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Stable Isotope Research in Southern African Birds

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1. Introduction

The use of stable isotopes in ornithological research has risen exponentially in the past few decades, mainly due to strides in technology that permit the processing of large numbers of samples at lower and lower cost. However, most likely because of the availability of resources in “developed countries”, studies are concentrated in predominantly Palaeartic and Nearctic countries. Africa is largely neglected but offers unique opportunities for both collaborative research on a global scale, and novel studies in uncharted fields. This chapter provides a brief summary of, 1) stable isotopes and some of the applications thereof in ornithology, 2) examples of the type of work currently completed and underway in Africa and how it might be applicable in a global perspective, and, 3) prospects for future studies in the use of stable isotopes for understanding African ornithology. Given the high diversity of birds in southern Africa (at least 950 species), associated with at least seven terrestrial biomes, e.g. fynbos, succulent Karoo, Nama-Karoo, grassland, savanna, forest, and thicket, numerous opportunities exist for addressing research questions of biological interest and conservation concern.

2. Stable isotopes

2.1 What are stable isotopes?

The atom of an element is defined by the number of protons within the nucleus which, together with the neutrons it contains, define its mass (Hoefs, 2009). For a particular element, additional neutrons within the nucleus will add mass to an atom but will not change its chemistry (Hoefs, 2009). These atoms of different mass are called isotopes, stable if they are not radioactive, and may behave differently during chemical reactions because of this difference in mass (Hobson and Wassenaar, 2008; Hoefs, 2009). Only 21 elements occur as pure elements, the rest are mixtures of at least two isotopes (Bigeleisen, 1965; Hoefs, 2009). However, a handful of elements, particularly light isotopes that are important in key life processes, e.g. hydrogen, carbon, nitrogen, oxygen and sulphur, are of interest to biologists (West et al., 2006; Hobson and Wassenaar, 2008).

Isotope fractionation, or the partial separation of light and heavier stable isotopes, may occur during physical processes, e.g. diffusion and evaporation, or biological processes, e.g.

photosynthesis and metabolism. The proportions of these isotopes in the environment will subsequently become disparate and it is the understanding of these differences, and how, when and why they occur, that are valuable for scientists in understanding complex interactions and processes in the world in which we live (Ehleringer, 1991; West et al., 2006).

Isotope ratios are expressed relative to arbitrary element-specific standards using delta-value (δ) notation (Bigeleisen, 1965; Ehleringer and Osmond, 1989; McKechnie, 2004; Hoefs, 2009). For numerous reasons absolute measurements are not reliable and it is more common to calculate these ratios relative to a standard reference material (Gonfiantini, 1978; Ehleringer and Osmond, 1989), e.g. standard mean ocean water (SMOW), or more recently Vienna standard mean ocean water (V-SMOW), for hydrogen (D/H) and oxygen ($^{18}\text{O}/^{16}\text{O}$) in water; *Belemnitella americana* from the Cretaceous Peedee formation, South Carolina (PDB or Peedee Belemnite), for carbon ($^{13}\text{C}/^{12}\text{C}$) and oxygen ($^{18}\text{O}/^{16}\text{O}$) in carbonates and organic material; atmospheric air (N_2) for nitrogen ($\text{N}^{15}/\text{N}^{14}$); and troilite (FeS) from the Canyon Diablo iron meteorite (Canyon Diablo meteorite, CD) for sulphur (Gonfiantini, 1978; Ehleringer and Osmond, 1989; Lee-Thorp and Thalma, 2000; McKechnie, 2004; Hoefs, 2009). The isotopic compositions of natural materials can be measured with great accuracy with a mass spectrometer (Peterson and Fry, 1987) and the accepted isotope ratio δ -value, expressed in parts per thousand (per mil, ‰), is calculated by:

$$\delta_{\text{sample}} (\text{‰}) = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where R represents the isotopic ratio (heavier to lighter isotope, e.g. $^{13}\text{C}/^{12}\text{C}$, $^{18}\text{O}/^{16}\text{O}$) of the sample and standard respectively (Peterson and Fry, 1987; Hobson and Wassenaar, 2008; Hoefs, 2009).

Thus, for example, the isotope ratio of carbon would be represented as follows;

$$\delta_{\text{sample}} (\text{‰}) = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}}/({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}} - 1] \times 1000 \quad (2)$$

Isotope standards, obtained from the IAEA (International Atomic Energy Agency), are often used to calibrate other laboratory standards that in turn are run with samples. This is because some of these original standards are long exhausted. Therefore, when expressing results, the standard used is always noted. This also facilitates conversions that relate to other standards, e.g. $\delta^{18}\text{O}_{\text{SMOW}} = 1.03091 \cdot \delta^{18}\text{O}_{\text{PDB}} + 30.91$, when comparing different studies (Friedman and O'Neill, 1977).

Stable isotopes have been used as a tool in palaeontological research for decades (Ehleringer and Osmond, 1989; Lee-Thorp and Thalma, 2000; Hoefs, 2009). Botanists have also long studied the patterns of ^{13}C distribution in plants resulting from climatic, altitudinal, latitudinal, and photosynthetic factors (Park and Epstein, 1960, 1961; Smith and Epstein, 1971; O'Leary, 1981; Dawson et al., 2002) and it is only recently that the technique has been applied in the zoological arena (Peterson and Fry, 1987), with a plethora of research publications appearing in recent decades (e.g. Lee-Thorp et al., 1989; Hobson & Clark, 1992a,b; Cerling and Harris 1999; Hobson et al. 2001; McKechnie, 2004; Herrera et al., 2003, 2006; West et al., 2006). The ratios of stable isotope signatures unique to particular environments, and the changes and variation in these ratios due to physical and biological processes, has gained popularity as a research tool for biologist's worldwide (Bigeleisen, 1965; Ehleringer and Osmond, 1989; Lee-Thorp and Thalma, 2000; McKechnie, 2004). The

reason for this is twofold; a reduction in the cost of analysing samples and improved technology that allows for the rapid processing of samples.

2.2 Carbon

Isotope compositions change in predictable ways as elements are cycled through ecosystems (Bigeleisen, 1965; Peterson and Fry, 1987). In incomplete reactions more of the lighter isotope is used up and the reaction products become depleted (i.e. they contain more of the lighter isotope). The unreacted material thus becomes enriched (i.e. containing more of the heavier isotope). In photosynthesis, the degree of carbon isotope fractionation is established during two rate-controlling processes; the diffusion of CO₂ into the chloroplasts, and the carboxylation process itself (Ehleringer and Monson, 1993; Hoefs, 2009). In photosynthesis there is thus a depletion of ¹²C in the remaining CO₂ because the light ¹²C is concentrated in the synthesized organic material (Hoefs, 2009). In C₃ plants (trees, shrubs and herbs, and temperate or shade grasses), where the initial product of photosynthesis is a three-carbon molecule, the CO₂ fixing enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) discriminates against ¹³C more strongly than another CO₂ fixing enzyme, PEP (phosphoenolpyruvate) carboxylase, that occurs in C₄ (mainly tropical grasses) and CAM (Crassulacean acid metabolism) plants (Park and Epstein, 1960, 1961; Smith and Epstein, 1971; Ehleringer, 1991). Plants exhibiting C₃ photosynthesis thus become more depleted in ¹³C relative to C₄ and CAM plants, with typical δ¹³C values for these different groups of plants as follows (Vogel et al., 1978; Ehleringer and Osmond, 1989; Ehleringer, 1991; Dawson et al., 2002);

-26.5‰ (-37 to -24‰) for C₃

-12.5‰ for (-16 to -9‰) for C₄

-17‰ (-19 to -9‰) for CAM

Implicit in the application of isotope techniques for biologists is the assumption that the isotope ratio of a consumers' tissue is related in some way to its diet (De Niro and Epstein, 1981; Ehleringer and Osmond, 1989; Hobson and Clark, 1992a,b). Typically the whole body of an animal is enriched in ¹³C relative to its diet by 1‰, although this fractionation can vary under different conditions (see later; De Niro and Epstein, 1978; Hobson and Clark, 1992). Because of this it may be necessary to establish levels of fractionation in the laboratory under controlled conditions (Gannes et al., 1997).

The use of stable isotopes has provided insight into the use of food resources by animal's not otherwise possible (Ehleringer and Osmond, 1989; Kelly, 2000; Dalerum and Angerbjörn, 2005). Whereas diet analyses have usually considered ingested material, gut contents or excreted matter to infer diets for animals, stable isotopes are able to provide an interpretation of assimilated matter using non-destructive means (Hobson and Clark, 1993; Phillips and Gregg, 2003).

The differences in the ratios of stable isotopes in different plants and environments are therefore useful in understanding more complex processes related to, for example, food chains and food webs, and sources of carbon. Carbon stable isotopes are thus used to reconstruct and quantify the proportions of isotopically distinct diets in different animals.

These dietary reconstructions rely on linear mixing models, with the proportions of two food sources in an animal's diet calculated by:

$$\delta X_{\text{tissues}} = p\delta X_A + (1 - p)\delta X_B + \Delta \quad (3)$$

where $\delta X_{\text{tissues}}$ is the isotope ratio in the animal's tissues, δX_A and δX_B are the isotope ratios of the respective food sources and p is the proportion of food A in the diet. The discrimination factor between the diet and the food source is represented by Δ (McKechnie, 2004; Hoefs, 2009). However, the dietary input for an animal is more often than not made up of more than two isotopic endpoints. Therefore, more isotopes and more sources can be used in multiple mixing models, e.g. IsoSource, MixSIR, ISOCONC1_01.xls, to quantify dietary proportions.

2.3 Nitrogen

Nitrogen isotopes are a useful tool in testing hypotheses concerning trophic levels and food web structure, and energy and nutrient transfer, because they are fractionated to a greater degree than carbon isotopes (De Niro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Mizutani et al., 1992; Hobson et al., 1994; Hobson and Wassenaar, 1999; McKechnie, 2004). Isotopic enrichment along a food chain is typically greater for ^{15}N than for ^{13}C , so the $\delta^{15}\text{N}$ values of a consumer's tissues becomes enriched by 3-5‰ relative to its diet (De Niro and Epstein, 1981; Minagawa and Wada, 1984; Fry, 1988; Mizutani et al., 1992; Hobson et al., 1994; Hobson and Wassenaar, 1999; McCutchan et al., 2003). This fractionation results from the differences between nitrogen assimilation and nitrogen excretion. An animals' trophic position can thus be estimated by:

$$\text{Trophic level} = \lambda + [(\delta^{15}\text{N}_{\text{secondary consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta_n] \quad (4)$$

where λ is the trophic position of the organism ($\lambda = 1$ for primary producers) used to estimate the $\delta^{15}\text{N}$ base, $\delta^{15}\text{N}_{\text{secondary consumer}}$ refers to the tissues of the consumer of interest, $\delta^{15}\text{N}_{\text{base}}$ is the corresponding value at the base of the food web, and Δ_n is the ^{15}N enrichment per trophic level (i.e. fractionation between diet and tissue).

The accuracy in determining the trophic position of an organism thus relies on, 1) a clear understanding of the food base on which a particular animal relies, and 2) the ^{15}N enrichment per trophic level (Hobson and Wassenaar, 2008). Also, for a clearer understanding of trophic positions reliable estimates of $\delta^{15}\text{N}$ at the base, and changing diet-tissue fractionation factors related to diet switches, particularly over a long period of time, are required (Post, 2002). This is one reason for the call for more controlled laboratory experiments in which stable isotopes under particular conditions can be better understood (Gannes et al., 1997; Martínez del Rio et al., 2009).

2.4 Research applications of carbon and nitrogen stable isotopes for birds

Stable isotope analysis has been used in the field of ornithology since the 1980s and has grown exponentially in the past few decades (Hobson, 2011). The biologically important stable isotopes of C, N, H, O and S have subsequently been measured in a variety of avian tissues to greater understand bird biology in mainly three realms; 1) diet and trophic relationships, 2) tracing the relative contribution of endogenous and exogenous nutrient

inputs into reproduction, and 3) determining the origin of migratory populations or individuals (Peterson and Fry, 1987; Kelly, 2000; Inger and Bearhop, 2008; Hobson, 2011). For other reasons including those stated above, and besides the fact that they are often measured concurrently on a mass spectrometer, combined use of carbon and nitrogen are useful in understanding carbon sources and interpreting trophic level interactions (Hobson et al., 1994). In particular they may be useful in understanding resource use and niche partitioning in diverse bird communities (Kelly, 2000; Herrera et al., 2003, 2006; Symes and Woodborne, 2009).

2.5 Hydrogen

2.5.1 Global fingerprint

The global distribution of hydrogen isotopes in precipitation (δD_p) has been used as a useful tool in determining the migratory connectivity of bird species in the Americas and Europe (e.g. Chamberlain et al., 1997; Hobson and Wassenaar, 1997; Chamberlain et al., 2000; Meehan et al., 2001; Wassenaar and Hobson, 2001; Hobson et al., 2004a,b; Clark et al., 2006). This is because of a significant and predictable change in δD_p across the globe, with a general depletion of δD (more negative δ values) in precipitation with an increase in latitude (Hobson, 1999; Bowen and Revenaugh, 2003; Lott and Smith, 2006; Inger and Bearhop, 2008; Hobson, 2011). A relatively robust model of hydrogen in precipitation across the globe, which also incorporates other variables such as distance from the sea, elevation and precipitation, has been developed (Bowen and Revenaugh, 2003). However, when making links between the hydrogen isotope values in feathers and the origins of migrating populations, it is important to have a sound understanding of moult and feather growth in the study species (Hobson and Wassenaar, 2008). This is because it is important to know where a feather is grown in its annual cycle (Clark et al. 2006). Also important is a sound understanding of fractionation processes from precipitation to feathers; for example most studies on raptor species show a depletion in δD of feathers from precipitation of 37–52‰ (Lott et al., 2003, Meehan et al., 2003; Hobson et al., 2009). However, it has been demonstrated that under different environmental conditions fractionation values may vary (McKechnie et al., 2004). Once again, for clearer interpretations regarding our understanding of bird migrations more laboratory and fieldwork experiments are required (Gannes et al., 1997; Martínez del Rio et al., 2009). Possible confounding factors that will obscure results of δD analysis include, for example, 1) animals consuming drinking water of very different isotopic composition when compared to food, 2) the enrichment of δD due to water stress in arid regions or during reproduction, 3) the change in δD patterns due to climate change, and 4) food webs relying on groundwater or lakes and wetlands (Hobson, 2005). Also, there must be clarity on the hydrogen component, i.e. exchangeable or non-exchangeable hydrogen, that is analysed. Feather samples must therefore be handled in a manner that ensures that hydrogen exchange between keratin and the ambient water is accounted for (Chamberlain, 1997; Hobson, 1999).

In Africa the hydrogen isotope gradient on either side of the equator is low so movements of birds within the continent are more difficult to study using stable isotopes (but see Yohannes et al., 2005, 2007, 2009, 2011; Wakelin et al., 2011). However, these challenges have not prevented research into African bird migrations using stable isotopes (see later).

2.5.2 Water turnover

Analysing hydrogen stable isotopes in tissues can provide valuable information in understanding the sources of water for organisms and water turnover, particularly in arid environments. To date, there has been no work conducted on understanding water sources of birds in southern Africa. However, in the Americas there have been investigations into the use of water sources in arid environments (Wolf and Martínez del Rio, 2003; McKechnie et al., 2004). For example, ratios of deuterium were used to determine the contribution of saguaro plant resources to water requirements of desert White-winged Doves *Zenaida asiatica mearnsii* (Wolf and Martínez del Rio, 2000; Wolf et al., 2002; Wolf and Martínez del Rio, 2003).

2.6 Tissue turnover

Important in interpretations of diet, water use, trophic level delineation etc., are assumptions regarding tissue turnover. Although it is not the task of this chapter to comprehensively review this topic, important points related to our understanding of avian biology and stable isotopes will be addressed.

The isotopic composition of a tissue that remains metabolically inert after formation should reflect that of the food and water consumed during synthesis (Chamberlain et al., 1997; Hobson, 1999; Hobson, 2005). Feathers are grown at least once a year and remain metabolically inert, so when moulted retain information of the previous location of moult. Claws of birds are metabolically inert but continuously grown, and can be useful to infer dietary and habitat information over a period of time from weeks to many months (Bearhop et al., 2003). Tissues that are metabolically active will reflect the average diet of the individual during a certain period into the past, according to the tissue's turnover rate, ranging from days (liver and blood plasma), to weeks (muscle and whole blood), to months, years or a lifetime (bone collagen) (Hobson and Clark, 1992a; Hobson, 1999; Hobson, 2005; Podlesak et al., 2005; Inger and Bearhop, 2008; Larson and Hobson, 2009; Hobson, 2011). Breath, reflecting immediately metabolised nutrients, and faeces representing the isotopic signature of a recent meal, may also be sampled non-destructively (Podlesak et al., 2005; Carleton et al., 2006; Voigt et al., 2008; Symes et al., 2011). Therefore, by analysing different tissues with different turnover rates temporal and/or spatial trophic shifts may be assessed.

Interpretations of temporal changes in $\delta^{15}\text{N}$ values, and associated trophic level shifts, can be complicated by insufficient knowledge on diet-tissue discrimination factors, dietary changes in different species and temporal changes in $\delta^{15}\text{N}$ of food sources, i.e. vegetation and insects. Numerous other factors can affect diet-tissue fractionation and studies to date have addressed these issues for a range of animal species, mostly under controlled conditions in captivity (see Post, 2002; Vanderklift and Ponsard, 2003; Robbins et al., 2005). For example, fractionation factors may be affected by, i) prey type, ii) prey quality, iii) temperature, iv) form of nitrogen excretion, v) habitat type, vi) water stress, and vii) nutritional status (including differences in dietary C:N ratios) (Ambrose, 1991; Hobson and Clark, 1992a,b; Hobson et al., 1993; Hobson et al., 1994.; Pinnegar and Polunin, 1999; Perkins and Speakman, 2001; Bearhop et al., 2002; Vanderklift and Ponsard, 2003; Pearson et al., 2003; Evans Ogden et al., 2004; Cherel et al., 2005; Robbins et al., 2005; Podlesak and McWilliams, 2006). In cases where we do not know more about discrimination factors

related to these factors we may be unable to make clear interpretations concerning trophic positions for particular species or animal communities.

Unfed animals have been found to show higher (enriched) $\delta^{15}\text{N}$ values due to recycling of endogenous nitrogen as body mass is lost without replacement of preferentially excreted ^{14}N (Hobson et al., 1993). Some studies may present contradictory results; in studies where animals have high C:N ratio diets (nitrogen becomes limiting at higher C:N ratios) the diet-tissue discrimination factor is shown to be higher (Adams and Sterner, 2000; McCutchan et al., 2003; Vanderkluft and Ponsard, 2003; Robbins et al., 2005; Tsahar et al., 2008), although Hobson and Bairlein (2003) found no significant difference in discrimination factor for different C:N diets for Garden Warblers *Sylvia borin*.

When Garden Warblers were fed a predominantly insect-based diet the diet-whole blood discrimination factor for carbon was 2.5‰ (Hobson and Bairlein, 2003), and House Sparrows *Passer domesticus* under different temperature conditions diet-whole blood discrimination factor was 1.5-1.8‰ (Carleton and Martínez del Rio, 2005). Fractionation factors for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for four tissues (plasma, breast muscle, cellular fraction of blood, whole blood, kidney, liver) of dunlin *Calidris alpina pacifica* fed controlled diets were 0.5-1.9‰ and 2.9-4.0‰ respectively (Evans Ogden et al., 2004). In calculating dietary proportions in tropical dry forest birds, Herrera et al. (2006) used derived values from other studies of birds; for carbon this was 1.4‰. It has commonly been accepted that diet-tissue discrimination factors for ^{13}C are lower than ^{15}N , in the order of 1-2‰ (Fry et al., 1978; Mizutani et al., 1992; Hobson and Wassenaar, 1999). In mammals controlled diet experiments on *Rattus rattus*, diet-whole blood discrimination factors for carbon ranged from -8.79‰ to 0.64‰ (Caut et al., 2008). Recent works therefore suggest that caution be applied in the use of isotope models because of uncertainty in diet-tissue fractionation factors for a wide variety of organisms and conditions (Caut et al., 2008b). Some have considered nectar feeding species and breath samples of broad-tailed hummingbirds *Selaphorus platycercus*, in a study that controlled diet, the diet-breath fractionation factor was calculated at -2.3‰ to -1.6‰ (Carleton et al., 2006).

To my knowledge no stable isotope laboratory studies have been done on African birds, and more specifically sunbirds. For wild caught birds $\delta^{15}\text{N}$ values for feathers of nectar feeding species were greater than expected; Southern Double-collared Sunbird *Cinnyris chalybeus* measured 7.5 ± 1.2 ‰ ($n = 5$; Symes and Woodborne, 2009) and Malachite Sunbird *Nectarinia famosa* 11.3‰ ($n = 1$; Symes et al., 2011). In 15 Northern Double-collared Sunbirds *Cinnyris reichenowi* the $\delta^{15}\text{N}$ values of feather samples ranged from 8.3-10.3‰ (Procházka et al., 2010); the range being less than that in a single White-bellied Sunbird *Cinnyris talatala* where samples from primary feathers ($n = 10$) ranged from 7.4-10.1‰ (mean value= 8.6 ± 0.8 ‰; Symes and Woodborne, 2011). Sunbirds have a diet that is typically low in nitrogen and to meet nitrogen requirements supplement their diet with insects (Skead, 1967; Daniels, 1987; Maclean, 1990, 1993; Markman et al., 1999, 2004; Gartrell, 2000; Roxburgh and Pinshow 2002). However, morphological and physiological features of nectarivores may be directed at utilizing a food source typically low in nitrogen. The reabsorption of nitrogen, and subsequent loss of lighter nitrogen isotopes, may thus explain the observed enrichment (Tsahar et al., 2005). Alternatively, the diet of arthropods may contain a high proportion of spiders, organisms with possibly high $\delta^{15}\text{N}$ values. For this reason diet-tissue fractionation rates were investigated in two sunbird species. White-bellied Sunbird and Amethyst

Sunbirds *Chalcomitra amethystina* (Nectariniidae), two common and broadly sympatric species on the South African highveld (Hockey et al., 2005), were captured and held under controlled laboratory conditions during a separate study investigating gastro-intestinal sucrase activity (Napier et al., 2008). They were fed a diet of sucrose [20% (w/w) sucrose] and protein supplement (2%; Ensure®, Abbott Laboratories, Johannesburg, South Africa) with a $\delta^{13}\text{C}$ value of $-13.1 \pm 0.1\text{‰}$ and $\delta^{15}\text{N}$ value of $1.1 \pm 0.8\text{‰}$. After 0, 5, 11 and 300 days 1-2 individuals of each species were euthanized and the carbon and nitrogen stable isotope signatures of blood, fat (dissected from a layer deposited on the pectoral muscle), feather, liver and muscle (pectoral) determined. In both species the values were greater than that reported for other bird species in the literature for South African birds (e.g. Symes and Woodborne, 2009, 2011). Although only one individual of each species was sampled on day 300, where tissue values had more than sufficient time to equilibrate with diet, the values are remarkable, given the known diet-tissue fractionation factors for other bird species (Table 1).

Tissue	Species	Carbon (‰)	Nitrogen (‰)
Liver	Amethyst Sunbird	3.4	5.5
	White-bellied Sunbird	4.1	8.3
Muscle	Amethyst Sunbird	4.1	6.7
	White-bellied Sunbird	4.5	8.0
Blood	Amethyst Sunbird	5.4	10.3
	White-bellied Sunbird	3.4	9.5

Table 1. Diet-tissue fractionation values for different tissues of White-bellied Sunbird *Cinnyris talatala* and Amethyst Sunbirds *Chalcomitra amethystina* ($n = 1$ for each value) determined in controlled laboratory experiments and euthanized at 300 days in captivity (Symes and Woodborne, 2011; Symes and Woodborne unpubl. data).

3. Links with the north – Migrant birds in southern Africa

3.1 Before stable isotopes

Bird ringing has been a valuable tool in tracking bird movements in the past (Nichols and Kaiser, 1999; Bairlein, 2003; Hartley, 2003). However, understanding movement patterns requires that ringed birds are recovered and when they are only the start and end points of movements can be determined. More recently, radar has been used to quantify migration in space and time, to determine the altitude of migration and to understand the influence of weather conditions on migration (Alerstam and Hedenström, 1998; Bairlein, 2003). For years the tracking of migrating species has proved difficult for all but conspicuous species (Chamberlain et al., 1997; Wassenaar and Hobson, 1998; Hobson, 1999; Wassenaar and Hobson, 2000; Hobson, 2002; Kelly et al., 2002; Rubenstein and Hobson, 2004; Hobson, 2005). Satellite telemetry, or radiotracking by satellite, allows for collection of migration data of greater detail both spatially and temporally (Meyberg et al., 1995; Nichols and Kaiser, 1999; Meyberg et al., 2001; Bairlein, 2003; Hartley, 2003). It also allows for tracking of species even when recoveries of birds are low, and aids in the identification of important stopover and refuelling sites (Bairlein, 1985, 2003). However, it was previously only be applied to relatively large species due to the weight of the transmitters (Bairlein, 2003). Birds can also be tagged with geolocation devices (which use real-time measurement of light intensity) and global positioning system devices (which use satellite data) to establish the geographic co-ordinates

of a bird as it travels, with or without recapture (Bairlein, 2003). Tracking birds in these ways is often far more efficient and informative than ringing, and can be used on small bird species. However, these less traditional methods can be time-consuming and expensive, and track only the routes of individual birds that in turn are used to infer patterns for a species.

Recently established chemical and molecular markers appear to be extremely useful in the study of bird migration. DNA analysis can be used to determine different populations and track their movements (Hobson, 1999; Bairlein, 2003; Clegg et al., 2003; Hartley, 2003; Rubenstein and Hobson, 2004).

The use of stable isotopes (hydrogen, carbon, nitrogen, strontium) in deciphering the movements of a number of species has proved successful and efficient (Hobson and Wassenaar, 1999; Hobson et al., 2001; Kelly et al., 2002; Graves et al., 2002). It has the advantage over marked-recapture techniques in which the same individual does not need to be recaptured again later. In addition it can include the study of smaller organisms such as migratory insects (Wassenaar and Hobson, 1998; Hobson, 2002). Stable isotopes may be used to pinpoint the movements of birds as they travel between distant locations with distinct isotopic composition and incorporate isotopic signatures into their tissues (Hobson, 1999; Bairlein, 2003; Szép et al., 2003; Inger and Bearhop, 2008). This is based on the principle that foodwebs from different regions differ in their isotopic signatures due to several biogeochemical processes, and birds that move from one foodweb to another isotopically distinct foodweb will retain the isotopic signature of their previous location (Hobson, 1999; Hobson, 2005; Podlesak et al., 2005; Larson and Hobson, 2009; Hobson, 2011). The use of stable isotope analysis requires only one sampling of an individual, is less time-consuming and will not influence the behaviour of the individual like an extrinsic marker (Hobson, 1999; Hobson, 2011). Retrospective studies on museum or archived samples are also possible (Hobson, 2011) and may even be used to study long term changes in bird diets brought about by anthropogenic changes (Chamberlain et al., 2005). Ringing cannot be completely replaced by stable isotope analysis (Bairlein, 2003), but the use of stable isotopes will no doubt enhance our understanding of the patterns and processes of migration in many species where very little is known.

Many migrant species are known to be currently undergoing population declines (Holmes, 2007). For birds that migrate, the sites of origin, stopover and destination are important during different stages of the annual period of migrants (Hahn et al., 2009). Thus studies into the largely unknown details of migration, e.g. differences in migration of age classes, sexes and populations; location of key stopover and wintering areas; connections between migration, moulting and breeding; migratory connectivity between populations of birds; carry-over effects between winter habitat occupancy and breeding success; and external factors regulating migration are required for use in conservation planning (Chamberlain et al., 1997; Hobson, 1999; Bairlein, 2003; Holmes, 2007).

Stable isotopes allowed Kelly et al. (2002) to report the leapfrog pattern of Wilson's Warbler *Wilsonia pusilla*. They analysed hydrogen stable isotope ratios (δD) in breeding, migrating and wintering warblers and established that northerly breeding populations migrated earliest in autumn, flying over southerly breeding birds (Kelly et al., 2002). These northern breeders migrated to the southern edge of the Wilson's Warbler's range in south Central America (Kelly et al., 2002), a phenomenon that would have been difficult to detect through other known research methods. Other species in which migratory connectivity have been

revealed include Cooper's Hawks *Accipiter cooperii* (Meehan et al., 2001), Ecuadorean hummingbirds (Hobson et al., 2003) and the Aquatic Warbler *Acrocephalus paludicola* (Pain et al., 2004), although these studies are confined to the Americas.

3.2 Intra-African migrants

Very few studies have used stable isotope analysis to interpret intra-African avian migratory patterns. This is probably due to two reasons. Firstly, limited resources in many African countries limit studies and secondly, and possibly more importantly, the isotopic gradient of the distribution of deuterium is not as great as that in the Americas and Palaeartic. However, despite these challenges some detailed studies have highlighted important findings. For example, Wakelin et al. (2011), used hydrogen, carbon and nitrogen stable isotopes to investigate migratory connectivity of the Blue Swallow *Hirundo atrocaerulea*, a threatened intra-African migrant with breeding populations in three geographically disjunct regions in southern Africa (Spottiswood, 2005). Their results indicated that there is overlap in the wintering ranges of at least two of the three major breeding populations (Wakelin et al., 2011). Because deuterium may not be a useful isotope to use in Africa, a multiple isotope approach may be more efficient (Wakelin et al., 2011).

3.3 Palaeartic migrants

Several fairly recent studies in Europe have dealt with Palaeartic-African migrants, i.e. those avian species that migrate between the Palaeartic (Europe, Africa north of the Sahara, and most of Asia north of the Himalayas) and Africa, south of the Sahara (Chamberlain et al., 2000; Symes and Woodborne, 2010). Examples of these studies are discussed below.

3.3.1 Amur falcon

In a study of Amur Falcon *Falco amurensis*, a small (138-160g, Schäfer, 2003) insectivorous raptor that undergoes a one-way migration between southern Africa and the eastern Palaeartic of ~13,000 km (Figure 1a; Ferguson-Lees and Christie, 2001; Mendelsohn, 1997; Jenkins, 2005), Symes and Woodborne (2010) demonstrated that South African populations do not show strong site fidelity but move widely across the subregion, feeding on a broad range of arthropods that become seasonally abundant during the austral summer. They have a wide breeding range in the eastern Palaeartic; through Mongolia, Siberia and northern China with a distribution range at least eight times that of the southern African range (Cheng, 1987, Mendelsohn, 1997; Ferguson-Lees and Christie, 2001; Greenberg and Marra, 2005; Global Raptor Information Network, 2008; Symes and Woodborne, 2010). They arrive late in southern Africa, compared to other migrants, during November to early-December, and roost in colonies that number thousands of individuals (Figure 1b & c; Benson, 1951; Cade, 1982; Tarboton and Allan, 1984). For a number of months they are a common sight on the eastern South African Highveld, before departing north to their breeding grounds in April to May (Mendelsohn, 1997; Jenkins, 2005). Although details on migration routes and feeding grounds were limited regarding stable isotope analyses, results did provide valuable information on the biology of Amur Falcons. The recent tracking of individual birds using satellite tracking devices may further contribute to a greater understanding of the movements and migration patterns of this species.



(a)



(b)



(c)

Fig. 1. a. Female Amur Falcons *Falco amurensis*; b & c. communal roost of Amur Falcons (Heidelberg, Gauteng, South Africa; 29 December; 26°30'11"S, 28°21'31"E, ~1,600m a.s.l.). Photographs: Craig Symes.

3.3.2 Willow Warblers

Hedenström and Pettersson (1987) noticed two different migratory directions within Willow Warbler *Phylloscopus trochilus* populations, and endorsed C and N stable isotope analysis as a method to determine wintering ranges of migrants in place of more traditional methods. It also emphasised the need for regional isotopic maps of feather keratin for migratory species in their African wintering grounds in order to pinpoint the exact localities of these areas.

Subsequently, a study by Chamberlain et al. (2000) used stable isotopes to investigate the migratory divide of Willow Warblers in Scandinavia. The breeding ranges of two subspecies of Willow Warbler occur adjacent to one another and overlap in a migratory divide. *Phylloscopus t. trochilus* is known to occur south of 61°N and *P. t. acredula* north of 63°N. The migratory divide should occur between these two ranges. Additionally, according to ringing recoveries, *P. t. trochilus* is thought to migrate to West Africa and *P. t. acredula* to East Africa. In this study $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures of feathers collected from males of both subspecies in Scandinavia were determined. The study found more enriched values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in *P. t. acredula*, suggesting that they do indeed winter in different regions of Africa. This is because East Africa, where *P. t. acredula* winters, has a more arid climate and more C4 plants than West Africa, where *P. t. trochilus* winters. The study also found intermediate $\delta^{15}\text{N}$ ratios in the birds of the contact zone, suggesting that they probably represent both subspecies.

A later study conducted stable isotope analysis in feathers of two Willow Warbler subspecies' in Africa, and attempted to map the subspecies wintering ranges (Bensch et al., 2006). However, many of the isotopic signatures documented in the Scandinavian study by Chamberlain et al. (2000) did not match those of the same subspecies in Africa as documented by Bensch et al. (2006). This prompts the need for more information before Willow Warbler wintering ranges can be effectively mapped (see proposed study later).

3.3.3 Aquatic Warblers

The globally threatened Aquatic Warbler *Acrocephalus paludicola* is threatened by anthropogenic habitat destruction and has a fragmented breeding population across the western Palaearctic with 90% of the population restricted to Belarus, Poland and Ukraine (Pain et al., 2004). Little is known about its wintering quarters which are assumed to be located in sub-Saharan Africa. Conservation of the species necessitates knowing where the wintering range occurs. Pain et al. (2004) sampled flight feathers of Aquatic Warblers in Europe and analysed δD , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios to determine whether different breeding subpopulations formed a single mixed population on the African wintering grounds. Neither $\delta^{15}\text{N}$ nor δD varied between subpopulations. Although this suggests that subpopulations do not differ in trophic level in their wintering ranges, it does not necessarily suggest that subpopulations winter in the same place, as similar δD ratios are found at many different latitudes in Africa. However, significant differences in mean $\delta^{13}\text{C}$ ratios between subpopulations suggest different wintering latitudes. Birds that breed further north or west in Europe possibly winter further north in Africa.

Subsequently, a study by Oppel et al. (2011) again collected feathers of the species across Europe to investigate $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, δD ratios and attempted to determine the species' wintering regions in Africa. Feathers were collected at the only known wintering site in Senegal. The feathers sampled in Africa showed similar degrees of variation in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$

and δD ratios to those sampled in Europe, little evidence to suggest that subpopulations wintered in different regions. Nevertheless, 20% of the samples in Europe fell outside of the range of isotopic values recorded in Senegal, suggesting an over-wintering region elsewhere in Africa. It was concluded that the large variability of feather isotopic signatures within sites of specialist species like the Aquatic Warbler, due to the large variation in plant isotope values at the base, makes it difficult to identify wintering sites using stable isotope analysis. According to Flade et al. (2011), ringing and molecular studies have also not provided conclusive evidence about African wintering regions, yet geolocators recently attached to Aquatic Warblers in the Ukraine could be promising.

3.3.4 Reed and Great Reed Warblers

Procházka et al. (2008) attempted to link the breeding and wintering grounds of the Reed Warbler *Acrocephalus scirpaceus* by analysing all relevant sub-Saharan ringing recoveries and conducting stable carbon and nitrogen isotope analysis on moulted feathers collected in Africa. This species is thought to experience a migratory divide in Central Europe, and birds from populations either side of the divide will either travel southeast or southwest during migration to different wintering quarters in Africa. Ringing recoveries suggested strong connection between breeding and wintering grounds in Africa. Higher $\delta^{15}N$ values of southeast migrating birds suggested that they occupied more arid biome types than southwest migrating birds, as was expected. More work is necessary before the precise wintering grounds can be identified, but the combination of ringing and stable isotope analysis was successful in understanding more about migration patterns of this species.

Similarly, Yohannes et al. (2008) used δD , $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of feathers of the Great Reed Warbler *Acrocephalus arundinaceus* to test whether isotope signatures of individuals remained consistent between years, and thus whether birds exhibited philopatry i.e. returned to the same location in successive years. The findings supported this behaviour, as similar isotopic signatures were obtained during different years. However, it could be that birds did not return from the same location as previous years, but rather that they returned from habitats with similar isotopic signatures. This study highlights the benefits of using multiple isotopes in stable isotope analysis of migration, and again highlights the effectiveness of using ringing data in combination with stable isotopes when attempting to understand bird movements.

4. Diet and trophic structure of southern African birds determined using stable isotopes

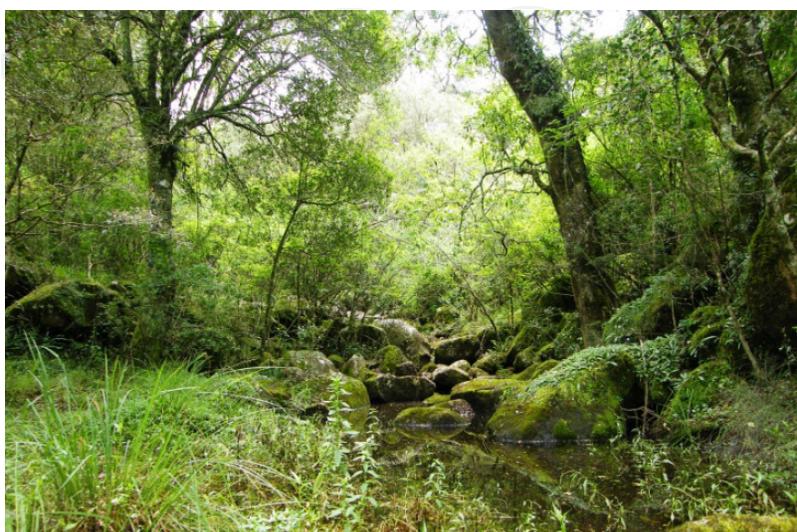
Numerous studies have demonstrated the complexities of links and trophic levels in avian food webs (Herrera et al., 2003, 2006; Symes et al., 2009). Usually this is done with tissues that can be sampled non-destructively such as feathers, blood, toe-nail and breath (Hobson and Wassenaar, 2008). However, in the case of feathers, interpretations using isotope values may be confounded by intra-individual variation (Symes and Woodborne, 2011). Recognising temporal dietary variation as represented in feathers grown at different times, e.g. moulting flight feathers, is thus important and needs to be critically assessed in any study of avian diets using stable isotope analysis. It may, however, be used advantageously where separate flight feathers are individually sampled to infer diet on a temporal scale (e.g. Ramos et al., 2009).

4.1 The forest-grassland matrix, and savannas and grasslands

The forest (C3 plant dominant) and grassland (C4 plant dominant) matrix in savanna and forest-grassland ecosystems of South Africa offers a suitable opportunity to understand carbon sourcing from two different vegetation types (Acocks, 1975). In each vegetation type the vegetation mosaic is different; in C3 forests the C4 grass environment usually surrounds the forest whilst in savanna the C4 grassy component occurs beneath the trees (Figure 2). However, grasslands are not entirely C4 and consist of an important C3 component of woody and herbaceous plants. Also, not all grasses in this biome are C4 and a gradient of increasing proportion of C3 grasses occurs with an increase in latitude south and an increase in altitude (Vogel et al., 1978). Never-the-less, in a montane forest the contribution of C3 (predominantly trees) and C4 (predominantly grasses, although few C4 grasses occur in forest) carbon to the diets of forest birds was investigated using stable isotope analysis of feathers (Symes and Woodborne, 2010). In addition, nitrogen isotopes were measured to investigate trophic partitioning. The forest bird community generally met predictions regarding known diets of different species, and overall very little isotopic partitioning of resources, as inferred from stable isotopes, was recognised. Birds, that are able to utilise the



(a)



(b)



(c)



(d)

Fig. 2. a. Mistbelt mixed *Podocarpus* forest in the KwaZulu-Natal midlands, South Africa, occurring naturally in fragments on south facing slopes, surrounded by grassland, note the well defined grassland-forest ecotone, b. forest interior with few grasses (usually in gaps) occurring in understorey, late-summer (March; 29°27'50"S, 29°52'43"E, ~1,530 m a.s.l.), c. savanna near Nelspruit, South Africa, showing extensive grassy understorey, early-spring (September), d. pale form of *Erythrina lysistemon*, an important nectar source for birds, in savanna near Nelspruit, early-spring (September; 25°34'22"S, 31°10'53"E, ~ 800 m a.s.l.). Photographs: Craig Symes.

environment in different ways to non-flying animals, may not need to partition resources in an "isoscape" (Bowen & West, 2006; West et al., 2010); partitioning resources may be more effectively recognised in space and time.

Current work on South African forest birds is now focussing on the suitability of stable isotopes in understanding bird diets. By sampling multiple "tissues", i.e. blood, faeces and feather, during different seasons, i.e. winter and summer, and comparing these data with comprehensive feeding observations in the forest, a clearer understanding of dietary acquisition and resource partitioning in a forest bird community can be obtained (Scott and

Symes unpubl. data). Preliminary results, that also analyse bird community census data, suggest that although there is very little change in avian diversity between seasons there is a significant seasonal turnover in the functional nature of the bird community between seasons (Scott and Symes unpubl. data). This turnover relates to the change in food resources available to birds between seasons (Scott and Symes unpubl. data).

4.2 Wetlands and marine environments

Stable isotopes provide a valuable tool in understanding the link between marine and terrestrial systems and numerous examples, from Alaskan Brown Bears *Ursus arctos* that derive marine nutrients through the consumption of migrating Pacific salmon (*Onchorhynchus gorbuscha*, *O. keta* and *O. kisutch*) (e.g. Ben-David et al., 2004) to numerous “maritime mammals” that consume intertidal energy resources and transfer these resources to the land (Carlton & Hodder, 2003). The ability of birds to fly enables them to transfer nutrients between terrestrial or marine systems and depositions of guano are testimony to the large amounts of nutrients transferred from sea to land. In marine feeding Great Black Cormorants *Phalacrocorax carbo* stable isotopes in feathers were used to show that birds had been feeding on an almost entirely freshwater prey source (Bearhop et al., 1999). Similarly, on the northern Chilean coast, two closely related songbirds (*Cinclodes nigrofumosus* and *C. oustaleti*) were shown, using stable isotopes ($\delta^{13}\text{C}$), to utilise coastal and freshwater environments quite differently; and the reliance on marine sources was accompanied by adjustments in the osmoregulatory mechanism (Sabat et al., 2006). As terrestrial productivity increased with an increase in latitude south so too did the incorporation of terrestrial carbon increase (Sabat et al., 2006). However *C. nigrofumosus* that lives exclusively on coastal environments, had a greater contribution of marine input and less variable $\delta^{13}\text{C}$ values than *C. oustaleti* which shifts seasonally from coastal to freshwater environments (Sabat et al., 2006). These studies are possible because of the distinct differences in marine and terrestrial food webs with marine organisms typically having more enriched isotope values for D, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$ and $\delta^{34}\text{S}$ (Hobson, 1999). Southern Africa’s extensive coastline offers suitable working examples to assess the marine contribution to terrestrial birds. For example, pelicans (*Pelecanus onocrotalus* and *P. rufescens*) occur in freshwater and marine systems across the sub-region but are thought not to be involved in significant movements (Crawford, 2005; Ryan, 2005). Much like the study of Klaassen et al. (2001) that demonstrated that capital resources are not important for breeding arctic waders (10 species) so too might stable isotopes be used to identify the importance of marine resources, at varying distance from the coast, for many birds, e.g. pelicans. Many studies have considered nutrient transfers between marine and terrestrial systems whilst others have used stable isotopes successfully to track the movements of seabirds within a marine environment (e.g. Barbraud and Chastel, 1998; Ramos et al., 2009). Unique stable isotope signatures of different feeding grounds (related to latitude, species composition, sea temperature, etc), together with other tracking techniques, may provide valuable information of the use of oceanic resources by seabirds.

The Mangrove Kingfisher *Halcyon senegaloides* has an almost exclusively coastal distribution along the east coast of Africa where, as its name implies, has a strong association with mangroves (Figure 3; Fry et al., 1988, 1992). Because of this association it is suggested that it has a strong reliance on marine resources. However, it has recently been discovered breeding in arboreal termitaria in woodland in central Mozambique (Davies et al., 2012). It is not yet clear whether this population is migratory and if they are what role resources

obtained from possible “overwintering” sites on the coast play in contributing to reproductive output and success (Davies et al., 2012). Stable isotopes might be a useful tool in answering this question. Additional species that might also rely on seasonal utilisation of marine and terrestrial resources, depending on their location and how they move across the landscape include, for example Pied Kingfisher *Ceryle rudis*, Reed Cormorant *Phalacrocorax africanus* and Greyheaded Gull *Larus cirrocephalus* (Hobson, 1987; Hockey et al., 2005).



(a)



(b)

Fig. 3. a. Mangrove swamp on KwaZulu-Natal north coast ($28^{\circ}58'51''S$, $31^{\circ}44'09''E$, $\sim 5m$ a.s.l.), site of Mangrove Kingfisher *Halcyon senegaloides*, b. arboreal termitarium on stem of *Sterculia* sp. (see arrow), used as nesting site by Mangrove Kingfisher in central Mozambique ($18^{\circ}09'17''S$, $35^{\circ}07'29''E$, $\sim 170m$ a.s.l.). Photographs: Craig Symes.

4.3 Specialist diets

Large tree-like CAM aloes such as *Aloe marlothii* and *A. ferox* are a conspicuous feature of the South African landscape (Figure 4), not unlike the saguaro cactus *Carnegeia gigantea* of the arid regions of the Americas (Fleming et al., 1996). Studies using stable isotopes in the Sonoran Desert have provided insight into the use of saguaro fruit for bird communities (Wolf and Martínez del Rio, 2000; Wolf et al., 2002; Wolf and Martínez del Rio, 2003). The fruit of saguaro cacti has a unique CAM stable isotope composition (Wolf et al., 2002). Using this feature, temporal analyses of $\delta^{13}\text{C}$ and δD revealed the importance of fruit as a source of nutrients and water for White-winged Doves *Zenaida asiatica mearnsii* (Wolf et al., 2002). These results were confirmed by a positive correlation between the $\delta^{13}\text{C}$ in dove liver tissues and percent saguaro fruit in the crop contents (Wolf and Martínez del Rio, 2000). Further investigations revealed that two different desert doves relied on saguaro fruit for different reasons; White-winged



(a)



(b)

Fig. 4. a. Flowering *Aloe marlothii* at Suikerbosrand Nature Reserve, Gauteng, South Africa, late-winter (August, 26°31'54"S, 28°10'11"E, ~1,630 m a.s.l.), b. Wattled Starling *Creatophora cinerea* feeding on *A. marlothii* nectar. Photographs: Craig Symes.

Doves predominantly perched atop saguaros and fed on flowers or fruit, whilst Mourning Doves *Zenaida macroura* fed exclusively on the ground (Wolf et al., 2002). These differences in feeding mode affected the importance of saguaro fruit for these two dove species. Saguaro provided an important source of nutrients and water for White-winged Doves, whereas for Mourning doves saguaro provided nutrients and less importantly water (Wolf et al., 2002). In South Africa, the importance of sugar in the dilute nectars of *A. marlothii* has been demonstrated as an important carbohydrate source for numerous opportunistic avian nectarivores (Symes et al., 2008; Symes, 2010; Symes et al., 2011). In particular the analysis of breath samples has indicated that ingested sugars are used as an income resource for a wide range of opportunistic nectar feeding species (Symes et al., 2011).

In southern Africa, specialised nectarivores are from the family Nectariniidae (sunbirds; 12 species) and Promeropidae (sugarbirds; 2 species) (Skead, 1967). However, additional opportunistic nectar feeders include white-eyes (Zosteropidae), weavers (Ploceidae), bulbuls (Pycnonotidae), barbets (Lybiidae), mousebirds (Coliidae) and starlings (Sturniidae) (Marloth, 1915; Oatley, 1964; Skead, 1967; Oatley and Skead, 1972; Jacot Guillarmod et al., 1979; Craig and Hulley, 1994; Oatley, 2001; Symes, 2010). Numerous studies have indicated the importance of nectar sources for bird communities in southern Africa (Frost and Frost, 1981; Daniels, 1987; Tree, 1990; Craig and Hulley, 1994; Symes et al., 2001; Symes, 2010) but only recently has this importance been quantified through the use of stable isotopes (Symes et al., 2011). The high diversity of aloes in southern Africa provides a valuable nectar source for many birds and although flowering occurs throughout the year there is a peak in the number of flowering species during the drier winter months (Figure 5).

The provision of fruit by saguaro cacti can be compared with the provision of nectar by aloes in southern Africa. *Aloe marlothii* is a CAM photosynthesizer (Eller et al., 1993), as is *A. arborescens* (Kluge et al., 1979); they display typical $\delta^{13}\text{C}$ values like many other aloes (*A. marlothii* $\delta^{13}\text{C}$ = -14.93 and -12.09‰; *A. greatheadii* var. *davyana* = -14.41‰; *A. arborescens* = -16.92‰; Figure 6). However, the $\delta^{13}\text{C}$ values of aloes vary for samples collected throughout Africa, ranging from -28.48‰ to -11.51‰ (mean \pm SD = 17.26 ± 4.94 ‰; Figure 6), so the application of isotope techniques, in assessing the value of nectar for opportunistic nectar feeders, needs to be conducted with a sound understanding of the isotopic environment.

Important in dietary studies determining the proportion of resources from different food items is an understanding of the isotope ratios of the food base on which birds are feeding, and the context of these food resources. In the study of the importance of *A. marlothii* nectar for birds Symes et al. (2011) were able to detect more enriched changes in the isotope signatures of the whole blood and breath of species that normally assimilated carbon from C3 sources outside of the flowering period (Wolf and Hatch, 2011). However, for seed eating species (granivores), such as Southern Masked Weaver *Ploceus velatus* that feed mostly on C4 plants (C4 grasses $\delta^{13}\text{C}$ = 14.7 ± 2.5 ‰) the shift in diet to nectar ($\delta^{13}\text{C}$ = 12.6 ± 0.5 ‰) was less obvious and any changes in diet were difficult to detect in tissues during the pre-flowering and flowering months (Symes et al., 2011). In this study nectars are comprised mostly of hexose sugars with very little protein and the emphasis of the study was to identify the routing of nectar carbohydrates in the system (Symes et al., 2011). In other circumstances the routing of protein using nitrogen stable isotopes may be studied (Herrera et al., 2006). For many nectar feeders the acquisition of nitrogen may be obtained from animal protein. Sunbirds (Family Nectariniidae) may regularly be observed feeding on insects and it is important that they feed nestlings this rich protein source (Hockey et al.,

2005; Markman et al., 1999). In Painted Honeyeaters *Grantiella picta* (Family Meliphagidae) and Mistletoebirds *Dicaeum hirundinaceum* (Family Dicaeidae) the isotopically distinct values of Grey Mistletoe *Amyema quandang* (Loranthaceae) fruit (mean $\delta^{15}\text{N} = 4.4\text{‰}$) and arthropods (mean $\delta^{15}\text{N} = 7.1\text{‰}$) allowed Barea and Herrera (2009) to determine that approximately half of their nitrogen was obtained from mistletoe fruit. Similarly, the opportunity may exist in Africa for stable isotope analyses to determine the importance of mistletoes for mistletoe feeding specialists such as tinkerbirds (Family Lybiidae).

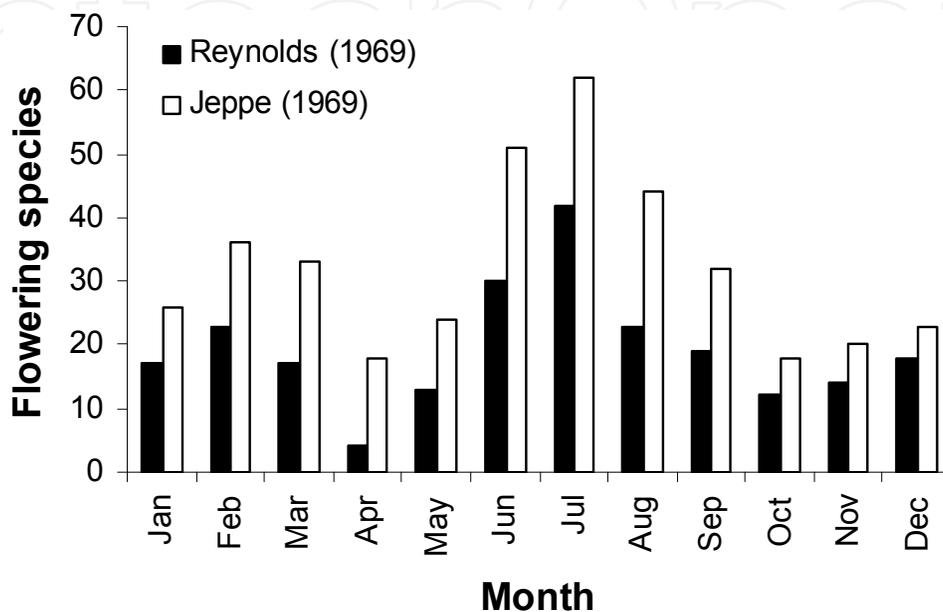


Fig. 5. Number of South African (after Jeppe, 1969) and southern African (after Reynolds, 1969, $n = 133$) *Aloe* species flowering in different months of the year. The different references may have included each *aloe* species flowering in more than one month.

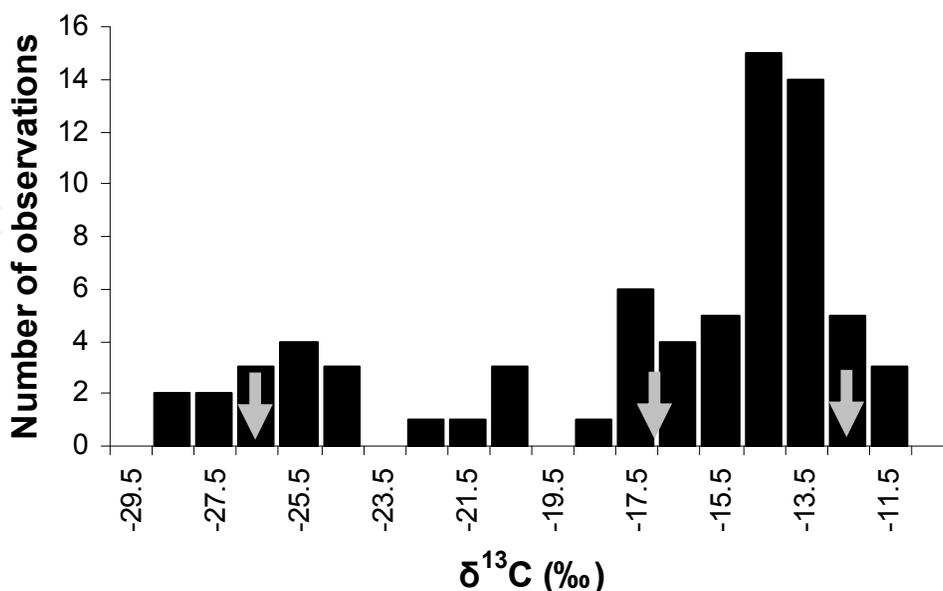


Fig. 6. Frequency distribution of $\delta^{13}\text{C}$ (‰) for 64 *Aloe* species ($n = 72$) (J. Vogel and S. Talma unpubl. data). Arrows indicate means for C₃ (-26.5‰), CAM (-17‰) and C₄ (-12.5‰) plants (Vogel et al., 1978; Ehleringer and Osmond, 1989; Ehleringer, 1991; Dawson et al., 2002).

5. Future research

5.1 Forging links

Scope for developing links between northern and southern hemisphere researchers and institutions is wide and collaborative efforts may strongly enhance our understanding of avian migration patterns. For any scientist the limiting factors in any research are a combination of resource availability and time. By thinking and working globally, rather than locally, broad questions regarding bird movements and behaviour can be addressed. In particular, questions relating to global change and the effects changes in the modern world are having on biodiversity can be addressed. Below I address in detail and give a number of possible studies on species with unique migration characteristics or patterns.

5.2 Deuterium and bee-eaters

Although there is a lack of a strong gradient in hydrogen isotopes distributed across Africa opportunities still remain for understanding the complexities of bird movements across the continent. The Palaearctic extends across a vast longitudinal range and from that wide region migrant species are funnelled down the African continent, many reaching South Africa (Chamberlain et al., 2000; Symes and Woodborne, 2010; Table 2).

Although there may be little conservation concern for certain species, rapid changes brought about by humans to the environment may significantly affect the long-term prospects for many of the world's birds, particularly those that migrate and that rely on habitats in two different hemispheres during different times of the year. It is of added importance to study these patterns in the context of a world affected by climate change (Drent et al., 2003).

The European Bee-eater *Merops apiaster* has a widespread distribution across the western Palaearctic and migrates to Africa during the austral summer (Cramp and Perrins, 1993; Snow and Perrins, 1998; Fry, 2001). In South Africa there are two morphologically indistinct populations (Underhill, 1997; Barnes, 2005). Palaearctic-breeding birds migrating to South Africa (where they undergo primary moult) are thought to originate from the east of their Palaearctic range; birds from the western Palaearctic migrate to West Africa (Barnes, 2005). On the other hand southern Africa breeding birds arrive from central Africa (where they have undergone a primary moult) (Brooke and Herroelen, 1988). The funnelling effect of different members of each sub-population into southern Africa therefore offers a unique opportunity to understand how these populations interact. With an understanding of moult patterns (Holmgren and Hedenström, 1995) and analysing stable isotopes of primary feathers of individuals at different roosts (breeding and non-breeding) across South Africa inferences on migratory origins and use of resources can be made.

Region	Number of species
West Africa	175
Sudan	198
Eastern Democratic Republic of Congo, Rwanda, Burundi	127
Kenya	147
Zimbabwe	75
South Africa (Western Cape, Eastern Cape, Northern Cape)	58

Table 2. Approximate numbers of species of Palaearctic migrants to different regions of Africa (From Maclean, 1990, Table 6.2).

5.3 Warblers and flycatchers

Understanding the migratory connectivity between breeding and non-breeding sites of migratory species, particularly species that may be difficult to study because they are small and inconspicuous, is of ecological and conservation importance (Pain et al., 2004). The Spotted Flycatcher *Muscicapa striata* and Willow Warbler *Phylloscopus trochilus* are two of southern Africa's most common Palaearctic migrants (Herremans, 1997a,b; Dean, 2005; Johnson, 2005). Both have similar distributions, arriving during the non-breeding season (austral summer) in most of equatorial and southern Africa (Salewski et al., 2002, 2004; Herremans, 1997a,b).

In southern Africa the Willow Warbler is widespread in woodland and Karoo habitats, although is thinly distributed in the south-western Kalahari basin and western Karoo, and absent from the Namib Desert (Herremans, 1997a). There is a decreasing abundance in southern Africa from north to south and from east to west (Underhill et al., 1992b). It is one of the earliest Palaearctic migrants to arrive where, in the north of the sub-region it arrives from mid-September, with mid-arrival dates in mid-October in the north and December in the south (Herremans, 1997a). Arrival is rapid and annually consistent (Herremans, 1994) with arrivals in the Eastern Cape in early-December (Underhill et al., 1992b). Departure is synchronised in the whole region with mid-departure in mid-April (Underhill et al., 1992b); males precede females on northward migration by 10 days (Underhill et al., 1992a) and few are present in early-May (Underhill et al., 1992b). This may explain why moulting females in southern Finland began moulting 10-15 days later than males (Tiainen, 1981). Recoveries in southern Africa include five birds in Finland and two in Sweden (Hedenström and Pettersson, 1987; Dowsett et al., 1988; Oatley, 1995). However, no South African ringed birds have been caught north of the equator. Of 35 ringed and recaptured, 12 were caught at the same site the following summer, with 10 at the same site >1 yr later (Safring, unpubl. data 2010). There has been a decline in numbers across Europe since 1980 and because of this there is cause for its conservation (Baillie et al., 2010).

Three subspecies of Willow Warbler are currently recognised (Dean, 2005) although they are difficult to identify (Table 3; Figure 7a; Svensson, 1992). *Phylloscopus t. yakutensis* undergoes the longest migratory journey for a passerine (Curry-Lindahl, 1981) (to southern Africa from eastern Asia) and comprises 10% of the population in the sub-region (Clancey, 1970; Irwin, 1981). *P.t. acredula* is the most common, being slightly larger and paler than nominate, *P.t. trochilus* which occurs at intermediate abundance (Clancey, 1980; Irwin, 1981; Hopcroft, 1984). Blaber (1986) reports *P.t. trochilus* as most common in KwaZulu-Natal although Urban et al. (1997) note that the nominate race is unlikely in southern Africa.

The Spotted Flycatcher is a more specialized insectivorous feeder than the Willow Warbler, being the only flycatcher in the region that specializes in long upward hawking (Herremans, 1997b). In northern southern Africa arrivals occur from early-October (Irwin, 1981; Tarboton et al., 1987; Herremans, 1994), with most arrivals in late-October and November (Herremans, 1997b). Peak arrival in the south is early-December (Herremans, 1997b) and in Bloemfontein, arrivals are mostly during 5-30 November (median 21 November) (Kok et al., 1991). In Johannesburg the earliest arrivals were the 2 November (Bunning, 1977) and in Queenstown, Eastern Cape, the 14 November (Anon, 1953). Departures are quick and simultaneous, occurring in late-March and April, although are sometimes recorded in late-April (Irwin, 1981). In Botswana the latest departures were 5 May (Herremans, 1994) and in Johannesburg

the latest departures were 25 March (Bunning, 1977). In Zimbabwe departures were 7-9 April (Borret, 1968; Tree, 1989, 1995). There is strong evidence of fidelity for non-breeding sites (Loske and Lederer, 1988; Maclean, 1993; Safring, unpubl. data 2010). Recoveries include four in Finland (Hunter and Hunter, 1970; Reed and Wells, 1957); one in Sweden (Underhill, 1994) and one in Britain (Tarboton et al., 1987; Underhill and Oatley, 1994).

Subspecies	Distribution	Breeding
<i>P.t. yakutensis</i>	To s Africa from e Asia (Curry-Lindahl, 1981); comprises 14.1% of the population in the sub-region, with likely concentration in e portion of South Africa (Clancey, 1970; Irwin, 1981)	Breeds e Siberia, from Taimyr Peninsula e to Anadyrland; from Ireland e & n through Europe to Russia & Ukraine (Snow & Perrins, 1998)
<i>P.t. acredula</i>	Winters e & s Africa, w to Cameroon and w to DRC; most common (54.7%)	Norway, n & s Sweden, ne Europe & Russia, e to Yenesei R
<i>P.t. trochilus</i>	Winters in w Africa, w to Cameroon (Urban et al., 1997); occurs at intermediate abundance (31.2%); Blaber (1986) reports <i>P.t. trochilus</i> as most common in Natal although Urban et al. (1997) note that it is unlikely in s Africa	Europe n to Sweden, e to s Poland & Romania (Urban et al., 1997)

Table 3. Distribution and breeding range of three subspecies of Willow Warbler *Phylloscopus trochilus* that are currently recognised (Dean, 2005) although difficult to identify (Svensson, 1992). All three are reported to winter in southern Africa (Clancey, 1970).

Five sub-species of Spotted Flycatcher are presently recognised (Table 4; Figure 7b; Clancey, 1980; Clancey et al., 1987; Johnson, 2005). In southern Africa *M.s. striata* is widespread and in Zimbabwe *M.s. neumanni* is most abundant (Benson et al., 1971). *M.s. balearica* is recorded in Damaraland, Namibia (Clancey, 1980), *M.s. sarudnyi* likely occurs in most of eastern southern Africa, and *M.s. inexpecta* is known in southern Africa from one moulting bird collected at Montclair, KwaZulu-Natal (31 Jan) (Clancey et al., 1987).

Subspecies	Distribution	Breeding
<i>M.s. striata</i>	Widespread in s Africa	Breeds w Europe e to w Siberia
<i>M. s. neumanni</i>	Massailand, n Tanzania, widespread in s Africa, most abundant subsp. in Zimbabwe (Benson et al., 1971)	Breeds e Mediterranean to Iran & w Siberia
<i>M. s. balearica</i>	Mallorca, Balearic Is, recorded Damaraland, Namibia (Clancey, 1980)	Breeds Balearic Island, w. Mediterranean
<i>M. s. sarudnyi</i>	e Iran & Transcapia; prob most in e of s Africa	Breeds Kazakhstan, s to e Iran
<i>M.s. inexpecta</i>	Tamak, Crimea, s Europe & Russia, known in s Africa from 1 moulting bird, collected 31 Jan (Montclair, KwaZulu-Natal; Clancey et al., 1987)	Breeds Crimean Peninsula

Table 4. Distribution and breeding range of the five subspecies of Spotted Flycatcher *Muscicapa striata* that are currently recognized (Clancey, 1980; Clancey et al., 1987).



(a)



(b)



(c)

Fig. 7. a. Willow Warbler *Phylloscopus trochilus* demonstrating new feathers moulted prior to migration north (Pretoria, 01 April; 25°46'33"S, 28°11'54"E, ~1,250m a.s.l.), b. Spotted Flycatcher *Muscicapa striata* (Pretoria, 01 April), c. Convergent moult in primary feathers of Spotted Flycatcher; arrow indicates primary feather moult direction, note three newly grown feathers (Colenso, KwaZulu-Natal, South Africa, 09 January; 28°41'21"S, 29°44'59"E, ~1,180m a.s.l.). Photographs: a. Graham Grieve; b & c. Craig Symes.

Although neither species are reported under threat in southern Africa (Herremans, 1997a,b) the Spotted Flycatcher has declined rapidly and consistently in the UK since the 1960's (Baillie et al., 2005) with a decrease by 81% over the past 25 years (Baillie et al., 2008). Decreasing numbers may have been caused by deteriorating habitats, or by conditions on wintering grounds or along migration routes (Vanhinsbergh et al., 2003). Very little is known on the migratory origins of these species although low recovery rates of ringed birds have added to our knowledge of movements. In southern Africa there is still debate concerning the origins of many migrating birds and although individuals are known to show strong site fidelity little is known of population movements. Therefore, the opportunity exists to use stable isotopes to understand aspects of the migration biology, from an austral perspective, of two species in which the moult cycle is fairly well known. A growing network of bird ringers in South Africa have the potential to contribute to a comprehensive study. The Spotted Flycatcher moults body plumage on its breeding grounds during July-September (Craig, 1983) so old body plumage feathers can be collected for analysis. Spotted Flycatchers have a convergent primary moult (Williamson, 1972) that is sometimes irregularly started before migration south, but suspended during migration (Figure 7c; Cramp and Perrins, 1993). Most birds, however, have a complete flight feather moult in Africa (Ginn and Mellville, 1983). An old flight feather can therefore also be collected for comparative purposes with body plumage feathers. The Willow Warbler, unlike many other migrating passerines, undergoes a complete moult twice a year, one in Africa and one in Europe (Ginn and Melville, 1983; Jenni et al., 1994; Hedenström et al., 1995). A primary flight feather can thus be collected from Willow Warblers caught across southern Africa. Old feathers, grown in Europe, will likely represent the isotopic environment from which they originated. Collecting a primary feather that is moulted later in the season (just prior to migrating) is likely to be more representative since the bird will have spent longer at that particular site and other body tissues (e.g. endogenous reserves that may contribute to feather production) will have had longer to equilibrate isotopically with the environment.

These three species accounts provide detailed information on the potential for migratory studies using stable isotopes, and offer insight into further research on many other species, for example African Hoopoe *Upupa africana*, Yellow-billed Kite *Milvus aegyptius*, Steppe Buzzard *Buteo vulpinus* and Red-backed Shrike *Lanius collurio*, to name a few.

5.4 The way forward – An armoury of research tools

Stable isotopes can transform the way we do science. Ultimately, multiple isotope approaches may be more powerful (Hobson, 1999; Hobson, 2011) and statistical methods may aid interpretation of complex and confusing stable isotope datasets (Inger and Bearhop, 2008). Elements other than C, N, O, and H which are known to show isotopic patterns can be incorporated into stable isotope analysis (Hobson, 2005). Furthermore, isotopic base maps can be combined with additional non-isotopic layers e.g. biome coverage maps that are relevant to the species under consideration (Hobson, 2005). The use of stable isotopes in ornithology, and in general, is often criticised. However, the difficulties and problems that stable isotope analysis may pose can be overcome by dealing with the inherent uncertainty, applying it only to situations where it is useful, using it in addition to other more traditional

methods like observation and faecal analysis, performing more controlled experiments to lay the foundation for interpretations, furthering the development of theory, and encouraging a more trans-disciplinary approach to ornithology that incorporates biology, chemistry and earth sciences (Kimura et al., 2002; Rubenstein and Hobson, 2004; Inger and Bearhop, 2008; Hobson, 2011).

The use of δD , $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$ and other stable isotopes in ornithology is in its relative infancy, and many more comprehensive studies and laboratory experiments are needed to fully realise the potential in this field of science. The use of a method that is as far reaching as birds travel can be applied reliably and non-destructively at a relatively low cost to contribute to the survival of birds in a rapidly changing world (Simmons et al., 2004; Gordo, 2007; Both and Malverde, 2007).

6. Acknowledgments

Katie Roller is thanked for her input in the preparation of this chapter, and Sam Scott for editorial assistance. Graham Grieve is thanked for the use of his Willow Warbler photograph. Dr John Vogel and Dr Siep Talma (Council for Scientific and Industrial Research, Pretoria) are thanked for providing raw data on stable isotopes in aloes. Numerous colleagues and friends are thanked for their support and academic input over the few years in which I have been involved in stable isotope research; including Dr Stephan Woodborne (CSIR, Pretoria), Prof. Andrew McKechnie (University of Pretoria) and Prof. Sue Nicolson (University of Pretoria).

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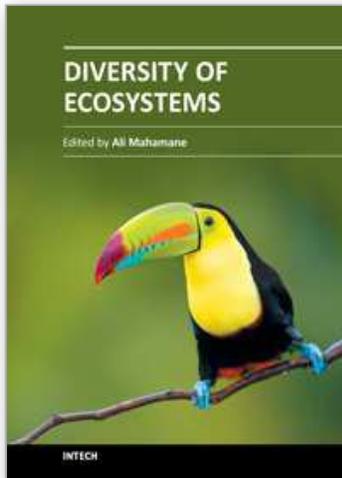
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Diversity of Ecosystems

Edited by Prof. Mahamane Ali

ISBN 978-953-51-0572-5

Hard cover, 484 pages

Publisher InTech

Published online 27, April, 2012

Published in print edition April, 2012

The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Craig T. Symes (2012). Stable Isotope Research in Southern African Birds, Diversity of Ecosystems, Prof. Mahamane Ali (Ed.), ISBN: 978-953-51-0572-5, InTech, Available from:

<http://www.intechopen.com/books/diversity-of-ecosystems/stable-isotope-research-in-southern-african-birds>

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