the principal components analysis (Figure 3.4), and a carbon and nitrogen isotope ratio for each feather type of South African breeding birds was also visualised (Figure 3.5).

The patterns revealed a large overlap between primary and secondary feathers, while tail feathers tended to be more distinct. This suggests that the wing feathers and tail feathers are not grown at the same time, and may potentially be grown in different locations.

Discussion

Differences among primary, secondary and tail feathers of South African birds

As it is known that the South African breeding Woodland Kingfisher are migratory, SAFRING data records have also shown that these birds do not spend much of their time in South Africa. During the time that they are in their breeding grounds, the main focus is on their breeding and they do not moult their flight feathers during this time. The analysis of wing feathers suggested that both primary and secondary feathers had more negative $\delta\ ^{2}H$, or they were enriched with more $\delta\ ^{2}H$ than that which I found in the tail feathers. This suggests that the South African-breeding Woodland Kingfishers moved from an isotopically positive or drier region (Neto et al. 2006) to a more negative or lower $\delta\ ^{2}H$ or moist region (Neto et al. 2006) between moulting their wing feathers and moulting their tail feathers. As it is known that the most common pattern of moulting flight feathers is wing feathers followed by tail feathers, it is likely that the migrating Woodland Kingfishers were moving between regions of differing $\delta\ ^{2}H$ isotopic values during the time when different flight feathers were moulted. That is, a set of flight feathers was moulted in one area before movement, and then the other set was also moulted in a different area, resulting in different isotopic signatures locked in different flight feather sets.

Differences among primary, secondary and tail feathers of Ghanaian and Ugandan birds

Woodland Kingfishers found in Ghana are local migrants that only move short distances. Birds found in Uganda are known to be resident, found in the area all year round. As I expected for the Ghanaian (Table 3.3) and Ugandan (Table 3.4) population, flight feathers of birds in these respective places did not show any significant differences. This goes to support the fact that they do not move between areas of different isotopic signatures (because they are non-migrants) and they will therefore reflect isotopic signatures that are not significantly different in the flight feathers.

Geographical influence on isotopic values

As much as we know about feather growth and other physiological factors influencing isotope values in migrating birds, the location of where the feather was grown has more influence on isotope values or signatures (Hobson & Clark 1992). One possibility that results in $\delta^{13}C$ values of primary and secondary feathers being more negative and $\delta^{15}N$ of primary and secondary being more positive than tail feathers is that wing feathers are normally moulted before tail and contour/body feathers. This is because wing feathers are more likely grown when the birds is at lower latitudes (with lower carbon and higher nitrogen values), but tail feathers are grown when the bird is at higher latitudes. So, wing feathers of South African birds may show these negative and positive isotope values for carbon and nitrogen, respectively as the Woodland Kingfisher might be feeding in isotopically different locations during the different moult phases (Dalerum & Angerbjörn 2005) or moving between areas of different habitats (Symes 2009, Alexander et al. 2018). All this would suggest that different geographical

areas yield different isotopic signatures and this was shown by having varying isotopic signatures/ratios across the different study areas.

Stable carbon abundance in nature is dependent on the existing photosynthesis type (O'Leary 1981), and it is also easy to isotopically trace if the consumer is dependent on a C3- or C4-based food-web (Alisauskas et al. 1998, Feret et al. 2003). Therefore, as with nitrogen, stable carbon isotopes also have the possibilities to distinguish xeric and mesic environments. The changes in isotopic values between feather types of the South African breeding birds suggest a possible movement and feeding on different food sources throughout the process of the moulting period (Farquhar & Richards 1984). This explains the possible differences in $\delta^{13}C$ and $\delta^{15}N$ between wing feathers of the migrating Woodland Kingfishers (South African breeding populations).

Assigning the South African breeding populations to non-breeding grounds

$\delta^{13}C$ values of Woodland Kingfisher feathers that are moulted in Uganda indicated a biome dominated by C4 plants and differed significantly from birds known to breed and moult in Ghana. Lower $\delta^{13}C$ values from Ghana indicated a C3-dominated biome. Feathers from birds caught in South Africa reflected C4-dominated food-webs. This is in agreement with predominantly grassland habitats occupied by Woodland Kingfishers in Uganda which lies right on the wet or wetter tropics. The fact that there was no significant difference in $\delta^{13}C$ values between the Ugandan and South African breeding birds may have been that the migrating South African birds are spending their non-breeding season and growing their wing feathers in the same isoscape band,

with predominant C4 vegetation around as the Ugandan population 10° N (Still et al. 2003) and, therefore, show similar $\delta^{13}C$ values. Based on our field observations during the breeding season and re-sighting reports of colour-ringed individuals, we are confident that the Ugandan population is resident, found in the same area all year round. Some studies have also suggested that the South African population migrate to central Africa after their breeding period in southern Africa, which corroborates the conclusion that the Woodland Kingfishers breeding in South Africa likely spend their non-breeding seasons in the same iso-scape as the resident Ugandan population (Tarboton & Tarboton 2014).

Feather $\delta^{15}N$ values of flight feathers that came from the South African breeding population differed significantly from $\delta^{15}N$ values of birds breeding in Ghana and Uganda. No significant differences were found between birds that breed in Ghana and those that breed in Uganda. Both these populations or breeding populations are known to be resident, found in their breeding areas all year round. Resident birds tend to feed at a higher trophic level than migrating birds (Ambrosini et al. 2014). The migrating Woodland Kingfisher (SA birds) could have been feeding at a different trophic level compared to their conspecific resident individuals, resulting in the differences being found between birds breeding in South Africa and Uganda.

Some studies have shown that $\delta^{2}H$ in precipitation and in animal tissue decreases with increasing latitude (Wakelin et al. 2019), and many isotopic studies of bird migration patterns have made use of this global pattern of variation in $\delta^{2}H$ (Hobson et al. 2004b, 2004c, Wakelin et al. 2019). In this study, however, flight feathers of the highest latitude Woodland Kingfishers (South Africa) exhibited the most

enriched feather δ ^{2}H values. Although this is the case, it is supported by the fact that Woodland kingfishers that migrate to the south for breeding, migrate northwards after breeding and they could be moulting their flight feathers on their non-breeding ground which have a relatively low altitude (see Chapter 1 for more details about the effect of latitude and altitude on δ ^{2}H values).

Using stable isotopes to track the movement of intra-African migrants is complicated by the positioning of the African continent. Africa is located over the Equator, and it thus lacks the unidirectional latitudinal gradients in precipitation that is observed in other continents such as North America and Europe. However, approaches that are stable isotope-based have proved to be useful in determining interspecific variation in stopover site selection in Palearctic migrants that moult along their migration route (Yohannes et al. 2007, Wakelin et al. 2019), this could also be implemented or used in intra-continental trans-equatorial bird migrants that moult in their non-breeding grounds. This approach can easily be used to infer migratory connectivity in populations that breed and winter in different parts of Africa (Wakelin et al. 2011). Yet, the analysis of stable isotopes requires knowledge of the moult patterns of the study bird species.

The Principal Component Analysis indicates extensive overlap of carbon and nitrogen ratios among feathers from South African kingfishers, and among kingfishers from Uganda and Ghana. The habitat used by Woodland Kingfishers in Ghana and Uganda is similar, resulting in similar isotope signals.

Tables and figures (Chapter 3)

Table 3.1: Sites of birds that were included in the study. The table below shows the place, the number of birds sampled and the mean stable isotope for the different feather types

Site	**Number of birds sampled per site**	**Stable Isotope mean**		
		$\delta^{13}C$	**$\delta^{15}N$**	**$\delta^{2}H$**
Ghana	10	-21.70	11.65	29.07
Uganda	18	-18.88	10.57	15.12
South Africa	48	-19.95	8.62	35.08

Table 3.2: Mean (± SD ‰) values and range (in parentheses) of δ ^{13}C, δ ^{15}N, and δ ^{2}H of South African breeding Woodland kingfishers for primary, secondary and tail feathers showing significant difference between feather groups (Kruskal Wallis H; $P < 0.05$).

Isotope	**Primary (range)**	**Secondary (range)**	**Tail (range)**	**Kruskal Wallis H**
δ ^{13}C	-19.86 ± 1.40 (-22.46 to 15.37)	-19.97 ± 1.15 (-22.12 to 17.36)	-18.30 ± 2.20 (-22.13 to 13.41)	56.22, df = 2, *P* = 0.0015
δ ^{15}N	8.05 ± 1.22 (6.16 to 11.55)	9.27 ± 1.29 (7.05 to 11.53)	9.17 ± 1.26 (6.67 to 11.62)	15.77, df = 2, *P* < 0.0001
δ ^{2}H	42.59 ± 18.321 (-38.10 to 74.60)	30.52 ± 30.12 (-43.60 to 62.50)	23.44 ± 16.06 (-14.80 to 49.10)	15.77, df = 2, *P* = 0.0008

Table 3.3: Mean (± SD ‰) values and range (in parentheses) of δ ^{13}C, δ ^{15}N, and δ ^{2}H of Ghanaian breeding Woodland kingfishers for primary, secondary and tail feathers showing significant difference among feather groups (Kruskal Wallis or ANOVA; P < 0.05).

Isotope	**Primary (range)**	**Secondary (range)**	**Tail (range)**	**Kruskal Wallis (H) or ANOVA (F)**
δ ^{13}C	-21.37 ± 1.99 (-23.23 to -16.40)	-21.71 ± 1.48 (-23.33 to -18.92)	-22.15 ± 1.88 (-25.34 to -19.05)	*H* = 0.42, df = 2, *P* = 0.8104
δ ^{15}N	12.11 ± 1.92 (9.51 to 15.23)	11.60 ± 1.85 (9.61 to 15.01)	11.03 ± 2.01 (8.64 to 14.07)	F = 0.5886, df = 2, denom df = 12.99, *P* = 0.5692
δ ^{2}H	22.29 ± 16.44 (-14.30 to 41.60)	38.36 ± 22.88 (3.30 to 75.80)	29.46 ± 20.26 (-3.30 to 61.10)	F = 1.2512, df = 2, denon df = 11.972 *P* = 0.321

Table 3.4: Mean (± SD ‰) values and range (in parentheses) of δ ^{13}C, δ ^{15}N, and δ ^{2}H of Ugandan breeding Woodland kingfishers for primary, secondary and tail feathers showing significant difference among feather groups (Kruskal Wallis or ANOVA; P < 0.05).

Isotope	**Primary (range)**	**Secondary (range)**	**Tail (range)**	**Kruskal Wallis (H) or ANOVA (F)**
δ ^{13}C	-18.70 ± 2.18 (-22.73 to -15.54)	-18.74 ± 2.50 (-23.11 to -16.45)	-19.40 ± 2.28 (-23.22 to -16.31)	*H* = 1.2342, df = 2, *P* = 0.5395
δ ^{15}N	10.38 ± 1.56 (7.15 to 12.11)	11.11 ± 1.02 (9.58 to 12.91)	10.41 ± 2.01 (7.03 to 12.74)	*H* = 0.62112, df = 2, *P* = 0.733
δ ^{2}H	13.82 ± 31.05 (-37.10 to 62.20)	13.17 ± 30.33 (-31.70 to 68.10)	21.92 ± 28.68 (-24.10 to 56.70)	F = 0.19245, df = 2 denom df = 12.94, *P* = 0.8273

Table 3.5: Mean (± SD ‰) values and range (in parentheses) of δ ^{13}C, δ ^{15}N, and δ ^{2}H of Woodland kingfishers from Ghana, South Africa and Uganda flight feathers showing significant difference among sample groups (Kruskal Wallis or ANOVA; P < 0.05).

Isotope	**Ghana (range)**	**South Africa (range)**	**Uganda (range)**	**Kruskal Wallis (H) or ANOVA (F)**
δ ^{13}C	-21.70 ± 1.78 (-25.34 to -16.40)	-19.51 ± 1.72 (-22.46 to -13.41)	-18.88 ± 2.24 (-23.22 to -15.54)	*F* = 17.83, df = 2, denom df = 51.26, *P* < 0.0001
δ ^{15}N	11.65 ± 1.90 (8.64 to 15.23)	8.62 ± 1.37 (6.16 to 11.62)	10.57 ± 1.56 (7.03 to 12.91)	*H* = 56.22, df = 2, *P* < 0.0001
δ ^{2}H	29.09 ± 19.89 (-14.30 to 75.80)	35.88 ± 22.95 (-43.60 to 74.60)	15.12 ± 29.69 (-37.10 to 68.10)	*H* = 15.77, df = 2, *P* = 0.0004

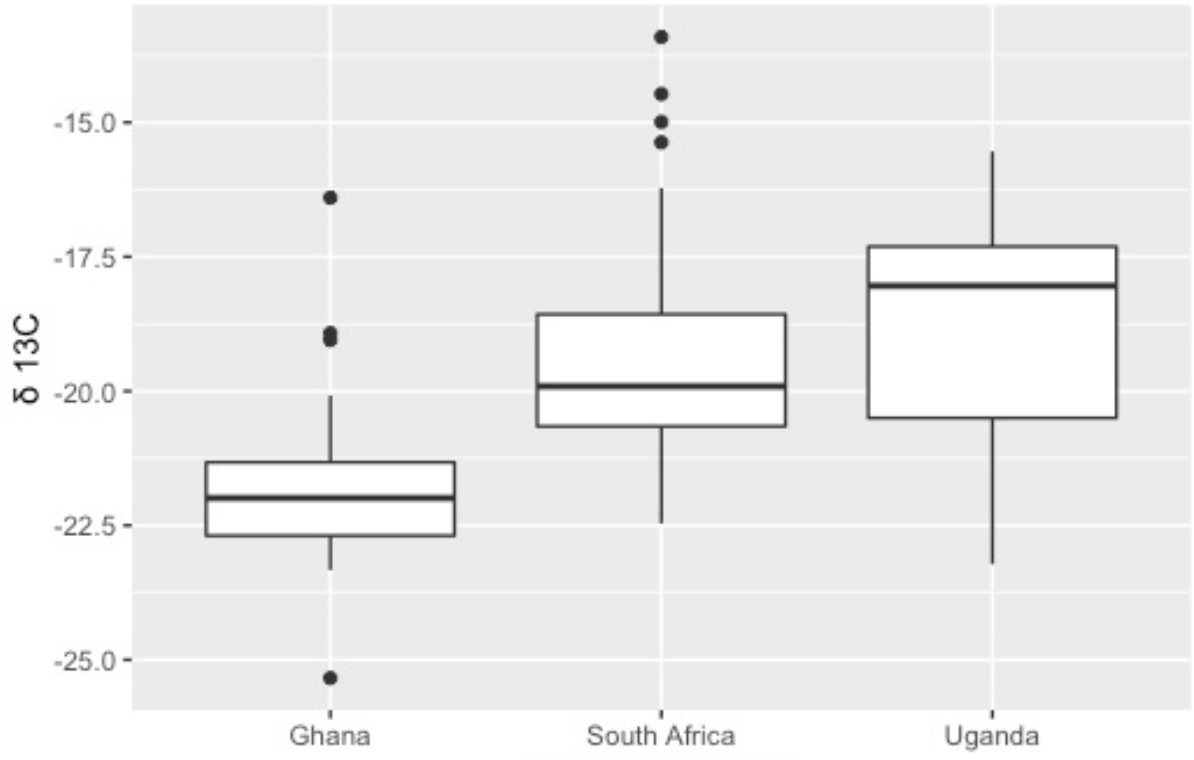

Figure 3.1: Mean (± SD) of carbon for Woodland Kingfishers caught in Ghana, South Africa and Uganda.

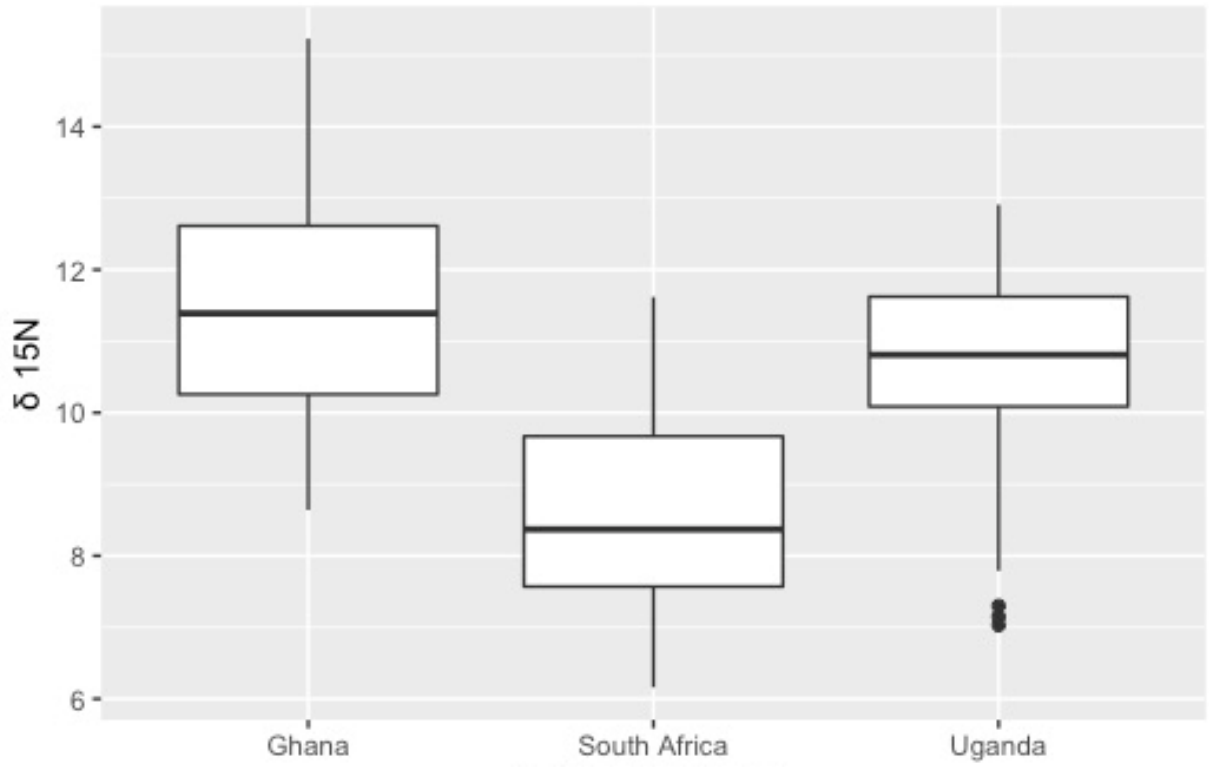

Figure 3.2: Mean (± SD) of nitrogen for Woodland Kingfishers caught in Ghana, South Africa and Uganda.

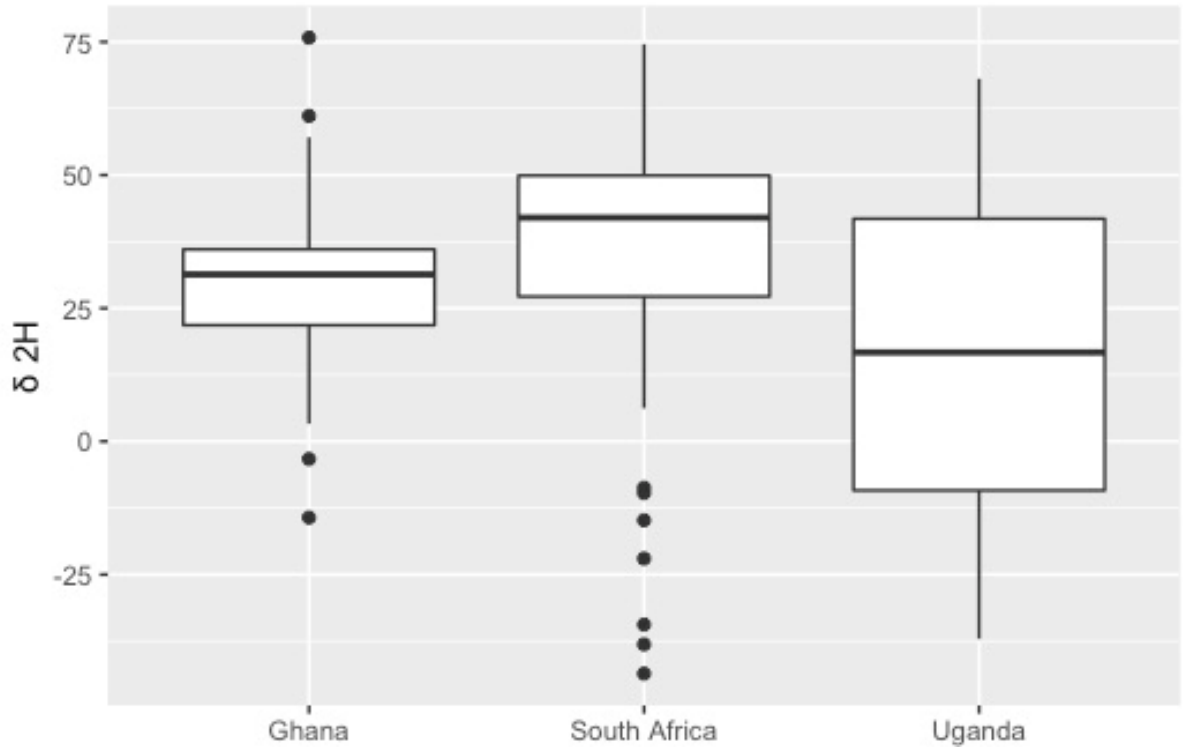

Figure 3.3: Mean (± SD) of deuterium for Woodland Kingfishers caught in Ghana, South Africa and Uganda.

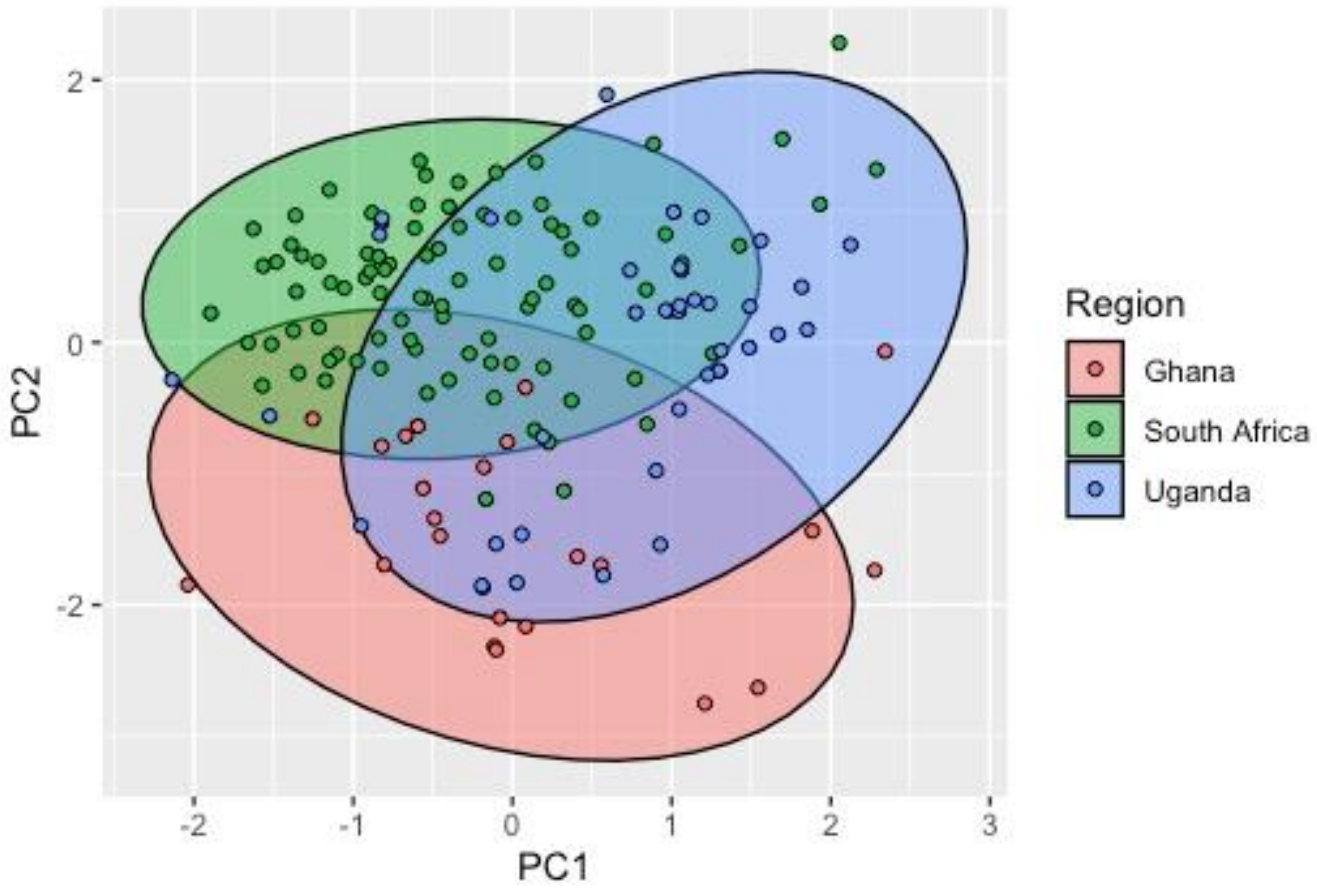

Figure 3.5: Two-dimensional ordination of carbon and nitrogen isotope ratios overlap for all Woodland Kingfisher flight feathers from Ghana, South Africa and Uganda.

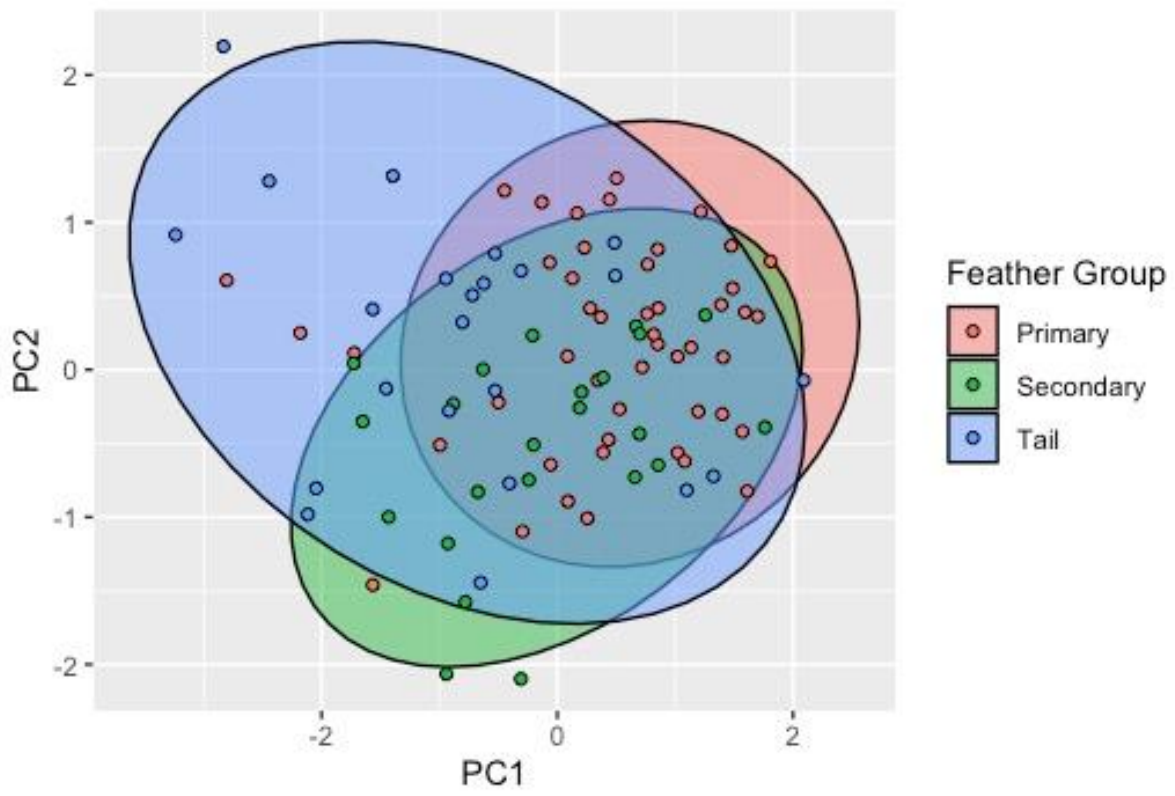

Figure 3.7: Relationship between carbon isotope ratios and nitrogen isotope ratios for the different flight feathers (primary, secondary and tail) of the South African breeding birds.

Chapter 4: Implication of the findings and recommendations for further research

Me inspecting a Woodland Kingfisher nest box in Mogalakwena, Limpopo, South Africa (Photo: Dr. Samuel T. Osinubi)

The main aim of the study was to explore the migratory behaviour of the Woodland Kingfisher through the analysis of flight feather moult and stable isotope. It is crucial to understand the movement patterns of migrant birds in general and specifically intra-African migrant land-birds. At present, there are only a few studies showing the movement and patterns of migration of intra-African birds (Nussbaumer & Jackson 2020). Because there is not enough information on when the Woodland Kingfisher moult, the first step for me was to ascertain the timing of flight feather moult in relation to the annual cycle of the Woodland Kingfisher. Chapter 2 shows that there is variation in timing of moult among individuals of the same population, especially for sedentary or resident populations. This only applied for the resident birds found in Accra, Ghana and Entebbe in Uganda. Chapter 2 also showed that long-distance migrating Woodland Kingfishers do not moult their primary feathers while in the breeding ground.

Within the scope of my MSc, it was not possible for me to obtain excellent results from each of the examinations or research questions because I was only able to collect data once for each group (Ghana, Uganda and South Africa). The intention was to explore the moulting pattern and timing of migrating Woodland Kingfishers that breed in southern Africa; this was going to help me infer the non-breeding grounds of the migrating Woodland Kingfisher. Although I had few birds in active moult, there were still lots of data from southern Africa to show that migrating Woodland Kingfishers definitely do not moult in the breeding area. Even though this was the case, the analysis of stable isotopes in different flight feather allowed me to infer “possible” non-breeding grounds of southern African breeding Woodland Kingfishers and this allowed me to hypothetically state where these birds may be moulting their flight feathers.

This study is one of few investigating the stable isotope analysis of *Halcyon* kingfisher feathers. I hypothesized that the stable isotope of different flight feathers of birds from different populations will differ significantly as a result of geographic differences, and that flight feathers of Woodland Kingfishers breeding in South Africa will show different isotopic signatures. I also hypothesized that isotopic signatures of different flight feathers (tail and wing) of Ugandan birds will not differ significantly as the Ugandan birds that are included in this study are known to be sedentary in the areas where I caught them. For this reason, primary, secondary and tail feathers of resident populations (Uganda) showed non-significant differences in isotopic signatures among individuals of this populations. The same was thought for Ghanaian breeding birds that I included in this study. No significant differences were found among flight feather of Woodland Kingfishers caught in Ghana. All these differences were thought to be as a result of both physiological and environmental factors (stress, food availability, low seasonality and dehydration; refer to Chapter 1).

The existence of distinct isotopic regions between the study areas and within the African continent was tested by comparing flight feather isotope signatures of Woodland Kingfishers across three different breeding grounds (South Africa, Ghana and Uganda). The proposed hypothesis was that the three study sites (breeding grounds identified in this study) were isotopically distinct because they belong to different vegetation biomes and they are far apart. I therefore conclude that moderately distinct isotopic regions exist in the African continent and these can be resolved with the use of multi-isotopic and time specific approaches to answer migratory questions of bird species that move between different areas within the African continent.

Feather differentiation

When using the application of stable isotope analysis to avian migratory studies, inferring the geographic origin of the sample in question is always important because it is not always possible to suggest the exact origin. This could sometimes prove to be a challenge to examine across the African continent because of the weak deuterium gradients and very little deuterium variations across the continent (Møller & Hobson 2004, Bowen et al. 2005). The equator runs directly through the African continent, and this means that there exist latitudinal variations to both the north and the south as one progresses from low to high latitudes (Nicholson 2017). The African continent is a complex continent isotopically and much more effort is still required to better improve the study of feather iso-scape to allow important and key studies on bird migration between African non-breeding and breeding grounds for a number of different intra-African migrant species. When applicable, it is important to suggested that multiple isotopes be analysed (Vogel et al. 1990, Hall-Martin et al. 1993, Veen et al. 2014).

I hypothesized that stable isotope values of Woodland Kingfishers from South Africa would differ significantly from those caught in Ghana, and differ less than kingfishers from Uganda because geolocators deployed on South African breeding birds suggest that they may occupy a similar isoscape as Ugandan breeding birds during the non-breeding season (Tarboton & Tarboton 2014). This hypothesis was supported as the isotope values of South African breeding birds differed significantly from Ghanaian breeding birds for $\delta^{13}C$ and $\delta^{15}N$ but not for $\delta^{2}H$. South African breeding birds also differed significantly from Ugandan breeding birds for $\delta^{15}N$ and $\delta^{2}H$ but not for $\delta^{13}C$. When comparing Ghanaian and Ugandan breeding birds, significant differences were only for $\delta^{13}C$. Birds in Ghana and Uganda are naturally

found in a distribution across central Africa, and they occur in areas that are dominated by C4 vegetation (Forshaw 2014) and their isotope signatures (Ghana: -21.70 ± 1.78‰; Uganda: -28.88 ± 2.24‰) reflect the isotope values of their C4 habitat (Chapter 2; (DeNiro & Epstein 1978, Pearson et al. 2003)).

I also hypothesized that there would be a difference in isotope values of different feather types of the migrating Woodland Kingfishers (South African breeding population). There are studies that have shown different isotope values among different feather types in other bird species or groups (Mizutani et al. 1992, Becker et al. 2007). A possible explanation for these differences may be as a result of different feather types that may be growing at different times of the year, therefore potentially growing in different geographical areas (Ramos et al. 2009, Marra et al. 2010). There were differences among the three isotopes and their values ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{2}H$). Feather types of Woodland Kingfishers caught in South Africa and the differences were not completely the same. Feathers that were the most positive for $\delta^{2}H$ were primary feathers, Secondary feathers were the most negative for $\delta^{13}C$ and most positive for $\delta^{15}N$, and tail feathers were the most positive for $\delta^{13}C$ and most negative for $\delta^{2}H$. These isotope differences between feather types creates inaccuracies when one is to compare isotopic values between individuals of the same species.

Summary of the findings

Based on moult records that I collected from the field during the respective field seasons for the three different regions that were included in this study, it is evident, without a doubt, that migrating Woodland kingfishers do not moult and breed at the same time. Stable Isotope analyses of carbon, nitrogen and hydrogen showed a clear

indication of this when South African birds closely resembled stable isotope values that were similar to the Ugandan birds (Figure 3.5). Also, based on both the condition of the wing feathers when these birds arrive in South Africa and the isotopic signatures that bear similarities to the Ugandan population, it appears that individuals breeding in South Africa moult their feathers in the same iso-scape as the Ugandan individuals and most likely do so just before migrating to the south to breed, having a pre-breeding moult.

Although the sample size for my study was small, the results I managed to get from the available data were clear enough to enable me to infer the possible non-breeding ground of the migrating Woodland Kingfisher. From what we know about the Woodland Kingfisher's distribution, it is easy to state where the Ghanaian and Ugandan populations are growing their primary flight feathers because birds found in these two areas are known to be sedentary. It is without a doubt that Woodland Kingfishers in Ghana and Uganda grow their flight feathers in Ghana and Uganda, respectively. Also, because there is little variation between their wing and tail feathers, this could be an indication that these birds are growing all their flight feathers in more or less the same area. There have also been reports or re-sightings at other times of the year outside the breeding time that suggests that they are indeed sedentary birds. This then corroborates what literature suggests about their distribution.

Implications of the study

Throughout this study it is clear and evident that the stable isotope analyses of Woodland Kingfisher feathers can be used to infer and determine non-breeding areas of migrating birds. This approach and the methods used can prove to be important in

identifying non-breeding grounds of the migrating Woodland Kingfisher that breed in South Africa. If the South African breeding Woodland Kingfishers have completed moult, the new feathers will lock in and incorporate the isotopic signatures of the area where the birds will be occupying during the time of moult (Bearhop et al. 2002). My study indicates that much more of ground work sampling and isotopic measurement of feathers of known moult origin are still required for Africa or intra-African migratory birds.

The use of moult, combined with stable isotope analyses, should be elaborated on and additional research should be conducted on more Woodland Kingfisher populations and other intra-African migratory species in an attempt to track and monitor their migratory patterns and/or behaviours.

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Appendices

APPENDIX 1

Birds caught during the different breeding seasons or times of three different sub-regions being South Africa, Ghana and Uganda. The data here dates from 2015 to 2019. The moult score was done following the SAFRING scoring style.

Bird number	**Sampling Date**	**SAFRING Score**	**Total Score (50)**	**Country**
1	2015/11/30	5555555555	50	South Africa
2	2015/11/30	5555555555	50	South Africa
3	2015/12/01	5555555555	50	South Africa
4	2015/12/03	5555555555	50	South Africa
5	2015/12/03	5555555555	50	South Africa
6	2015/12/03	5555555555	50	South Africa
7	2015/12/05	5555555555	50	South Africa
8	2015/12/05	5555555555	50	South Africa
9	2015/12/08	5555555555	50	South Africa
10	2015/12/08	5555555555	50	South Africa
11	2015/12/09	5555555555	50	South Africa
12	2015/12/09	5555555555	50	South Africa
13	2015/12/21	5555555555	50	South Africa

14	2015/12/26	5555555555	50	South Africa
15	2016/11/28	5555555555	50	South Africa
16	2016/11/28	5555555555	50	South Africa
17	2016/12/01	5555555555	50	South Africa
18	2016/12/02	5555555555	50	South Africa
19	2016/12/12	5555555555	50	South Africa
20	2016/12/13	5555555555	50	South Africa
21	2016/12/15	5555555555	50	South Africa
22	2016/12/16	5555555555	50	South Africa
23	2016/12/17	5555555555	50	South Africa
24	2016/12/20	5555555555	50	South Africa
25	2017/01/04	5555555555	50	South Africa
26	2017/01/05	5555555555	50	South Africa
27	2017/01/05	5555555555	50	South Africa
28	2017/12/07	5555555555	50	South Africa
29	2017/12/14	5555555555	50	South Africa
30	2017/12/17	5555555555	50	South Africa
31	2017/12/17	5555555555	50	South Africa
32	2017/12/18	5555555555	50	South Africa
33	2017/12/19	5555555555	50	South Africa
34	2017/12/20	5555555555	50	South Africa
35	2017/12/21	5555555555	50	South Africa
36	2017/12/22	5555555555	50	South Africa
37	2017/12/27	5555555555	50	South Africa

38	2017/12/28	5555555555	50	South Africa
39	2017/12/28	5555500005	30	South Africa
40	2018/12/30	5555555555	50	South Africa
41	2018/12/31	5555555555	50	South Africa
42	2019/01/10	5555555555	50	South Africa
43	2019/01/11	5555555555	50	South Africa
44	2019/01/12	5555555555	50	South Africa
45	2019/01/12	5555555555	50	South Africa
46	2019/01/12	5555555555	50	South Africa
47	2019/01/15	5555555555	50	South Africa
48	2019/01/15	5555555555	50	South Africa
49	2019/01/23	5555555555	50	South Africa
50	2016/07/13	5555555555	50	Ghana
51	2016/07/13	5555555555	50	Ghana
52	2016/09/08	5555555555	50	Ghana
53	2018/06/22	5555555555	50	Ghana
54	2018/06/22	5555555555	50	Ghana
55	2018/06/26	5555555555	50	Ghana
56	2018/06/27	5430000000	47	Ghana
57	2018/06/28	5555555555	50	Ghana
58	2018/06/28	5400000000	45	Ghana
59	2018/06/29	5555555555	50	Ghana
60	2016/08/10	5554100000	40	Uganda
61	2016/08/16	5555555555	50	Uganda

62	2016/08/16	5555555555	50	Uganda
63	2018/07/26	5555555555	50	Uganda
64	2018/07/26	5555555555	50	Uganda
65	2018/07/26	5555555555	50	Uganda
66	2018/07/26	5555555555	50	Uganda
67	2018/08/09	5555540000	39	Uganda
68	2018/08/09	5555555555	50	Uganda

APPENDIX 2

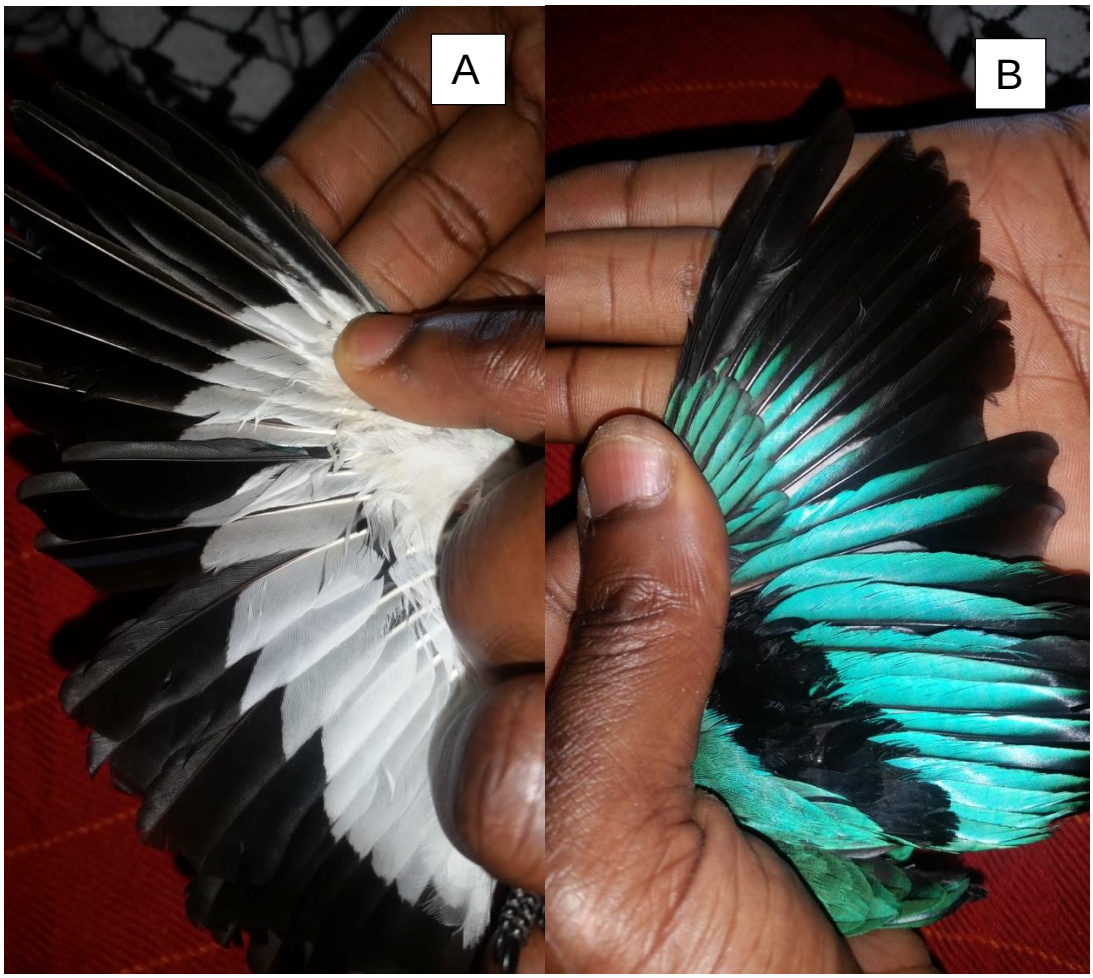
Woodland Kingfisher caught in Ghana on 2018/06/27. This individual was found in active moult, growing its p2 and p3 on both wings. (A) shows the left wing while (B) shows the right wing

APPENDIX 3

Woodland Kingfisher caught on 2018/06/27, same individual as Appendix 2. This bird was also growing its tail feathers.

APPENDIX 4

Woodland Kingfisher caught on 2018/06/28 in Ghana appears to be replacing a feather a result of mechanical damage. Only one feather on the right wing was being replaced.



APPENDIX 5

Woodland Kingfisher caught on in 2018/08/09 in Uganda with its wings spread out.

APPENDIX 6

Woodland Kingfisher caught on 2018/08/09 in Uganda.

APPENDIX 7

Woodland Kingfisher moult data extracted from the SAFRING dataset. This data includes birds from South Africa, Zimbabwe, Botswana, Zambia and Malawi.

Year	**Month of capture (number of Woodland Kingfishers caught)**											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1970	1	-	-	-	-	-	-	-	-	-	-	-
1991	1	-	-	-	-	-	-	-	-	-	-	-
1992	1	-	-	-	-	-	-	-	-	-	-	-
1994	-	-	-	-	-	-	-	-	-	-	-	2
1995	-	-	-	-	-	-	-	-	-	-	2	1
2000	1	-	-	-	-	-	-	-	-	-	-	-
2001	1	-	-	-	-	-	-	-	-	-	4	6
2002	5	1	4	-	-	-	-	-	-	1	-	2
2003	2	1	6	-	-	-	-	-	-	-	1	5
2004	1	5	3	-	-	-	-	-	-	-	-	4
2005	2	7	5	-	-	-	-	-	-	-	1	12
2006	4		6	-	-	-	-	-	-	-	3	21
2007	1	6	4	1	-	-	-	-	-	-	3	1
2008	1	15	1	-	-	-	-	-	-	-	-	4
2009	8	5	6	-	-	-	-	-	-	-	3	10
2010	6	4	4	2	-	-	-	-	-	-	1	5
2011	1	4	4	2	-	-	-	-	-	-	1	5

2012	15	4	6	-	-	-	-	-	-	-	-	4
2013	28	6	9	-	-	-	-	-	-	-	-	2
2014	19	14	3	-	-	-	-	-	-	-	10	4
2015	8	9	3	-	-	-	-	-	-	-	-	5
2016	5	2	4	-	-	-	-	-	-	-	3	5
2017	7	-	-	-	-	-	-	-	-	-	-	1

APPENDIX 8

Statistical differences between flight feathers types of Woodland Kingfishers breeding in South Africa for each isotope (P<0.05), * shows statistically significant difference between sub-regions.

Feather type	**Statistic (paired t-Test/Wilcoxon Signed-Rank test)**
$\delta^{13}C$	
Primary = Secondary	*W* = 12.94, *df* = 2, *P* = 1.0000
Secondary vs Tail	*W* = 12.94, *df* = 2, *P* = **0.0068***
Primary vs Tail	*W* = 12.94, *df* = 2, *P* = **0.0025***
$\delta^{15}N$	
Primary vs Secondary	*W* = 18.58, *df* = 2, *P* = **0.0010***
Secondary = Tail	*W* = 18.58, *df* = 2, *P* = 1.0000
Primary vs Tail	*W* = 18.58, *df* = 2, *P* = **0.0020***
$\delta^{2}H$	
Primary = Secondary	*W* = 14. 18, *df* = 2, *P* = 1.0000
Secondary = Tail	*W* = 14.18, *df* = 2, *P* = 0.2161
Primary vs Tail	*W* = 14.18, *df* = 2, *P* = **0.0002***

APPENDIX 9

Statistical significant differences between flight feathers of Woodland Kingfishers from Ghana, Uganda and South Africa for each isotope (P<0.05)

Feather region	**Statistic (t-Test/Wilcoxon Signed-Rank test)**
$\delta^{13}C$	
Ghana < South Africa	t =17.83, df = 2, P < **0.0001**
South Africa = Uganda	t = 17.83, df = 2, P = 0.2048
Ghana < Uganda	t = 17.83, df = 2, P < **0.0001**
$\delta^{15}N$	
Ghana > South Africa	W = 56.2, df = 2, P < **0.0001**
South Africa < Uganda	W = 56.2, df = 2, P < **0.0001**
Ghana = Uganda	W = 56.2, df = 2, P = 0.2600
$\delta^{2}H$	
Ghana = South Africa	W = 15.77, df = 2, P = 0.0517
South Africa > Uganda	W = 15.77, df = 2, P = **0.0012***
Ghana = Uganda	W = 15.77, df = 2, P = 0.2977