Using stable isotopes to trace the movements of ducks in southern Africa

Candidate: Gregory Lilgee Mutumi
Supervisor: Graeme Cumming

Thesis presented for the degree of Master of Science in the Department of Zoology, University of Cape Town. August 2010

Two roads diverged in a wood, and I took the one less travelled by, and that has made all the difference. ‘Robert Frost’

Contents

	Page
GENERAL ABSTRACT……..	1
GENERAL INTRODUCTION……..	3
Stable isotopes in movement ecology studies……...	3
Feather Moult in Ducks and isotope signature integration from the environment...	7
Objectives and hypotheses of the study……	10
Literature cited……..	13
STUDY SITES, MATERIALS AND METHODS	
Study sites…….	16
Barberspan, South Africa (BAR)……..	16
Strandfontein, South Africa (STR)……...	17
Manyame catchment, Zimbabwe (MAN)…….	18
Lake Ngami, Botswana (NGA)……	19
Lake Chuali, Mozambique (CHU)……	19
Study Species……	20
Collection of feather samples……...	20
Sample selection for Isotope Analysis……...	21
Pre-treatment of samples for δ^{15}N and δ^{13}C analysis……	22
Feather isotope analysis…….	23
Expected outcome…….	25
Limitations of the study…….	27
Literature cited……...	27
CHAPTER 1: FEATHER STABLE ISOTOPES DISTINGUISH SOME SOUTHERN AFRICAN DUCKS FROM DIFFERENT MOULTING LOCATIONS	
Abstract……..	30
Introduction……	30
Methods…….	32
Results……..	33
Site differences…….	34
Seasonal differences…….	37
Annual differences……	38
Discussion……..	41
Between site differences in isotope signatures…….	41
Seasonal differences in isotopic signatures……..	44
Between year differences in isotopic signatures……...	44
Deuterium…….	45
Conclusions……	46
Literature cited……...	47
CHAPTER 2: CAN FEATHER STABLE ISOTOPES REVEAL DIFFERING MOBILITY AMONG SOUTHERN AFRICAN DUCKS?	
Abstract……..	52

Introduction…… 53
Methods…… 55
Results…… 57
Discussion…….. 61
Spatial variations in isotope signature distinctions……... 62
Temporal isotope signature variations…….. 62
Inter-species variations in feather isotope distinctions……. 63
Inter-individual variations……. 64
Mobility…… 64
Conclusions……..... 66
Literature cited……... 67

CHAPTER 3: USING STABLE ISOTOPES TO STUDY THE FORAGING ECOLOGY OF DUCKS IN SOUTHERN AFRICA
Abstract…….. 70
Introduction…… 71
Methods……. 73
Results…… 74
Inter-species Comparisons…… 76
Inter-individual Comparisons……... 77
Discussion…….. 87
Inter-species isotope signature patterns…… 88
Inter-individual Isotope signature patterns……... 88
Temporal signature patterns…….. 90
Conclusions…… 90
Literature cited……... 91

SYNTHESIS…….. 94
Literature cited……... 98

AKNOWLEDGEMENTS……. 99

Appendix 1: Ecology of some of the study species……... 100
Appendix 2: Ducks present at each site during the research……. 102
Appendix 3: Capture across the five study sites during different years…… 106
Appendix 4: Descriptive statistics for chapter 1…… 110
Appendix 5: Descriptive statistics for chapter 2…… 115
Appendix 6: Descriptive statistics for chapter 3…… 118
Appendix 7: Paired t-test results…… 124
Appendix 8: Turkey-type multiple comparisons test for differences among variances……..... 126
Appendix 9: Inter-individual isotopic variances per species, site, season and year….. 129

Using stable isotopes to trace the movements of ducks in southern Africa

G. L. Mutumi, MSc Zoology, University of Cape Town, August 2010

GENERAL ABSTRACT

Despite the importance of movement ecology studies, the field faces a prevailing challenge of methodological limitations in tracking individual organisms. This research investigated the utility of the stable isotope technique to trace movements of ducks in southern Africa. I sampled and analysed feathers of ten duck species for stable isotope proportions of Carbon (δ^{13}C), Nitrogen (δ^{15}N) and Hydrogen (δD), from five wetlands (Strandfontein and Barberspan in South Africa, the Manyame catchment in Zimbabwe, Lake Chuali in Mozambique, and Lake Ngami in Botswana) as test cases.

Sampling was carried out at different seasons to account for seasonal isotope signature variations. Isotope signatures of feathers grown at different moulting locations were compared to test whether southern Africa shows stable isotope spatial patterns (distinct isotopic regions). Feathers grown at different life-phases were compared to test whether different sites had been used and if more mobile species showed more and stronger isotope distinctions. Finally, growing flight feathers grown at moulting locations were compared across species to query how much information on diet and foraging behaviour can be inferred from southern African duck feather stable isotopes.

Feather isotope signatures were distinct by site in at least one of the tested isotopes, for the majority of ducks tested. Strandfontein had more and stronger distinctions of isotope signatures between feathers grown at different life phases. This site is the closest to the sea and most likely to have marine-influenced isotope signatures especially in δ^{15}N, it falls within the Mediterranean climatic conditions experiencing winter rainfall unlike all the other sites. Vegetation compositions (C_3 and C_4 plant distributions) therefore vary across sites influencing δ^{13}C patterns. More mobile species (only Egyptian Goose *Alopochen aegyptiacus* from Strandfontein, and Cape Shoveler *Anas smithii* from Barberspan; determined by mobility scores from other studies) had more and stronger distinctions between flight and body feathers. All the other species did not comply with mobility scores. They showed weaker and fewer tissue signature distinctions than their mobility scores suggested. There were high isotopic signature overlaps in δ^{13}C and δ^{15}N across and within feeding guilds at

each moulting site implying dietary overlaps during moulting. More overlaps occurred during the dry seasons (summer in Strandfontein and winter in Lake Chuali, Manyame catchment site, and Lake Ngami). Higher isotopic variances (higher dietary flexibility) were associated with isotope signature divergence to mobility scores especially in Cape Teals and Yellow-billed Ducks.

The isotope technique is flawed with uncontrollable sources of variation which potentially confound movement inferences. It is best used when accompanied by conventional methods to detect and counter against species specific biology and dietary behaviour imposed biases in tissue isotope signatures. Further research on how species specific biological processes affect the reflection of spatial patterns of isotopes in feathers is recommended. Multi-isotope time explicit approaches and trace element analysis were also recommended. Scientists should be wary about basing management strategies or building theory about movement patterns of species based on the technique at least in stochastic environments such as southern Africa. My results provide empirical evidence that the technique is unreliable at this scale of analysis. In particular, the majority of ducks in this region are not good candidates for use of isotopic signatures in distinguishing movement patterns of southern African ducks.

GENERAL INTRODUCTION

Stable isotopes in movement ecology studies

The study of movement is a central theme in ecology but has only recently been recognized as a sub-discipline and an 'emerging paradigm' in its own right (Nathan 2008). For many organisms, survival and reproduction are strongly dependent on movement; and dispersal capability at different scales can have profound influences on the demography of mobile species (Erwin 2002; Nathan 2008).

Ducks exploit a wide range of geographic and climatic conditions by employing a variety of flexible movement and foraging behaviours (Todd 1996). Duck species may use a variety of wetlands and/or a suite of habitats within a given wetland for different activities (e.g., breeding, foraging, roosting and moulting). In south east Asia, Greenland and Iceland, ducks are migratory, using sites separated by over 4000km (Scott and Rose 1996). On Africa's offshore islands they are mainly sedentary (Scott and Rose 1996). Within Africa, duck movements are best described as nomadic; their annual movements vary from a few hundred metres to over a thousand kilometres depending on the availability of forage and wetlands (Hockey et al. 2005). Movements are complex and difficult to predict, partly because they are influenced by the availability of resources, which in southern Africa are relatively unpredictable in comparison to northern temperate environments (Scott and Rose 1996).

The analysis of the movement patterns of southern African ducks presents a methodological challenge. Bird counts and atlasing efforts are inadequate data sources from which to draw strong inferences about movement (Hobson and Wassenaar 2004; Thomas 2008). Ringing data from southern Africa (Harrison et al. 1997; Underhill et al 1999) are insufficient to document detailed movement patterns because of scarce returns and biases in ringing sites and sampling effort (Thomas 2008). Satellite telemetry is an alternative approach to studying movement, but it is expensive and the cost limits the number of individuals that can be tracked. It is therefore important for our understanding of waterbird ecology that alternative approaches to documenting and analysing movements are developed. Stable isotope techniques, the focus of this thesis, offer a potential solution. They have the benefits that they are cheaper and less invasive than tagging alternatives and are not dependent on recaptures (Wassenaar and Hobson 1998; Wassenaar and Hobson 2001; Hobson 2005).

Isotopes are elements that have the same number of protons but differ in their number of neutrons. These different forms of an element have different atomic masses. Isotopes that do not undergo radioactive decay are called stable isotopes (Hobson and Wassenaar 2008; West et al 2010). Biogenic substances in nature contain significant amounts of isotopes of light elements such as Hydrogen, Oxygen, Carbon, Nitrogen and Sulphur. For example Carbon predominantly exists in two forms, Carbon of atomic mass 13 (^{13}C) and Carbon of atomic mass 12 (^{12}C). The difference in the abundance of the two forms expressed as a ratio of the rare (the heavier) to the common (the lighter) is represented by 'δ' (e.g. $\delta^{13}C$) and is reported in units of parts per thousand (‰; West et al. 2010). During nutrition uptake processes (ingestion, digestion, assimilation and excretion), the heavier isotopes are preferentially retained over the lighter form of elements (Inger and Bearhop 2008). Hence organisms higher on the trophic ladder accumulate higher stable isotope proportions than those of lower trophic rank. This is termed trophic isotope enrichment (Hobson 2005; Quillfeldt et al. 2005). On a global scale, owing to seasonality and differences in altitude and latitude, isotopes are globally dispersed in distinguishable patterns as a result of spatial variation in isotope fractionation processes.

Isotope-based movement studies are dependent on the existence of such patterns (Hobson et al. 1999; Hebert and Wassenaar 2001). Spatial and temporal differences in isotopic ratios are reflected in animal tissues (Hobson et al. 1999). An essential premise in using stable isotopes in movement studies is that predictable spatial patterns exist among isotopes in the environment and that study species do not introduce huge or unpredictable variations in isotopic ratios during nutrient uptake processes (Hobson 2008).

For instance (Table 1 and 2), the abundance of Carbon isotopes is mainly influenced by the photosynthetic pathway used by the primary producers in a particular ecosystem. Three pathways exist, Calvin (C_3), Hatch-Slack (C_4) and Crassulacean Acid Metabolism (CAM; Hobson 2005). In the C_3 pathway, plants incorporate atmospheric CO_2 by carboxylation of Ribulose Biphosphate (RuBP) producing first a three-Carbon molecule. C_4 plants use the Hatch Slack pathway and incorporate CO_2 by carboxylation of Phosphoenol pyruvate (PEP) producing initially a four-Carbon molecule. The enzymes involved (RuBP-carboxykinase and PEP-carboxykinase respectively) discriminate differently towards ^{13}C in the two pathways resulting in C_3 based systems' $\delta^{13}C$ ranging from -32 to -20‰ and C_4 from -14 to -9‰. CAM plants have an intermediate range from -34 to -11 because they can shift their major site of CO_2 via the PEP or RuBP carboxykinases in response to environmental

conditions (O'Leary 1981; Ehleringer and Rundell 1989). $\delta^{13}C$ increases from C_3 to C_4, and from C_3 to CAM based ecosystems, and decreases from C_4 to CAM based ecosystems (Hobson 1999; Kelly 2000; Rubenstein and Hobson 2004).

This study offers a first assessment of the value of stable isotope methods for tracking the movements of southern African waterbirds, focusing on the *Anatidae* (ducks and geese). Some ducks offer an interesting test case because they lose all their flight feathers at the same time and re-grow them in a single location, thereby experiencing a flightless moult (Todd 1996; Hockey et al. 2005). Isotope signatures in growing flight feathers are taken from the moulting site. Because different sites may be used for breeding and moulting (Todd 1996), comparisons of isotope signatures of tissues grown during different life phases can yield information on whether diverse sites have been used and on the variation of mobility across species; if the area has distinct isotopic regions (Hobson 2005).

Ten duck species occurring in southern Africa, from three different feeding guilds were selected for the study. Yellow-billed Duck (*Anas undulata*), Cape Teal (*Anas capensis)*, Hottentot Teal (*Anas hottentota*), Red-billed Teal (*Anas erythrorhyncha)* and Cape Shoveler (*Anas smithii*) are predominantly water surface feeders. They forage by dabbling, sieving and up-ending (Owen and Black 1990; Baldassarre and Bolen 2006). The African Pygmy Goose (*Nettapus auritas*), forages by diving and feeding under water. Egyptian Goose (*Alopochen aegyptiacus),* Spur-winged Goose (*Plectropterus gambensis*) and White-faced Duck (*Dendrocygna viduata)* feed mostly on land by grazing. South African Shelduck (*Tadorna cana*) feeds mainly on algae, aquatic invertebrates and occasionally on crops (Geldenhuys 1977). Appendix 1 contrasts the ecological traits of some of the ducks in this study. It can be seen that their feeding habits are flexible across guilds and depend on the availability of resources (Ogilvie & Pearson 1994). For example, even though the Egyptian Goose is predominantly a grazer, it sometimes dabbles when the land is arid. I considered ducks from different feeding guilds because stable isotope signatures should be incorporated from diet, assuming that different dietary items contain different stable isotope proportions (Swap et al. 2004).

Table 1: Processes that influence stable isotope patterns in the environment (adapted from Rubenstein and Hobson 2004).

Stable Isotope	Processes That Influence Isotope Abundance		Natural Environmental Patterns		
	Biological and/or biogeochemical	*Anthropogenic*	*Terrestrial*	*Terrestrial versus Marine*	*Marine*
δ^{13}C	Vary in plant tissue with: • Isotopic fractionation during photosynthesis in C_3, C_4 and CAM species[a] • Ambient conditions that limit enzymatic reactions during photosynthesis or alter stomatal opening	Agricultural crops (i.e. C_4 based) in natural (i.e. C_3 based) atmospheric or aquatic point source pollution.	Decreases with increasing latitude [b,c] Increases with altitude [b] Mesic habitats more enriched than xeric in C_3 based systems [d]	Marine more enriched compared to terrestrial [f]	Decreases with increasing latitude [b,c] Northern oceans more enriched than southern oceans [e] Benthic more enriched than pelagic [e]
δ^{15}N	Vary in plant tissue according to how plants fix N: • Symbiotic fixation • Direct conversion of atmospheric N	Agricultural origin e.g. fertilizer Land use practices that result in ammonification or the differential loss of ^{14}N	Xeric habitats more enriched than mesic habitats	Marine more enriched compared to terrestrial [g]	Northern oceans more enriched than southern oceans [h]

a – because plants use different types of photosynthetic pathways (C3 or C4 or CAM that utilise different CO2 fixing enzymes and result in varying ranges of δ13C values

b- Mainly due to temperature differences

c- Determined by differences in abundance of C4 plants

d- Owing to difference in water use efficiency

e- Because of temperature differences, surface water CO2 concentrations and differences in plankton biosynthesis or metabolism

f- Owing to bi-carbonate as a Carbon source and slower diffusion of CO2 in marine environment

g- Owing to the age of bed rock (and thus decay rate of the isotope)

h- Reasons are unclear

Table 2: Trends in stable isotope distribution (after Hobson 2005)

Contrast	Isotope pattern
C_3 to C_4, C_3 to CAM	$\delta^{13}C$ increases
C_4 to CAM	δD increases
Terrestrial to marine	$\delta^{13}C$ $\delta^{15}N$ $\delta^{34}S$ δD $\delta^{18}O$ increases
Benthic to pelagic	$\delta^{13}C$, $\delta^{34}S$ decreases
Xeric to mesic	$\delta^{13}C$, $\delta^{15}N$ decreases
Increase in altitude	$\delta^{13}C$ increases, but δD and $\delta^{18}O$ decreases.
Canopied to open forest or agriculture	$\delta^{13}C$, $\delta^{15}N$ increases
Older soils to younger soils	$\delta^{87}Sr$ decreases
Anthropogenic inputs to background	$\delta^{13}C$, $\delta^{15}N$ $\delta^{34}S$ δD $\delta^{18}O$ varies
Latitudinal effects	$\delta^{13}C$ decreases with increasing lattitude

Feather Moult in Ducks and isotope signature integration from the environment

For a bird to maintain flight, heat insulation and waterproofing, worn out feathers have to be replaced through the process of moulting. As a rule, each feather is replaced once a year (Todd 1996). Moulting may be induced by changes in photo-period, temperature, food availability, rainfall, or disturbance (Kear 2005). It is an energetically and nutritionally demanding process (feathers make up 25% of body protein) and thus timed to coincide with seasons of food abundance (Todd 1996). Moult timing might be also influenced by mating requirements and brood rearing duties. Males may need to look attractive to females (i.e., with fresh plumage) during breeding season and females may delay moulting in order to first replenish reserves used during breeding (Hockey et al. 2005).

Timing of moult can be highly flexible for birds living in areas with dynamic weather patterns that show a high level of variation in resource availability (Baldassarre and Bolen 2006). Southern African ducks therefore display spatial and temporal variability in timing of moult (Table 3) and this allows for spatial and temporal comparisons of isotope signatures.

Several authors have highlighted the primary dependence of feather moult on foraged food rather than stored nutrients (Kear 2005; Moorman et al 1993; Ankney 1984) because of the timing and duration of moult. Additionally, Baldassarre and Bolen (2006) attributed declining body mass (during flightless moult) to mobilisation of stored lipids to meet

everyday energy requirements, so that most of the proteins acquired in diet are channelled to feather synthesis. Southern African ducks arrive at the moulting grounds and become flightless approximately a week before dropping feathers; feathers are worn out and the root weakens as the moulting process is initiated (Ogilvie and Pearson 1994; Baldassarre and Bolen 2006; Ndlovu et al. 2010). Exploitation of food reserves commences before moulting thus increasing the dependence on foraged food from the moulting grounds as feather growth begins. It is also documented for instance that Egyptian Geese do not store fat prior to moulting like northern hemisphere ducks (Ndlovu et al. 2010). Southern hemisphere ducks exhibit phenotypic flexibility to hasten feather growth and to shorten the flightless period. In particular, the gizzard muscles actually increase in order to maximise nutrient extraction from the poor moulting diet (Ndlovu et al. 2010). Additionally the cost of moulting is composed of several energy requirements (King 1981): 1) energy content of the feathers, 2) costs of biosynthesis of feather materials, 3) heat loss due to decreased insulation during the moulting period. The process often results in a 25% loss of the bird's lean dry mass, which is then regenerated over a period of days to weeks as the moult progresses (King 1981). Dry waterfowl feathers are about 86% protein. Large amounts of sulphur amino acids, mainly cystine, are required for the production of keratin, the protein constituent of feathers. The net energetic efficiency of feather synthesis is only 6.4% (Ringelman 1990). Combination of low conversion efficiency, overall high protein demand and specific amino acid requirements causes moult to be nutritionally and energetically costly. There is a primary dependence on foods, although internal reserves provide a buffer against periods of high protein demand or food shortage (Ringelman 1990). It is reasonable to conclude that energy reserves' contribution to the isotopic composition of feathers in southern African ducks is negligible. However, further research is necessary to verify this assumption.

Table 3: Timing of moult in southern African ducks (*based on information from Hockey et al. 2005*)

Species	Peak Moulting Period	Weight Loss	Duration
Egyptian Goose	Wing moult recorded all months in South Africa predominantly March-October. Peak April to Aug in Barberspan (BAR) & Vogelvlei, S.A	Weight decreases by 19-25%	Takes 40 days to replace flight feathers. Open undisturbed sites close to crop fields and grasslands chosen.
Red-billed Teal	Moults during and after breeding. In Zimbabwe, June-July (n=45), in Northwest Province of S.A, in Feb-Nov, with 90% in June-August & in Western Cape, March-Sept.	25% of weight is lost Takes 1-3 days shedding feathers timing of moult varies spatially	28 days growth replacement, 70-80% grown feathers can fly.
Yellow-billed Duck	3-4 months after breeding peak,		27-37 days to re-grow flight feathers Becomes flightless at 4 to 8 days before feathers are dropped.
White-faced Duck	Wing moult timing varies spatially. Coldest months avoided		
Cape Teal	Complete post breeding moult, timing varies from year to year according to breeding activity. Summer moulting peak (BAR) In KZN, Nov, in Zimbabwe Sept		Takes 22-23 days to re-grow flight feathers.
South African Shelduck	Mid-summer (late October-end Feb, mainly Nov-Dec in S.A. Remiges shed over 1-6 days.	25- 30% weight is lost	Takes 28-40 days flightless
Hottentot Teal	Moulting peaks in Feb to May. Also moults in September to November in Botswana		

African Pygmy Goose			28 days flightless
Spur-winged Goose	Annual wing moult in winter (93% of birds at Barberspan, May-July). I week to lose remiges,	20% of initial body mass lost.	7 weeks flightless
Cape Shoveler	In NW Province of S.A mainly April-June, and Oct –Jan (either side of breeding peak Jul-Sept). In Western Cape, July to December, Oct-Nov post breeding peak		Takes 29-35 days to re-grow flight feathers.

KZN = Kwazulu Natal (Durban)

BAR = Barberspan

S.A = South Africa

Objectives and hypotheses of the study

Recent studies have revealed variations of stable isotope patterns with season, location, species and years; animal tissue of known origin can only be used as a proxy of the site's signature with careful consideration of these sources of variation (Wunder et al. 2005; Langin et al. 2007; Rocque et al. 2009). In order to test the feasibility of the stable isotope technique in southern Africa, feathers from 10 duck species were sampled from five different wetlands and analysed for stable isotope proportions, ^{15}Nitrogen : ^{14}Nitrogen (δ^{15}N), ^{13}Carbon : ^{12}Carbon (δ^{13}C) and Deuterium : Hydrogen (δD). Sampling was carried out across different seasons and years (2007 to 2009) to test for temporal variation. The data were analysed to answer three key questions.

(1) To determine whether distinct 'isotopic regions' exist within southern Africa.

Growing flight feather isotope signatures (δ^{13}C, δ^{15}N and δD) were compared across three different sites (Strandfontein, Barberspan, and Manyame catchment) by species to address three fundamental questions:

- Do feather signatures from different sites show consistent variation to distinguish birds from different locations?
- Does the isotopic signature of duck feathers vary with season?
- Does the isotopic signature differ across years?

(2) To investigate whether different sites were used during different life-phases.

Body feathers from moulting and non-moulting ducks i.e., growing flight feathers from moulting ducks, and fully grown flight feathers from non-moulting ducks were analysed for $\delta^{13}C$, $\delta^{15}N$ and δD and the signatures were compared with body feathers. The data were used to address two questions,

- Do local populations of more mobile species show greater signature variation than less mobile species in feathers grown during different life-stages?
- Does this variation change across study sites.

(3) To compare diet and foraging behaviour across species.

Growing feathers were analysed for $\delta^{13}C$, $\delta^{15}N$ and δD and these isotope signatures were compared across different species at each moulting site. Three questions were addressed,

- Is there convergence in diet during moulting?
- Do different individuals of the same species show variation in isotopic signature?
- At different times of the year, do intra and inter-species signature variations change?'

Moulting of flight feathers in ducks is synchronous. This means that all flight feathers are lost and regrown at a fixed location, the moulting site (Hockey et al. 2005). Growing feathers (which are not capable of carrying the duck in flight) were therefore analysed and used as proxies to the moulting site signature. Feather stable isotopes were compared across three different sites by species, year and season of moulting. As a standard, the second secondary feather (S2) was used throughout the study for the flight feather. δD was run for a selected few Egyptian Goose and Red-billed Teal feather samples because it was three times more costly than $\delta^{13}C$ and $\delta^{15}N$ combined.

Since chapter one addressed the question of whether the sites belonged to isotopically distinct regions, I selected those species occurring over more than one site and used only freshly grown feathers. Not all of the sampled species were captured from two or more sites, I selected feathers from Egyptian Geese, Red-billed Teals, Yellow-billed Ducks, and Cape Teals. These birds came from three sites: Strandfontein, Barberspan, and the Manyame catchment. South African Shelducks and White-faced Ducks from single sites were included to give a stronger case for seasonal comparisons.

Chapter two then compared flight feathers locally grown at each moulting site (growing S2) and fully grown flight feathers (fully grown S2) of unknown moulting origin against body feathers (back feather) grown at unknown breeding sites. I used samples from 7 southern African ducks (Egyptian Geese from Strandfontein and Barberspan, Spur-winged Geese from Strandfontein and Barberspan, Red-billed Teals from Lake Ngami; South African Shelducks, Cape Shovelers, Yellow-billed Ducks, and Cape Teals from Barberspan). The main aim was to test whether different diets and/or sites had been used for different life phases. Patterns of isotopes $\delta^{13}C$, $\delta^{15}N$ and δD in the environment respond to latitude, vegetation composition, and precipitation; consequently, these characteristics differ from one site to another. Ducks using more distinct sites at different life stages should show more or stronger isotope signature distinctions between different feathers (Bearhop et al. 2004). I used mobility scores generated in other studies (Cumming et al. 2008) to verify through comparative means how reliably the isotope technique could detect differing mobility among southern African ducks.

Even though chapter two showed possible movement patterns implied by isotope signatures, there still remained the question of whether the observed variation was predominantly related to movements and use of different sites. This is because diet and foraging habits as well as intra and inter-individual variations in isotope assimilation rates modify signature patterns reflected in feathers (Weimerskirch et al. 2009). Chapter three queried the diet and foraging habits of ducks using feather isotope signatures in growing flight feathers. I compared inter-individual variation using $\delta^{13}C$ and $\delta^{15}N$ variances per species to separate generalist from specialist foragers. I also compared isotope signatures across different species (inter-species variation) to investigate dietary overlaps during moulting. Revisiting chapter one and two, I then compared diet and foraging behaviours to isotope-based site distinction and movement information. The aim was to relate diet and foraging behaviours shown in chapter three to how each species performed on the movement and site distinction tests in chapters one and two.

A comprehensive overview of the pros and cons of using the isotope technique in southern Africa is given in the synthesis chapter, incorporating recommendations for areas of future research needs.

Literature cited

Baldassarre, G.A., Bolen, E.G. 2006. *Waterfowl Ecology and Management*. New York: John Wiley and Sons.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology,* 73, 1007-1012.

Cumming, G.S., Hockey, P.A.R., Bruinzeel, L.W., Du Plessis, M.A. 2008. Wild bird movements and avian influenza risk mapping in southern Africa. *Ecology And Society*, 13, 26 [online] URL: http://www.ecologyandsociety.org/vol13/iss2/art26/

Ehleringer, J.R., Rundel, P.W. 1989. Stable isotopes: history, units, and instrumentation. In: Rundel, P.W., Ehleringer, J.R., Nagy, K.A. (eds). *Stable isotopes in ecological research*. pp. 1-15, New York: Springer-Verlag.

Erwin, R.M. 2002. Beyond the conventional integrated management of waterbirds. *International Journal of Waterbird Biology*, 25, 5-12.

Geldenhuys, J.N. 1977. Feeding habits of South African Shelduck. *South African Journal of Wildlife Research,* 7, 5-9.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremens, M., Tree, A.J., Parker, V., Brown, C.J. (eds). 1997. *The atlas of southern African birds.* Johannesburg: BirdLife South Africa.

Hebert, C.E., Wassenaar, L.I. 2001. Stable Nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environmental Science and Technology,* 35, 3482-3487.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia,* 120, 314-326.

Hobson, K.A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions,* 11, 157-164.

Hobson, K. A. 2008. Applying isotopic methods to tracking animal movements. In: Hobson, K.A. and Wassenaar L.I., (eds). *Tracking animal migration with stable isotopes*. pp. 45-78, London: Elsevier

Hobson, K.A., Wassenaar, L.L. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable Hydrogen isotopic analysis of feathers. *Oecologia,* 109, 142-148.

Hobson, K.A., Wassenaar, L.I. 2008. *Tracking Animal Migration Using Stable Isotopes*. London: Elsevier.

Hobson, K.A., Atwell, L., Wassenaar, L.I. 1999. Influence of drinking water and diet on the stable-Hydrogen isotope ratios of animal tissues. *Proceedings of the National Academy of Sciences of the United States of America,* 96, 8003-8006.

Hobson, K.A., Aubry, Y., Wassenaar, L.I. 2004. Migratory connectivity in Bicknell's Thrush: Locating missing populations with Hydrogen Isotopes. *Condor,* 106, 905-909.

Hockey, P.A.R., Dean, W.R.J., Ryan, P.G. (eds). 2005. *Roberts' birds of southern Africa*. Cape Town: Trustees of the John Voelcker Bird Book Fund.

Inger, R., Bearhop, S. 2008. Applications of stable isotope analyses to avian ecology. *Ibis*, 150, 447-461.

Kelly, J.F. 2000. Stable isotopes of Carbon and Nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, 78, 1-27.

Langin, L.M., Reudink, M.W., Marra, P.P., Norris, D.R., Kyser, T.K., Ratcliffe, L.M. 2007. Hydrogen isotopic variation in migratory bird tissues of known origin: implications for geographic assignment. *Oecologia,* 152, 449-457.

Nathan, R., 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19050-19051.

O'Leary, M.H. 1981. Carbon isotope fractionation in plants. *Phytochemistry,* 20, 553-568.

Ogilvie, M. and Pearson, B. 1994. *Wildfowl Behaviour Guide*, Melbourne: Hamlyn.

Owen, M., Black, J.M. 1990. *Waterfowl Ecology*. Glasgow: Blackie.

Pardo, L.H., Nadelhoffer, K.J. Using Nitrogen stable isotopes to assess terrestrial ecosystems at regional and global scales. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (eds). 2010. *Isoscapes: Understanding movement, pattern and process on Earth through isotope mapping*. London: Springer. pp 221-245

Quillfeldt, P., McGill, R. and Furness, R.W. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine Ecology Progress Series*, 295, 295-304.

Rocque, D.A., Ben-David, M., Barry, R.P., Winker, K. 2009. Wheatear moult and assignment tests: ongoing lessons in using stable isotopes to infer origins. *Journal of Ornithology*, 150, 931-934.

Rubenstein, D.R., Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution,* 19, 256-263

Scott, D.A., Rose. P.M. 1996. *Atlas of Anatidae populations in Africa and western Eurasia*. Wetlands International Publication No. 41. Wagenigen: Wetlands International.

Swap, R.J., Aranibar, J.N., Dowty, P.R., Gilhooly, W.P., Macko, S.A. 2004. Natural abundance of $\delta^{13}C$ and $\delta^{15}N$ in C_3 and C_4 vegetation of southern Africa: patterns and implications. *Global Change Biology*, 10, 350-358.

Thomas, H.L. 2008. (Unpubl. MSc Thesis, Univ. of Cape Town). Are current monitoring programs adequate to understand movements of African waterbirds?

Todd, F. 1996. *Natural history of the waterfowl*: California: San Diego Natural History Museum.

Underhill, L.G., Tree, A.J., Oschadleus, H.D., Parker, V. 1999. *Review of ring recoveries of waterbirds in southern Africa*, Cape Town: Avian Demography Unit, University of Cape Town.

Wassenaar, L.I., Hobson, K.A. 1998. Natal origins of migratory Monarch Butterflies at wintering colonies in Mexico: New isotopic evidence. *Proceedings of the National Academy of Sciences of the USA*, 95, 15436-15439.

Wassenaar, L.I., Hobson, K.A. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology*, 35, 1845-1850.

Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K., Aurioles, D. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Marine Ecology Progress Series*, 391, 267-278.

West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. 2010. *Isoscapes: Understanding movement, pattern, and process on earth through isoscape mapping*. London: Springer

Wunder, M.B., Kester. C.L., Knoff, F.L., Rye, R.O. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia,* 144, 607-617.

Study sites

As test cases, I sampled birds at five sites spread along a north-south gradient and falling within different vegetation biomes. The sites were between 1000 and 2500 kilometres apart (Fig. 1).

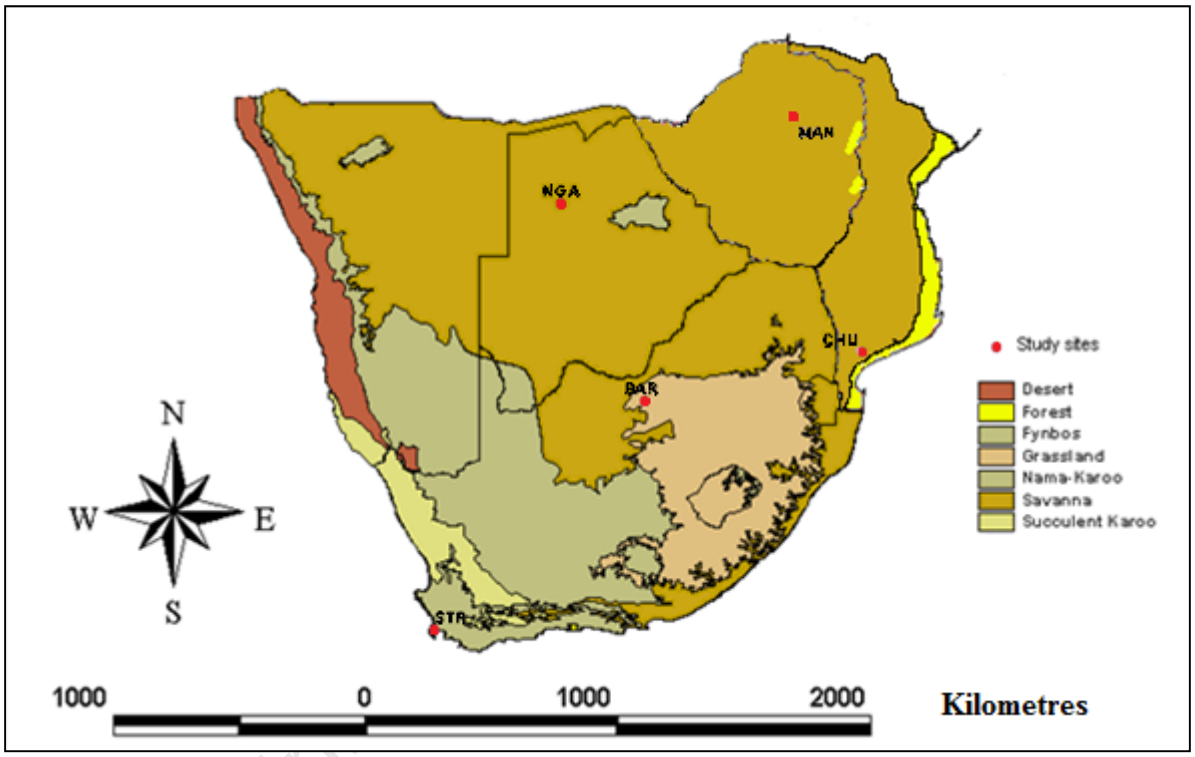


Figure 1: Map of southern Africa's vegetation biomes showing study sites Barberspan (BAR), Strandfontein (STR), Lake Ngami (NGA), Lake Chuali (CHU), Lakes Manyame and Chivero (MAN).

Barberspan, South Africa (BAR)

Barberspan is situated 15 km north-east of Delareyville in the North West Province of South Africa (26° 36′ S, 25° 36′ E). It is a 2 000 ha shallow (10 m maximum depth) alkaline lake and has a catchment of 30 km^2, receiving an average annual rainfall of 560 mm. Barberspan is connected by a narrow channel to Leeupan, a saline pan in the proximity (a kilometre to the north) with more variable water levels that dries up in most winters. Prior to 1913 Barberspan was perennial, after which a channel was dug to divert water from the Harts River to the pan.

During dry seasons (April to October) most surrounding small wetlands in the district dry up and birds move to the pan in large numbers. Most waterfowl in the district moult at the site. Barberspan supports over 20 000 individuals of 360 species of birds and was designated a wetland of international importance 'a RAMSAR site' by the Convention on Wetlands of International Importance in 1975. It hosts one of the largest Red-knobbed Coot *Fulica cristata* populations of any single water-body in South Africa (Cumming et al. 2011).

Vegetation composition is predominantly open flat grassland dominated by Rooigrass (*Themeda triandra*). Scattered shrubs of Bloubos (*Diospyros lycioides*), Buffalo Thorn (*Zizyphus mucronata*) and thickets of Sweet Thorn (*Acacia karoo*) are found in the site. Blue gums (*Eucalyptus globulus*) have been planted on various sites and have also become important roosting sites for birds in Barberspan (Taylor et al. 1999). Barberspan is located within an ecotone of three biomes. Agriculture is the main land use surrounding the site. Neighbouring farms have been predominantly cultivated for summer crops, such as maize, sunflowers, and groundnuts. However, about 60% of the area surrounding the pan consists of fully grown lands in various stages of succession.

During the study (2007-2009), the most abundant study species was the Egyptian Goose with an average relative abundance expressed in number of individuals per hectare per count of 432 ducks/ha, followed by Yellow-billed Ducks (191 ducks/ha), Spur-winged Geese (49 ducks/ha) and South African Shelducks (39 ducks/ha; appendix 2). Egyptian Geese and South African Shelducks were relatively more catchable than all the other duck species at this site (appendix 3). Other duck species counted were Cape Shovelers (24 ducks/ha), Cape Teals (26 ducks/ha), White faced Ducks (7 ducks/ha), and Hottentot Teals (1 ducks/ha; appendix 2).

Strandfontein, South Africa (STR)

Strandfontein (34° 05′ S, 18° 30′ E) is a wastewater treatment site in Cape Town of South Africa on the north edge of the False Bay at an altitude ranging from 0-20m. It is characterised by a system of shallow and deep treatment ponds once used to settle and remove *Escherichia coli* prior to release into the ocean. The ponds and their immediate surroundings offer a range of semi-natural habitats, including aquatic vegetation, grasses, and beds of invasive *Typha* reeds. The water bodies are characterised by algae and copepods on which birds forage (Kaletja-Summers et al. 2001; Birdlife International 2009, www.birdlife.org).

Strandfontein site is almost entirely man-made; before the sewage works was established, the site used to have a small temporary marsh Tamatievlei. By 1976 the marsh had been converted into 34 settling ponds covering over 306 ha and this has been gradually increased over time. A range of semi-natural habitats occur; deep and shallow open water, seasonal open ponds, canals, reed, rush and sedge beds, and vegetated shorelines and islands. The sewage works functions through algal decomposition using a large number of shallow ponds; this facilitates an abundance of algae and copepods, a favoured food source by many bird species (Birdlife International 2009, www.birdlife.org).

The Cape experiences Mediterranean climate characterised by winter rainfall (peaking in July) and a dry summer from November to March (Dallman 1998). It is also the most human-influenced among my study sites; being surrounded by suburban areas, with the Pelican Park to the east and Muizenberg to the west, as well as a landfill site in the north-west.

A total of 168 bird species have been recorded at Strandfontein among which 76 are fresh water wetland species and 18 are coastal species that visit the area to roost or breed; 45 species have been confirmed to breed at the site (Cumming et al. 2011). The proximity of the site to the coast and its diversity in wetland habitats facilitates bird diversity. Individuals have reached 23 200 between 1980-1990 and during extreme years the number can reach up to 30 000 (Birdlife International 2009, www.birdlife.org). During the study (2007-2009), the most abundant among study species were Cape Shovelers (436 ducks/ha), followed by Cape Teals (154 ducks/ha), and Red-billed Teals (83 ducks/ha; appendix 2). However, these species were less catchable than Egyptian Geese (77 ducks/ha). Other duck species counted were the Yellow-billed Ducks (59 ducks/ha), Spur-winged Geese (25 ducks/ha) and White-faced Ducks (0.5 ducks/ha; appendix 2).

Manyame catchment, Zimbabwe (MAN)

Lakes Chivero (17°54′ S 30°47′ E) and Manyame (17°49' S 30°36' E) taken as one study site Manyame catchment, lie to the west of the city of Harare in dry Miombo woodland. Lake Chivero covers an area of 65 km^2, and Lake Manyame covers 185 km^2. They are surrounded by a mosaic of agricultural fields, protected areas, and small human settlements. Manyame has more bird habitats for feeding because it has more beaches and shallows than Chivero. Lake Chivero is however more utilised as breeding and moulting habitat by waterfowl. Lake Chivero is the source of Harare's drinking water and was created for this purpose in 1952.

Both Lakes receive inflow from the Manyame River which falls in the Zambezi catchment. Manyame River is heavily polluted in places from sewage and industrial waste (Birdlife International 2009, www.birdlife.org; Cumming et al. 2011).

Water levels in both lakes fluctuate seasonally; the lakes fill up during summer (the rainy season) from December to March, and then decrease gradually across winter. Part of Lake Chivero is a protected area. Lake Manyame is surrounded by farms mostly utilised for tobacco and maize farming, as well as poultry and ostrich rearing (Cumming et al. 2011).

During the study, Red-billed Teals (347 ducks/ha) and White-faced Ducks (294 ducks/ha) were the most abundant species at this site. Egyptian Geese reached 32 ducks/ha even though they were the least catchable at this site (appendix 3). Other ducks counted were Spur-winged Geese (6 ducks/ha), Cape Shovelers (3 ducks/ha), Hottentot Teals (3 ducks/ha), African Pygmy Geese (3 ducks/ha), Cape Teals (1 ducks/ha; appendix 2).

Lake Ngami, Botswana (NGA)

Lake Ngami (20° 30′ S, 22° 40′ E) is one of the three (Makgadikgadi pans, Mababe pans, Lake Ngami) fault controlled sedimentary basins that lie at the distal end of the Okavango Delta. Lake Ngami is a dead-end channel receiving inflow from the Delta and surrounding seepage, reaching approximately10 km in length when full. It is in an arid/savannah, acacia dominated woodland mostly used as pasture land. The wetland shows seasonality, almost drying up during the dry season and filling up as rains resume. It has in the past dried up for several years (Burrough et al. 2007). Lake Ngami is used seasonally by large flocks of waterbirds and serves as an important resource rich habitat for waterbirds in the arid region of Botswana.

During the study, Red-billed Teals were most abundant (369 ducks/ha), followed by White-faced Ducks (50 ducks/ha) and Egyptian Geese (55 ducks/ha). Other ducks counted were Hottentot Teals (6 ducks/ha), African Pygmy Geese (5 ducks/ha), Yellow-billed Ducks (<0 ducks/ha), Cape Teals (<0 ducks/ha) and Spur-winged Geese (<0 ducks/ha; appendix 2). Duck catchability was low at this site (appendix 3). Birds were very timid and difficult to catch in large numbers using baited walk-in traps.

Lake Chuali, Mozambique (CHU)

Lake Chuali (15° 29' S, 30° 28' E) is in a mesic woodland surrounded by agricultural fields and sugar-cane plantations. It is a permanent, 28 km^2 wetland used to irrigate sugar

plantations 100 km north of Maputo (Cumming et al. 2011). Fishing, cattle ranging, agriculture and bird hunting are the main land-uses within and around the Lake. Spur-winged Geese and Red-knobbed Coots are mostly hunted for food; during sampling I encountered hunters carrying these species.

During the study (2007-2009), the most abundant species counted were White-faced Ducks (29 ducks/ha). Other ducks counted include the Red-billed Teals (7 ducks/ha), Spur-winged Geese (4 ducks/ha), Cape Shovelers (0.3 ducks/ha; appendix 2), Yellow-billed Ducks (0.2 ducks/ha), and Egyptian Geese (<0 ducks/ha). Duck captures were low at this site (appendix 3).

Study Species

I analysed samples from the ten southern African ducks for which we could obtain sufficient samples (White-faced Ducks*,* Egyptian Geese*,* South African Shelducks, Cape Teals, Yellow-billed Ducks, Hottentot Teals, African Pygmy Geese, Spur-winged Geese, Cape Shovelers and Red-billed Teals). Egyptian Geese and Spur-winged Geese are grazing ducks; the other species are dabbling ducks, although Cape Teal have comb-like serrations on the edges of their culmina and consume finer particulate matter than the others (Ogilvie and Pearson 1994).

Collection of feather samples

Standardised sampling was carried out at two monthly intervals in Barberspan, Strandfontein and Manyame catchment. In the more difficult to access sites (Lake Chuali and Lake Ngami), sampling was done at four monthly periods. At each site, between 12 and 16 points were selected and marked using a GPS system. This was done to fix capture and counting sites. All counting, trapping and water quality assessment was undertaken at these points. Baited walk in traps (2m by 2m) and duck mist-nets were used to capture birds at selected counting sites (at least 4 points) over a week. A 1-3 day habituation baiting phase (with the traps open and baited, allowing birds free access and feed) was carried out during each sampling mission, before capturing.

From the captured birds, morphometric measurements were taken (weight, wing length, head length and tarsal length). A total of 1 940 ducks was captured from the five study sites (appendix 3). I selected samples from 406 individual ducks for stable isotope

analysis (appendix 4, 5 and 6). Among these ducks, 371 were moulting (I collected growing flight feathers from these) and 135 were not moulting (I collected fully grown flight feathers from these). A total of 224 back feathers from randomly selected moulting (89) and non-moulting birds (135) were also analysed. This gave a total of 630 feathers analysed for $\delta^{13}C$ and $\delta^{15}N$, amongst which 105 growing flight feathers were sub-sampled and analysed for δD (appendix 5 and 6). Fewer samples were run for δD due to budgetary constraints. For δD, I analysed 56 growing feathers and 51 fully grown feathers, limited to two species (Egyptian Goose and Red-billed Teal) from three sites, Strandfontein, Barberspan and Manyame catchment (Appendix 4).

From each bird, the tip of the second secondary feather (S2) about 1cm long was clipped off for isotope analysis. A small piece of body feather (1cm long) was collected from the back. Samples were stored in paper envelopes until analysis. The moult status of each bird was scored using the method of De Beer et al. (2001), in which each feather is scaled as a proportion of the whole feather, as follows: 0 - a fully grown feather, 1- fully grown feather missing or new feather completely in pin, 2 - new feather just emerging from sheath, up to about one third grown, 3 - new feather between one and two thirds grown, 4 - new feather more than two thirds grown but waxy sheath still at its base, and 5 - new feather fully grown with no trace of sheath at its base. For the growing feathers, only feathers with moult status 2 to 4 were selected because these feathers are not long enough to carry the bird to and from significantly distant places beyond the moulting locality. Fully grown feathers of moult status '0' (fully developed and worn out) were considered for comparative analysis.

Sample selection for Isotope Analysis

Species catchability and Anatid community composition varied with study site, season and year. This resulted in patchy sample coverage (appendix 3). I excluded all juveniles from the analysis but did not separate sexes because the study did not test for effects between different sexes. When using isotope analysis to trace movements, adults' growing feathers are recommended as proxies to site signatures since the juveniles' signature may be distorted by the signature of the parental breeding location (Hobson and Wassenaar 2008). To exclude juveniles, each captured bird was inspected and measured carefully. Birds were aged following criteria listed in the Roberts Birds of Southern Africa (Hockey et al. 2005). If there was any doubt with a bird's age, it was excluded from the analysis.

More non-moulting than moulting individuals were caught; I graded captures into classes of moult status, 'fully grown' (feathers past stage 5 and worn out) and 'growing' (feathers at moult status from two to four). Chapter one used growing feathers to answer the question of whether the sites belonged to isotopically distinct regions and if this was reflected in feathers. I therefore selected those species occurring over more than one site and with only growing feathers (259), for chapter one. Egyptian Goose, Red-billed Teal, Yellow-billed Duck and Cape Teal were selected and these came from three sites: Strandfontein, Barberspan, and Manyame catchment. Moulting White-faced Ducks and South African Shelducks from single sites (Manyame and Barberspan respectively) were included to present a stronger seasonal case. Chapters two used only individual birds from whom two feathers (body and flight) were collected (224); 135 birds from which both fully grown flight feathers and body feathers, and 89 birds from whom both Growing flight feathers and body feathers were collected. Chapter three therefore used more ducks (371) across more sites than chapter one and two because isotope signature comparisons were done across species by study site, among only growing flight feathers.

Pre-treatment of samples for $\delta^{15}N$ and $\delta^{13}C$ analysis

Since duck feathers are coated in natural oils during preening, I checked that lipids were not biasing the results. Fifteen feathers were treated for oils and compared against the same fifteen non-treated in a pair-wise comparison. Oil extraction treatment involved soaking in 2:1 chloroform: methanol mixture for 30 minutes followed by several rinses with distilled water. Samples from two species (Egyptian Goose and South African Shelduck) were used. Egyptian Geese were from Strandfontein and Barberspan and South African Shelducks were from Barberspan. The samples were randomly selected from 2007 up to 2008 captures.

The overall mean $\delta^{15}N$ signature for treated and non-treated samples (Table 4) differed with 0.13‰ (non-treated mean $\delta^{15}N$ was 12.53 ± 4.36‰ as compared to treated, 12.40 ± 4.41‰; no significant difference using a paired t-test, $t_{1;\,14} = 1.11$; $P > 0.05$). The $\delta^{13}C$ signature followed a similar trend with treated samples having values closely related to the non-treated samples (-17.32 ± 5.71‰ as compared to -17.42 ± 5.72‰ of the treated samples; no significant difference using a paired t-test, $t_{1;\,14} = 1.06$; $P > 0.05$). Trophic levels are typically separated by 0.4‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$ (Post et al. 2002).

These data corroborate the findings of Mizutani et al. (1992); Knoff et al. (2001); Paritte and Kelly (2009). Oil treatment might be necessary when using 'blood feathers' in the

initial stages of growth which have not emerged from the rachis; they are contaminated with blood lipids, or when using heavily soiled/contaminated feathers. Feather samples collected in this research were clean and they all comprised of fully emerged tips. Quillfeldt et al. (2010) omitted the acid cleaning protocol since it has been suggested that cleaning agents can change feather isotope values, either through residues or 'agent to feather' atom exchange. I thus decided not to apply an acid based cleaning protocol; instead, I used several rinses with distilled water.

Table 4: Descriptive statistics for tests of the effects of oils on feather isotope signatures

		Not treated for oils		Treated for oils		Not treated for oils		Treated for oils	
	N	Mean δ^{13}C	SD δ^{13}C	Mean δ^{13}C	SD δ^{13}C	Mean δ^{15}N	SD δ^{15}N	Mean δ^{15}N	SD δ^{15}N
EG Total	8	-21.87	3.72	-21.97	3.62	15.74	3.26	15.68	3.15
2007	5	-21.23	4.68	-21.49	4.59	15.71	3.53	15.44	3.35
BAR	1	-13.35	-	-13.64	-	9.96	-	9.75	-
STR	4	-23.21	1.80	-23.46	1.56	17.15	1.68	16.87	1.22
2008	3	-22.93	1.43	-22.77	1.50	15.79	3.52	16.07	3.45
STR	3	-22.93	1.43	-22.77	1.50	15.79	3.52	16.07	3.45
SAS Total	7	-12.11	1.10	-12.23	1.27	8.86	1.59	8.65	1.74
2007	5	-12.49	1.08	-12.47	1.43	9.12	0.64	8.89	0.44
BAR	5	-12.49	1.08	-12.47	1.43	9.12	0.64	8.89	0.44
2008	2	-11.16	0.38	-11.62	0.65	8.22	3.51	8.05	4.05
BAR	2	-11.16	0.38	-11.62	0.65	8.22	3.51	8.05	4.05
Grand Total	15	-17.32	5.73	-17.42	5.71	12.53	4.36	12.40	4.41

SD= Standard deviation, EG= Egyptian Goose, SAS= South African Shelduck, BAR= Barberspan, STR= Strandfontein

Feather Isotope analysis

Analyses for Carbon and Nitrogen were carried out in the archaeology isotope laboratory at the University of Cape Town (UCT). Washed feathers were oven dried for 24 hours at 40ºC (Wassenaar and Hobson 2001; Wunder et al. 2005). Approximately 0.6 mg (0.55-0.65) of tissue was loaded into pressed tin capsules for δ^{13}C and δ^{15}N analysis. Samples were analysed by continuous flow methods using an elemental analyser coupled to a micro-mass Optima mass spectrometer: they were oxidized in a Finnigan Flash EA 1112 series elementals analyser coupled to a $\text{Delta}_{\text{plus}}$ XP isotope ratio mass spectrometer via a Finnigan Conflo III gas control unit. Stable isotope proportions of Carbon (δ^{13}C) and Nitrogen (δ^{15}N) were reported relative to Pee Dee Belemnite (PDB) and air standards respectively using three

internal laboratory standards (Merck gelatine, Sucrose ANU, and Valine). Analytical errors for Carbon and Nitrogen isotopes were accounted for in the final readings by comparing and correcting against three standards for every fifteen feathers, allowing any instrument drift over a typical 14-hour run to be corrected. Furthermore, based on internal standards, the analytical precision (± 1 SD) equalled ± 0.17‰ for δ^{15}N and ± 0.28‰ for δ^{13}C.

The analysis for Deuterium (δD) was carried out at the CSIR isotope laboratory in Pretoria. Samples were degreased in a 2:1 toluene : ethanol mixture and were allowed to equilibrate their exchangeable H for approximately two days. In each batch on the spectrometer, three running standards and a feather from a local Hadeda Ibis (*Bostrychia hagedash*) were run as comparison samples between batches. The standards had been previously calibrated for exchangeable H so it was assumed that if the local equilibration time was long enough, then the exchangeable component would be the same for unknowns and knowns. These values were regressed against each other under the assumption that they would have the same percentage of exchangeable H and that this exchangeable component would be the local signal (i.e., it would have the same value for all samples). The result given is therefore the non-exchangeable component of the feather (Hobson et al. 2006). Running standards had known values of: -108, -138, and -187 parts per thousand (‰). The Hadeda feather gave a δD value of -29‰.

Isotopes in precipitation were calculated from an online isotope calculator (Bowen 2009, www.waterisotopes.org). The Global Network of Isotopes in Precipitation (GNIP) online database keeps record of δD isotopes in rainfall and these are linked to the altitude and geographical coordinates of the site of interest. By inputting the geographical coordinates and the altitude of each of the study sites, I managed to retrieve their respective annual average δD in precipitation (δD_p).

All isotope values were reported as the ratio between the heavy and the light isotopes compared to international standards. For Nitrogen and Carbon isotopes, the standards are air Nitrogen (N_2) and PDB respectively. For Hydrogen, the standard is the Vienna Standard Mean Ocean Water (VSMOW). The deviation (δ) of the ratio (R) is expressed in parts per thousand (‰) as shown in the equation ($\mathbf{\delta X = [(R_{sample}/R_{standard}) - 1] * 1000}$) where X is the heavier isotope and R is the corresponding ratio between the heavier and lighter isotope (Forero and Hobson 2003).

Expected Outcome

Because stable isotope signatures vary with geographic location, anthropogenic inputs, climate, seasonality and vegetation composition patterns in the environment (Rubenstein and Hobson 2004), I expected signature patterns to vary by site. Each of the selected sites belonged to a different vegetation biome (Fig. 1). An ideal outcome (workable scenario) that would allow us to draw inferences of movement would be represented by clear isotope signature distinctions by site, with seasonal and annual variations as consistent as possible (Pardo and Nadelhoffer 2010; Hobson and Wassenaar 2008). I set up criteria to define whether feather isotope signature patterns presented a workable scenario or not. Criteria were based on: 1) variation between the sampled study sites, 2) variation between species, 3) variation between seasons, and 4) variation between years.

Relative scaling of stable isotope signature variation of each of the factors, i.e., whether High (H) or low (L) were be based on statistical level of significance and multivariate analyses' measures of effects of variables using Wilk's lampda. Tables 5a to 5c represent the possible outcome scenarios (combinations of variations), their implications and how the research would address each one of them (if workable) in order to infer information relevant to movement ecology of southern African ducks. The four sources of variation (site, species, seasons, and years), produced a spectrum of possible outcome combinations which were grouped under three main scenarios: a) Workable (movement information can be interpreted with ease), b) Workable with difficulty (movement information can be interpreted but with a lot of calibration), and c) Not workable (intractable information).

a) Workable

All cases with a strong variation among sites would be ideal for movement inferences (table 5a). This would depict that the chosen sites belonged to isotopically distinct regions and duck feathers can reflect regional isotopic patterns. Movement inferences can be drawn with ease as long as all the other sources of variation are not significant.

Table 5a: Workable scenario showing sites with a predominantly high strength of variation relative to other sources of variation.

	SITES	SPECIES	SEASONS	YEARS
Variation	*H*	*L*	*L*	*H*
Variation	*H*	*L*	*H*	*H*
Variation	*H*	*L*	*L*	*L*

L= low variation (not significant)

H= High variation (significant)

b) Workable with difficulty

Even though the site differences are strong in this scenario, other sources of variation are significant, which necessitates stringent calibration techniques. This scenario would require a species, season, and year specific approach.

Table 5b: Workable with difficulty scenario showing sites with a strength of variation almost equalled to each of the other sources of variation.

	SITE	SPECIES	SEASONS	YEARS
Variation	*H*	*H*	*H*	*H*
Variation	*H*	*H*	*H*	*L*
Variation	*H*	*H*	*L*	*L*

L = low variation (not significant)

H = High variation (significant)

3. Not workable

As long as there are no significant site signature differences, either the sites chosen do not belong to distinct isotopic regions or the tissues and species chosen are not capable of representing biogeographic isotope patterns in the environment. It would be impossible then to draw meaningful movement inferences from such a scenario.

Table 5c: A non-workable scenario showing isotopically similar sites (with low signature variation).

	SITES	SPECIES	SEASONS	YEARS
Variation	*L*	*L*	*L*	*L*
Variation	*L*	*L*	*L*	*H*
Variation	*L*	*L*	*H*	*H*

L= low variation (not significant)

H= High variation (significant)

Limitations of the study

It was not possible to get a uniform sample size across study sites, seasons, years, and species due to variations in the catchability of some ducks. This resulted in a patchy sample coverage which limited the robustness of inferences that could be drawn.

Supporting resource data in the form of background isotope values of the environment: plants and water (Cerling et al. 2009), was not analysed due to time and logistical constraints. This limited the research's ability to account for within patch variability of isotope signatures. Although study areas are relatively homogenous in δD signatures, within patch variability of isotope signatures (δ^{13}C and δ^{15}N) can be high depending on habitat variability and anthropogenic influences, these influences potentially confound comparative analyses (Pardo and Nadelhoffer 2010). Further research is needed to analyse within site variability of δ^{15}N and δ^{13}C. Ideally, within site heterogeneity must be considerably smaller than between site variation for the chosen isotope signatures to distinguish between different sites.

Literature cited:

Bird Life International. 2009. Important Bird Area factsheet: Robert McIlwaine Recreational Park, Zimbabwe. Downloaded from the Data Zone at http://www.birdlife.org on 11/8/2009

Bowen, G.J. 2009. The Online Isotopes in Precipitation Calculator, http://www.waterisotopes.org.

Burrough, S.L., Thomas, S.G., Shaw, P.A., Bailey, R.M. 2007. Multiphase quaternary highstands at Lake Ngami, Khalahari Northern Botswana. *Palaeogeography Paleoclimatology Plaeoecology,* 253, 280-299.

Cerling, T. E., Wittemyer, G., Ehleringer, J. R., Remien, C.H. Douglas-Hamilton, I. 2009. History of animals using isotope records (HAIR): A 6-year dietary history of one family of African elephants. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 8093-8100.

Cumming, G.S., Caron, A., Abolnik, C., Cattolli, G., Bruinzeel, L., Burge, C.E., Chiweshe N., Mochotlhoane, B., Mutumi, G.L., Ndlovu, M. 2011. The ecology of influenza A viruses in wild birds in southern Africa, Ecohealth. http://www.ncbi.nlm.nih.gov/pubmed/21516374

Dallman, P.R. 1998. *Plant Life in the World's Mediterranean Climates: California, Chile, South Africa, Australia, and the Mediterranean Basin.* Los Angeles: Carlifornia University Press. pp 1-19.

De Beer, S.J., Lockwood, G.M., Raijmakers, J.H., Raijmakers, J.M., Scott,W.A., Oschadleus, H.D., Underhill, L.G., 2001. *SAFRING Bird Ringing Manual,* Cape Town: South Africa Bird Ringing Unit, Avian Demography Unit.

Forero, M.G., Hobson, K.A., 2003. Using stable isotopes of Nitrogen and Carbon to study seabird ecology: applications in the Mediterranean seabird community. *Scientia Marina*, 67, 23-32.

Hobson, K.A., Clark, R.G. 1992. Assessing avian diets using stable isotopes: Isotope Turnover of δ^{13}C in tissues. *Condor*, 94, 181-188.

Hobson, K.A., Van Wilgenburg, S., Wassenaar, L.I., Hands, H., Johnson, W.P., O'Meilia, M., Taylor, P. 2006. Using stable Hydrogen isotope analysis of feathers to delineate origins of harvested Sandhill Cranes in the central flyway of North America. *Waterbirds,* 29, 137-147.

Hobson, K.A., Wassenaar L.I. 2008. (eds). *Applying isotopic methods to tracking animal movements*. London: Elsevier

Kaletja-Summers, B., McCarthy, M., Underhill, L.G. 2001. Long-term trends, seasonal abundance and energy consumption of waterbirds at Strandfontein, Western Cape, South African, 1953-1993. *Ostrich,* 72, 80-95.

Knoff, A.J., Macko, S.A., Erwin, R.M. 2001. Diets of nesting Laughing Gulls (*Larus atricilla*) at the Virginia Coast Reserve: Observations from stable isotope analysis. *Isotopes in Environmental and Health Studies*, 37, 67-88.

Mizutani, H., Fukuda, M., Kabaya, Y. 1992. δ^{13}C and δ^{15}N enrichment factors of feathers of 11 species of adult birds. *Ecology*, 73, 1391-1395.

Ogilvie, M., Pearson, B. 1994. *Wildfowl Behaviour Guide*, Melbourne: Hamlyn Limited.

Pardo, L.H., Nadelhoffer, K.J. Using Nitrogen stable isotopes to assess terrestrial ecosystems at regional and global scales. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (eds). 2010. *Isoscapes*: *Understanding movement, pattern and process on Earth through isotope mapping*. London: Springer. pp 221-245

Paritte, J.M., Kelly, J.F. 2009. Effect of cleaning regime on stable-isotope ratios of feathers in Japanese Quail *Coturnix japonica*. Auk, 126, 165-174.

Quillfeldt, P., Voigt, C.C., Masello, J.F. 2010. Plasticity versus repeatability in seabird migratory behaviour. *Behavioral Ecology and Sociobiology,* 64, 1157-1164

Rubenstein, D.R., Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution*, 19, 256-263

Taylor, P.B., Navarro, R.A., Wren-Sargent, M., Harrison, J.A., Kieswetter, S.L. 1999. *Total CWAC Report: Coordinated Waterbird Counts in South Africa, 1992-97*. Cape Town: Avian Demography Unit, University of Cape Town.

Wassenaar, L.I., Hobson, K. A. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology*, 35, 1845-1850.

Wunder, M.B., Kester. C.L., Knopf, F.L., Rye, R.O. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia,* 144, 607-617.

CHAPTER 1

FEATHER STABLE ISOTOPES DISTINGUISH SOME SOUTHERN AFRICAN DUCKS FROM DIFFERENT MOULTING LOCATIONS

Abstract

Meaningful applications of stable isotope measurements to infer movements and origins of biological material require understanding of isotopic regions within the area of interest. Biological tissue grown in a known location can be used as a proxy for the site's signature, assuming that the organism of interest takes up its signature from a local diet. Movement can therefore be traced if the spatial scale of the study area has discernable patterns of stable isotope signatures in space (regions of distinct isotope signature patterns). This study compared δ^{15}N, δ^{13}C, and δD data for growing feathers from six duck species. Four duck species (Egyptian Goose, Yellow-billed Duck, Red-billed Teal and Cape Teal) were sampled from across three different wetlands across seasons in three years. Two species (White-faced Duck and South African Shelduck) were sampled from single wetlands. Three of the species sampled across different wetlands (Egyptian Goose, Red-billed Teal and Cape Teal) showed spatial variation in at least one of the isotopes δ^{13}C, δ^{15}N and δD. Egyptian Geese showed the clearest separation of sites in all three isotopes. For the majority of samples, isotope signatures showed seasonal and yearly effects (including White-faced Ducks and South African Shelducks sampled from single sites), implying the need for season and year specific approaches to isotope techniques. I therefore concluded that southern Africa has regions of distinct isotopic signatures and these are moderately reflected in some duck species. Consequently movements, origins and feeding habits of some but not all southern African ducks can be inferred from feather isotopes.

Introduction

Dispersal is a fundamental ecological process. The ways in which organisms move through landscapes influences their overall demography, their role as pathogen and disease dispersers, and their responses to stochastic environments and anthropogenic perturbations (FAO 2006; Sinclair et al. 2005). Dispersal ability is also an important determinant of species distributions

and community composition. It enables mobile species to use a succession of resources as and when they occur, thus increasing their chances of persistence (Baldassarre and Bolen 2006).

Empirical studies of dispersal in animals have been complicated by the difficulties of tracking individual organisms over long distances (Nathan et al. 2003; Nathan 2008). Bird movements are better understood than those of many other animals through ringing (banding) programmes which rely on active participation from the public. However, ringing returns for many southern African birds are inadequate to derive strong inferences about movement. Although larger birds can be tracked using telemetry, satellite transmitters are needed for birds that fly long distances over potentially inhospitable terrain. Satellite telemetry is expensive and hence difficult to apply to large numbers of birds (Hobson and Wassenaar 1997; Hobson 2005).

The use of dietary signatures, as quantified using ratios of stable isotopes in feathers, offers a potentially useful alternative to standard tracking approaches (Rubenstein and Hobson 2004). The stable isotope technique nullifies the need to recapture individuals, making information interpretable from as large a sample as one can capture; it offers a non-destructive sampling option; and it is far cheaper than satellite telemetry. However, even though stable isotope techniques continue to develop (West et al. 2010), research is biased towards areas outside southern Africa. No data have been published to date on southern African Ducks (using ISI Web of Knowledge search engine). A considerable amount of additional research is thus needed within the region before we can determine whether the method has relevance for understanding duck movements in southern Africa.

In this study I focused on ducks in southern Africa. Ducks offer an interesting test case because they undergo a 4-5 week period of flightless moult every year, regrowing their wing feathers synchronously in a single location (Ogilvie and Pearson 1994; Todd 1996; Hockey et al. 2005). This means that stable isotopes in growing wing feathers offer an assay of the isotopic signature of the moulting site (Hobson and Wassenaar 2008).

Since wing feather moult is generally undertaken at a large wetland that the bird can be sure will not dry up during moult, a substantial amount of movement in duck populations occurs to and from moulting sites. By contrast, body feathers (breast and back) are regrown annually at feeding sites which may be far removed from moulting sites (Hockey et al. 2005; Baldassarre and Bolen 2006). One of the central questions in applying isotope analysis to the dispersal of southern African birds is that of whether southern Africa as a region is composed of "isotopic regions" distinct enough to yield significantly different signatures (Hobson 1999;

Hebert and Wassenaar 2001). Stable isotopes can vary with location, season (Cabanellas-Reboredo et al. 2009), year (West et al. 2006), and intra/inter species dietary and metabolic rate differences (Fox and Kahlert 1999), and anthropogenic influences (Rubenstein and Hobson 2004). The research analysed growing flight feathers for three different isotope ratios: ^{13}Carbon: ^{12}Carbon (δ^{13}C), ^{15}Nitrogen: ^{14}Nitrogen (δ^{15}N), and ^{2}Hydrogen: ^{1}Hydrogen (δD). These data allowed three questions to be asked: (1) Do feathers moulted at diverse sites have isotopic signatures sufficiently distinct to discern birds from different locations? (2) Does the isotopic signature of duck feathers vary with season? (3) Does the isotopic signature at each site differ between years.

Methods

To test for the potential utility of stable isotope analysis as a tool for understanding the movements of nomadic ducks in southern Africa, I sampled duck feathers over two different years from three study sites within southern Africa. Locally growing flight feathers (2nd secondary feather as a standard) were used as proxies to the site's signature because ducks are immobile during flight feather replacement. This means that the signature of feathers is predominantly from the moulting site. All sampling and stable isotope analysis methods are discussed in the general methods section. Statistical procedures are:

The data were tested by species for normality using a one sample Kolmogorov-Smirnov test in Predictive Analysis Software (PASW) version 18 (Zuur et al. 2009). The data were normally distributed and therefore nested parametric Multivariate Analysis of Variance (MANOVA) was carried out on each species to compare season, year and site differences of signatures using Statistica version 9. Main effects were used because interaction effects did not make any biological sense. Analysis of variance (ANOVA) was chosen for its robustness. In addition, small deviations from the assumptions are less influential to the overall results, and thus catered for the unequal sample sizes (Sokal and Rohlf 1994). Where significant differences were detected (Table 1.3), single ANOVAs followed by post hoc tests (Unequal N HSD) were carried out. Unequal N HSD was used because different numbers of birds were captured during different seasons, years, and sites. Separate ANOVAs were also run for δD which was run for a smaller subsample than δ^{13}C and δ^{15}N; δD analysis was more expensive than δ^{15}N and δ^{13}C analysis. Additionally, δD isoscape maps have shown a limited range of δD values within southern Africa, implying its limited utility in southern African environments (Bowen and Ravenaugh 2003).

For seasonal comparisons, the months September to March were grouped as summer and April to August as winter, using information from Nicholson (2000). Note that the timing of rainfall differs between my sites, with Strandfontein falling in a winter rainfall region, Barberspan in a highly variable but dominantly summer rainfall region, and Manyame catchment in a summer rainfall area.

Results

A total of 259 freshly grown feathers were analysed from six duck species as shown in Tables 1.1 and 1.2. However, because of the variations in catchability and abundance of ducks across sites, it was not possible to obtain a uniform sample size across sites. The degree of separation of feather sample signatures by site varied with species, season and year (appendix 4). The majority of the feathers that were analysed, with the exception of the samples from Egyptian Geese, showed strong yearly and seasonal differences in δ^{13}C and δ^{15}N. δD was sensitive to seasonal and yearly changes in the two species tested (Egyptian Goose and Red-billed Teal; appendix 4). Table 1.1 shows that Strandfontein ducks were generally δ^{15}N enriched (15.59 ± 3.39 compared to 10.33 ± 3.20 and 10.69 ± 2.33) and δ^{14}C depleted (-20.96 ± 2.75 compared to -13.36 ± 3.49 and -18.98 ± 3.98) relative to Barberspan and Manyame catchment ducks respectively. The following sub-sections describe the isotope signatures in detail, first by spatial and then by temporal variation.

Table 1.1: Mean values of Carbon and Nitrogen Isotopes (δ^{13}C and δ^{15}N) in freshly grown duck feathers

	STR			BAR			MAN			T/N
	N	δ^{15}N	δ^{13}C	N	δ^{15}N	δ^{13}C	N	δ^{15}N	δ^{13}C	
EG	56	15.26	-21.44	44	9.66	-12.54	2	12.68	-16.41	102
RBT	4	12.21	-18.28	11	11.25	-14.12	48	9.41	-19.53	63
YBD	3	15.68	-21.70	14	10.60	-13.92				17
WFD							41	12.10	-18.47	41
CT	7	20.14	-18.27	8	12.99	-17.81				15
SAS				21	10.04	-12.14				21
T	70			98			91			259

T/N = Total N, T = Total, EG = Egyptian Goose, RBT = Red-billed Teal, YBD = Yellow-billed Duck, WFD = White-faced Duck, CT = Cape Teal, SAS = South African Shelduck.

Table 1.2: Mean values of Hydrogen Isotopes (δD) in freshly grown feathers

	STR		BAR		MAN		T/N
	N	δD	N	δD	N	δD	
EG	10	-70.21	10	-63.92	2	-93.44	22
RBT	3	-48.68	9	-53.31	22	-76.77	34
T	13	-65.24	19	-58.90	24	-78.16	56

T/N = Total N, T = Total, EG = Egyptian Goose, RBT = Red-billed Teal, YBD = Yellow-billed Duck, WFD = White-faced Duck, CT = Cape Teal, SAS = South African Shelduck.

Site differences

Egyptian Geese showed the clearest separation by site in both isotopes, δ^{13}C ($F_{2, 96} = 182.30$; $P < 0.001$), δ^{15}N ($F_{2, 96} = 73.72$; $P < 0.001$). Cape Teals were distinct only in δ^{15}N ($F_{1, 95} = 5.72$; $P < 0.05$) and not in δ^{13}C ($F_{1, 95} = 0.13$; $P > 0.05$) and the isotopic signature of their feathers varied significantly with season and year of moult (Fig. 1.1 and 1.2). Only the Yellow-billed Ducks could not be separated by site using δ^{13}C and δ^{15}N.

An unequal N HSD post hoc test on Egyptian Geese showed that Strandfontein ducks were distinct from Barberspan ducks in both δ^{13}C and δ^{15}N (Table 1.4; Fig. 1.1 and 1.2). Manyame duck feather signatures were not unique from either Barberspan or Strandfontein in both δ^{13}C and δ^{15}N. The isotope δD offered a useful alternative as it was distinct by site ($F_{2, 18} = 4.32$; $P < 0.05$); it distinguished Barberspan ducks from Manyame ducks. δD could not distinguish Strandfontein ducks from those in either Manyame or Barberspan.

Red-billed Teals were also distinct according to site in both isotopes, δ^{13}C ($F_{2, 25} = 3.48$; $P < 0.05$) and δ^{15}N ($F_{2, 25} = 5.64$; $P < 0.01$). An unequal N HSD post-hoc test showed that ducks from Manyame were distinct from Barberspan but Strandfontein ducks were not distinct from either Barberspan or Manyame in δ^{13}C (Table 1.4). The Red-billed Teals from the three sites were significantly different from each other in δ^{15}N. Different sites could not be resolved for Red-billed Teals using δD ($F_{2, 25} = 3.15$; $P > 0.05$; Fig. 1.3).

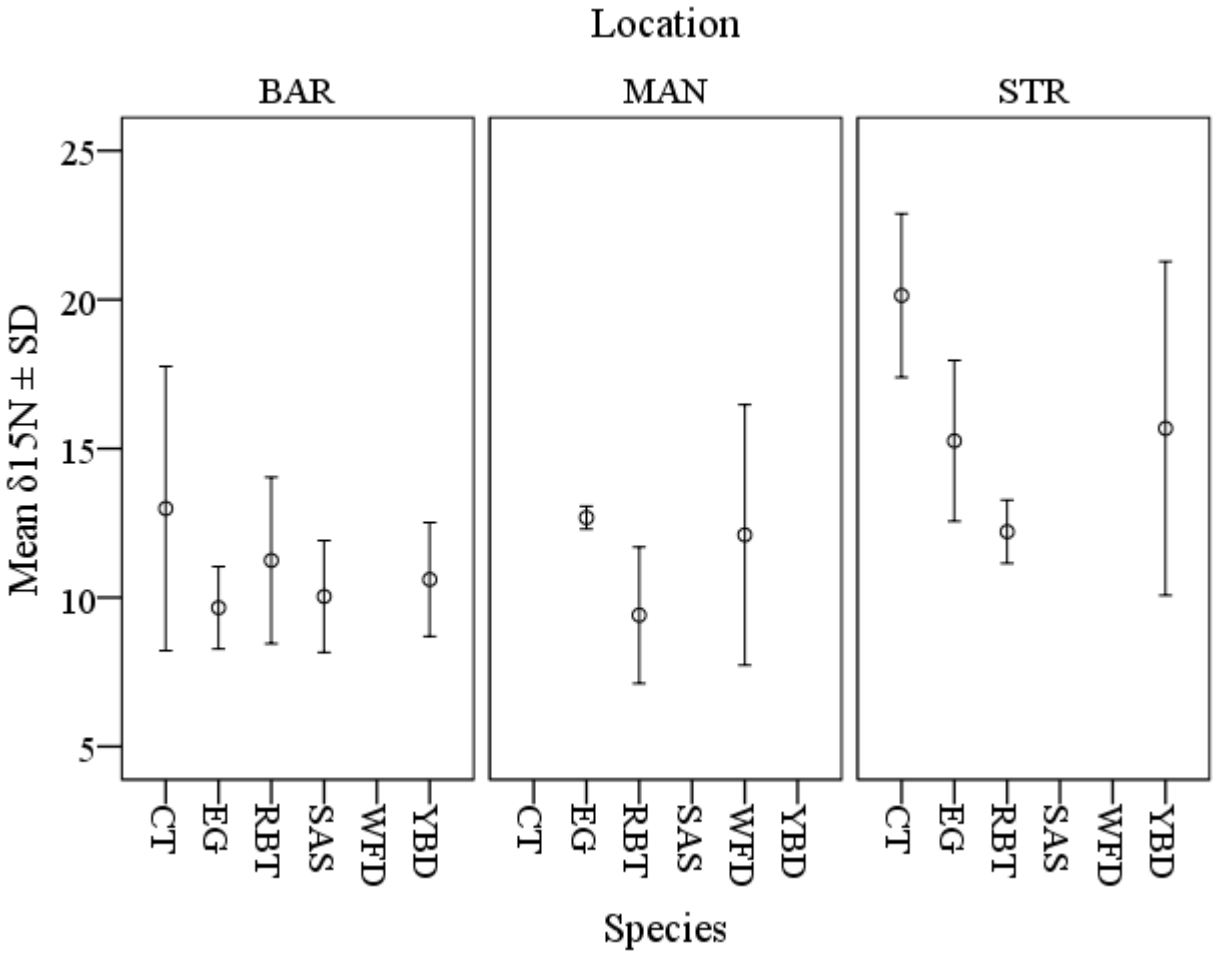


Figure 1.1: Mean ± SD of isotopic proportions of Nitrogen (δ^{15}N) in growing flight feathers of different ducks from each study site, Strandfontein (STR), Barberspan (BAR) and Manyame catchment (MAN). Cape Teal (CT) and Yellow-billed Duck (YBD) were captured from two sites (Barberspan and Strandfontein), White-faced Ducks (WFD) and South African Shelducks (SAS) were from single sites. Whereas Egyptian Geese (EG) and Red-billed Teals (RBT) were captured from three sites (Barberspan, Strandfontein and Manyame)

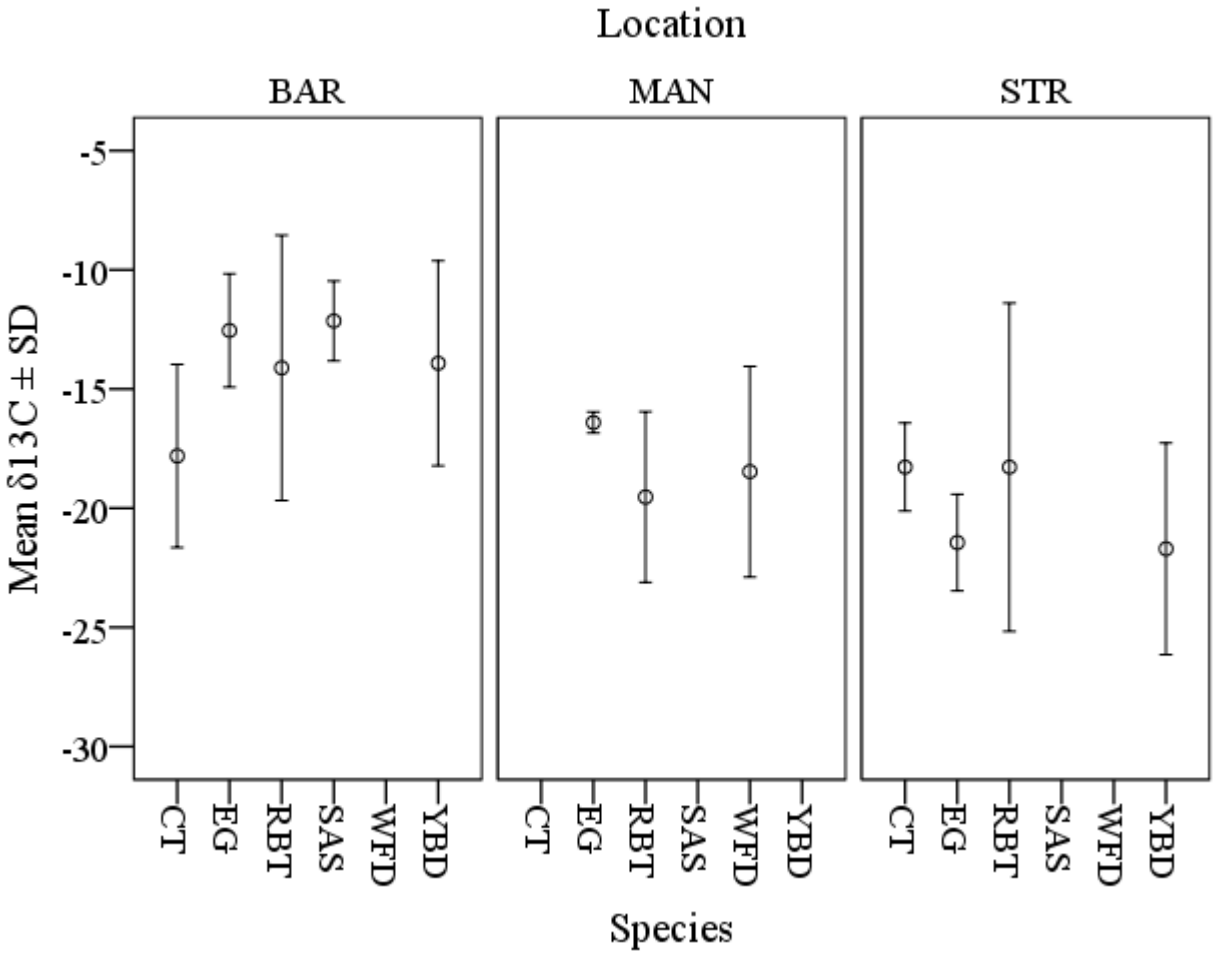


Figure 1.2: Mean ± SD of isotopic proportions of Carbon ($\delta^{13}C$) in growing flight feathers of different ducks from each study site, Strandfontein (STR), Barberspan (BAR) and Manyame catchment (MAN). Cape Teals (CT) and Yellow-billed Ducks (YBD) were captured from only two sites (Barberspan and Strandfontein). White-faced Ducks (WFD) and South African Shelducks (SAS) were from single sites, whereas Egyptian Geese (EG) and Red-billed Teals (RBT) were captured from three sites (Barberspan, Strandfontein and Manyame)

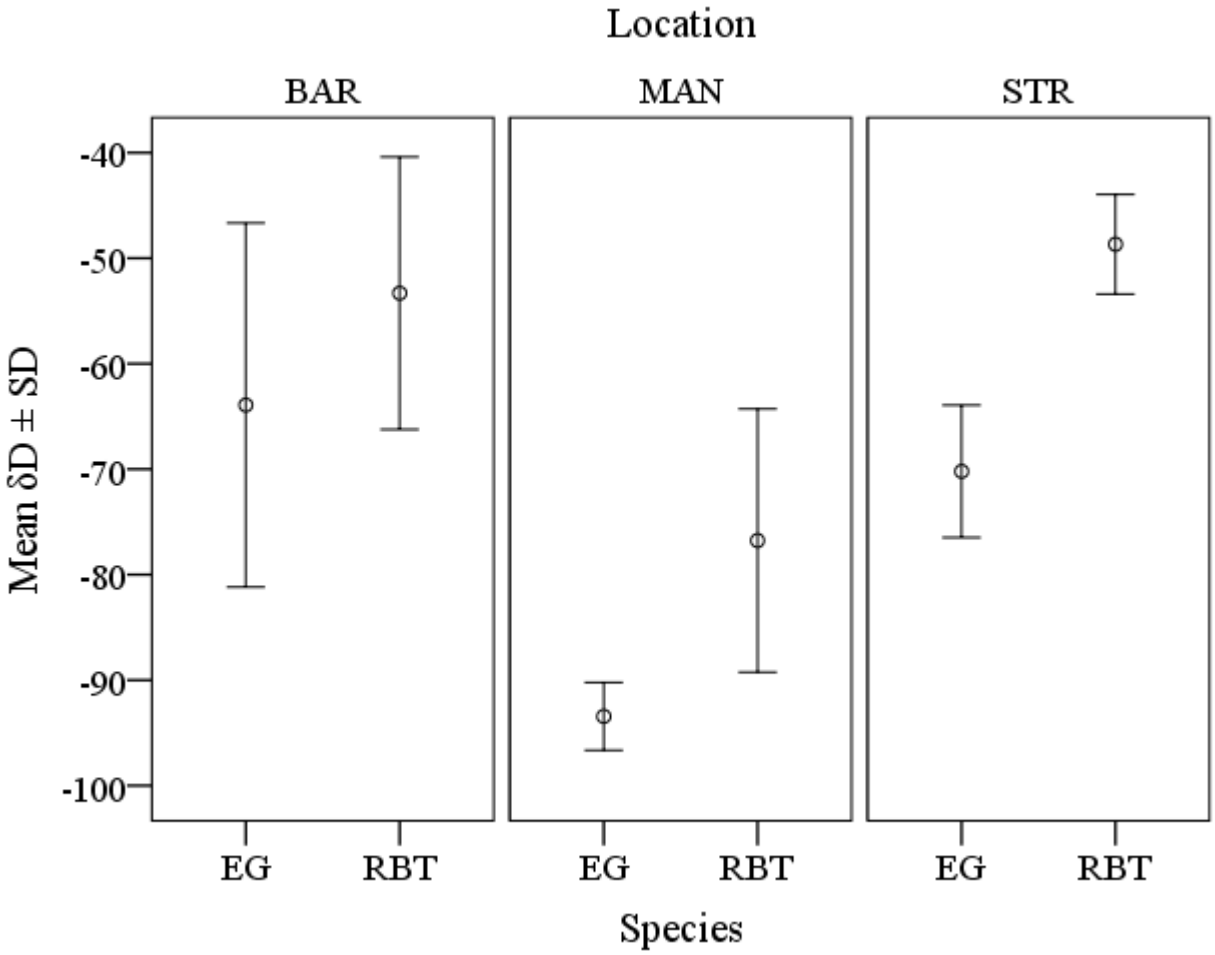


Figure 1.4: Mean ± SD of stable isotope proportions of Hydrogen (δD) in growing flight feathers of Egyptian Geese and Red-billed Teals from Strandfontein (STR), Barberspan (BAR) and Manyame catchment (MAN).

Seasonal differences

Egyptian Geese feather isotope signatures did not change significantly between summer and winter in either δ^{13}C ($F_{1, 96} = 1.34$; $P > 0.05$) or δ^{15}N ($F_{1, 96} = 1.02$; $P > 0.05$). δD differed significantly between different seasons ($F_{1, 18} = 5.58$; $P < 0.05$), showing summer moulting ducks to be significantly more δD depleted than winter moulting ducks. Cape Teals did not show significant variation across different seasons in either δ^{15}N ($F_{1, 95} = 0.48$; $P > 0.05$) or δ^{13}C ($F_{1, 95} = 1.80$; $P > 0.05$). South African Shelducks showed significant seasonal variations in δ^{13}C ($F_{1, 18} = 12.91$; $P < 0.01$) but not in δ^{15}N ($F_{1, 18} = 3.26$; $P > 0.05$; ref appendix 4 for descriptive statistics).

The same pattern was shown by White-faced Ducks, with δ^{13}C significantly different across seasons ($F_{1, 37} = 13.43$; $P < 0.001$) but not δ^{15}N ($F_{1, 37} = 0.56$; $P > 0.05$). Red-billed Teals moulting in summer had a different signature from ducks moulting in winter in δ^{13}C

($F_{1, 25}$ = 11.69; P < 0.01) but not in δ^{15}N ($F_{1, 25}$ = 0.47; P > 0.05). The δD signature of feathers from Red-billed Teals moulting in summer was not distinct from ducks moulting in winter ($F_{1, 25}$ = 1.19; P > 0.05; ref appendix 4 for descriptive statistics).

Annual differences

The isotopic signatures of Egyptian Geese feathers differed across years in δ^{15}N ($F_{2, 96}$ = 3.54; P < 0.05) but not in δ^{13}C ($F_{2, 96}$ = 1.84; P > 0.05). Post hoc tests showed feathers grown across different years to be similar in both δ^{13}C and δ^{15}N (Table 1.4). Yellow-billed Ducks did not show annual differences in feather signatures in either δ^{15}N ($F_{2, 95}$ = 1.26; P > 0.05) or δ^{13}C ($F_{2, 95}$ = 1.26; P > 0.05). Cape Teals did not show significant variation across years in either δ^{15}N ($F_{1, 95}$ = 1.26; P > 0.05) or δ^{13}C ($F_{1, 95}$ = 0.41; P > 0.05).

The isotopic signatures of Red-billed Teal feathers varied significantly across years in both δ^{15}N ($F_{2, 25}$ = 4.91; P < 0.05) and δ^{13}C ($F_{2, 25}$ = 3.42; P < 0.05). Unequal N HSD post-hoc tests showed that 2007 moulting ducks were distinct from 2008 moulting ducks (Table 1.4). South African Shelduck feather signatures differed significantly between 2007 and 2008 in δ^{13}C ($F_{1, 18}$ = 6.89; P < 0.05) but not in δ^{15}N ($F_{1, 18}$ = 0.01; P > 0.05). For White-faced Ducks, feather isotope ratios differed significantly in δ^{15}N ($F_{2, 37}$ = 6.33; P < 0.01) but not in δ^{13}C ($F_{2, 37}$ = 2.76; P > 0.05). An unequal N HSD post hoc test also showed that the signature of ducks from 2007 was distinct from 2008, but that the 2009 signature was not distinct from either 2008 or 2007 in δ^{15}N (Table 1.4). All years were statistically similar for δ^{13}C in White-faced Duck feathers.

Table 1.3: Multivariate tests of significance of stable isotopes proportions, Carbon (δ^{13}C), Nitrogen (δ^{15}N), and Hydrogen δD in growing feathers of ducks across three moulting locations (Strandfontein, Barberspan and Manyame catchment) in southern Africa.

Effect	Test	Value	F	Effect df	Error df	p
			Egyptian Goose using δ^{15}N, δ^{13}C, and δD			
Intercept	Wilks	0.017338	302.27	3	16	0.000000
season	Wilks	0.521259	4.90	3	16	0.013315
Location	Wilks	0.317125	4.14	6	32	0.003472
			Egyptian Goose using δ^{15}N and δ^{13}C			
Intercept	Wilks	0.059906	745.41	2	95	0.000000
season	Wilks	0.974249	1.26	2	95	0.289618
Year	Wilks	0.904922	2.43	4	190	0.048918
Location	Wilks	0.147856	76.03	4	190	0.000000
			Red-billed Teal using δ^{15}N, δ^{13}C, and δD			
Intercept	Wilks	0.013027	580.87	3	23	0.000000
season	Wilks	0.315036	16.67	3	23	0.000006
Location	Wilks	0.376611	4.83	6	46	0.000678
			Red-billed Teal using δ^{15}N and δ^{13}C			
Intercept	Wilks	0.172339	134.47	2	56	0.000000
season	Wilks	0.808632	6.63	2	56	0.002612
Year	Wilks	0.792544	3.45	4	112	0.010635
Location	Wilks	0.721075	4.97	4	112	0.000997
			Yellow-billed Duck using δ^{15}N and δ^{13}C			
Intercept	Wilks	0.035569	149.13	2	11	0.000000
season	Wilks	0.987822	0.07	2	11	0.934829
Year	Wilks	0.866705	0.41	4	22	0.801013
Location	Wilks	0.740791	1.93	2	11	0.192011
			White-faced Duck using δ^{15}N and δ^{13}C			
Intercept	Wilks	0.045863	374.47	2	36	0.000000
season	Wilks	0.725502	6.81	2	36	0.003101
Year	Wilks	0.714757	3.29	4	72	0.015561
			Cape Teal using δ^{15}N and δ^{13}C			
Intercept	Wilks	0.043779	98.29	2	9	0.000001
season	Wilks	0.808651	1.06	2	9	0.384525
Year	Wilks	0.744205	0.72	4	18	0.591667
Location	Wilks	0.633474	2.60	2	9	0.128168
			South African Shelduck using δ^{15}N and δ^{13}C			

			Yellow-billed Duck using δ^{15}N and δ^{13}C			
Intercept	Wilks	0.016470	507.60	2	17	0.000000
season	Wilks	0.560725	6.66	2	17	0.007318
Year	Wilks	0.710269	3.47	2	17	0.054587

Table 1.4: Post hoc tests for Egyptian Geese and Red-billed Teals across three sites and three years.

Egyptian Goose				Red-billed Teal			
δ^{15}N							
LOCATION	STR	BAR	MAN	LOCATION	STR	BAR	MAN
	15.26	9.66	12.68		12.21	11.25	9.41
STR		0.000105	0.451429	STR		0.808864	0.17526
BAR	0.000105		0.336275	BAR	0.808864		0.128596
MAN	0.451429	0.336275		MAN	0.17526	0.128596	
YEAR	2007	2008	2009	YEAR	2007	2008	2009
	13.093	11.999	13.14		9.1358	10.63	9.9921
2007		0.130197	0.996424	2007		0.028079	0.958754
2008	0.130197		0.126785	2008	0.028079		0.976917
2009	0.996424	0.126785		2009	0.958754	0.976917	
δ^{13}C							
LOCATION	STR	BAR	MAN	LOCATION	STR	BAR	MAN
	-21.44	-12.54	-16.41		-18.28	-14.12	-19.53
STR		0.000105	0.056613	STR		0.266502	0.88478
BAR	0.000105		0.179901	BAR	0.266502		0.003725
MAN	0.056613	0.179901		MAN	0.88478	0.003725	
YEAR	2007	2008	2009	YEAR	2007	2008	2009
	-17.21	-18.28	-17.18		-17.15	-19.72	-20.3
2007		0.150181	0.997955	2007		0.027674	0.823624
2008	0.150181		0.15136	2008	0.027674		0.993355
2009	0.997955	0.15136		2009	0.823624	0.993355	

Unequal N HSD post hoc tests of growing feather stable isotopes of Carbon (δ13C) and of Nitrogen (δ15N) across three sites, Strandfontein (STR), Barberspan (BAR), and Manyame catchment (MAN). Underlined figures yielded statistically significant post hoc results.

Egyptian Goose ($\delta 15$N) Unequal N HSD; Approximate Probabilities for Post Hoc Tests Error: Between MS = 4.55, df = 96

Red-billed Teal ($\delta 15$N) Unequal N HSD; Approximate Probabilities for Post Hoc Tests Error: Between MS = 4.78, df = 57

Egyptian Goose ($\delta 13$C) Unequal N HSD; Approximate Probabilities for Post Hoc Tests Error: Between MS = 4.68, df = 96

Red-billed Teal ($\delta 13$C) Unequal N HSD; Approximate Probabilities for Post Hoc Tests Error: Between MS = 14.05, df = 57

Discussion

Key findings are that the majority of species were distinct by site in at least one of the isotopes tested and that isotope signatures were not always consistent across seasons and years. These findings yielded a 'workable with difficulty scenario' meaning that isotope-based movement studies with southern African Ducks need to be species, season and year specific. The Egyptian Goose, Cape Teal and Red-billed Teal feather signatures were consistent across seasons and years but South African Shelducks, White faced Ducks and Yellow-billed Ducks were not. The following subsections give possible explanations for isotope signature variations between sites, years and seasons.

Between site differences in isotope signatures

Habitat

Even though the majority of feathers were distinct by site, the degree of distinction (in terms of number of distinct isotopes) varied with species, season and year. Some species showed clearer spatial signature patterns than others (Fig. 1.1 and 1.2). Egyptian Goose signatures showed the clearest distinctions by site (Fig. 1.1, 1.2 and 1.3) in all isotopes tested. Red-billed Teal and Cape Teal signatures were distinct by site only in δ^{15}N. Yellow-billed Ducks were not distinct by site in both δ^{15}N and δ^{14}C.

Varying compositions of plants of C_3 and C_4 photosynthetic pathways yield different δ^{13}C signatures. Plants that are C_4 based are more enriched (with a mean of about -13‰) than C_3 plants (with a mean of about -27‰; Koch et al. 1995). Food webs dominated by C_4 would result in higher δ^{13}C values of bird feathers. Even if the bird does not directly feed from the vegetation, other organisms lower on the food web relative to the bird can pass on the isotope signatures to the bird. Additionally, within C_3 plants, δ^{13}C is more enriched in drier than in moister areas (Marra et al. 1998; Rubenstein and Hobson 2004). Higher δ^{13}C values are also related to water-use efficiency in C_3 plants (Rubenstein & Hobson 2004). The patterns described above offer an explanation why the Barberspan birds had higher δ^{13}C values than birds from other sites. Barberspan is dominated by grasses and it is surrounded by farms predominantly cultivated for maize (C_4 plants), it is drier than Strandfontein and Manyame. Strandfontein is coastal and moister than Barberspan and Manyame.

Even though δ^{15}N is primarily used to assess trophic position in food webs, higher δ^{15}N values are linked to animals foraging in arid environments (Ambrose 1991).

Additionally, anthropogenic inputs such as fertilizer, tilling of soils and sewage effluent can influence food web isotope signature patterns (Hobson 1995; Das et al. 2003). Rubenstein and Hobson (2004) also noted than marine ecosystems are δ^{15}N enriched. The influence of the ocean and the high salinity of lower-lying ponds at Strandfontein may explain why Strandfontein birds were generally δ^{15}N enriched relative to Barberspan and Manyame catchment birds. It is also possible that Strandfontein birds are nutritionally or water stressed, which can further lead to high δ^{15}N values (Hobson and Clark 1992).

Because Egyptian Geese showed separation of sites in both isotopes whilst other duck species did not (Cape Teals and Red-billed Teals were only distinct in δ^{15}N), there appear to be inter-species differences in stable isotope composition variation. This can indicate different habitat usage, different diet and foraging behaviours and different metabolic rates across species as proposed by Marra et al. (1998); Yohannes et al. (2008) and Jaeger et al. (2009). Such findings suggest that biological processes do not always allow efficient tissue reflection of isotope patterns in the environment (Cherel et al. 2006; Rocque et al. 2006). This reduces the reliability of the isotope technique in movement studies. Overall the results showed a moderate distinction of sites using stable isotopes in growing feathers of ducks.

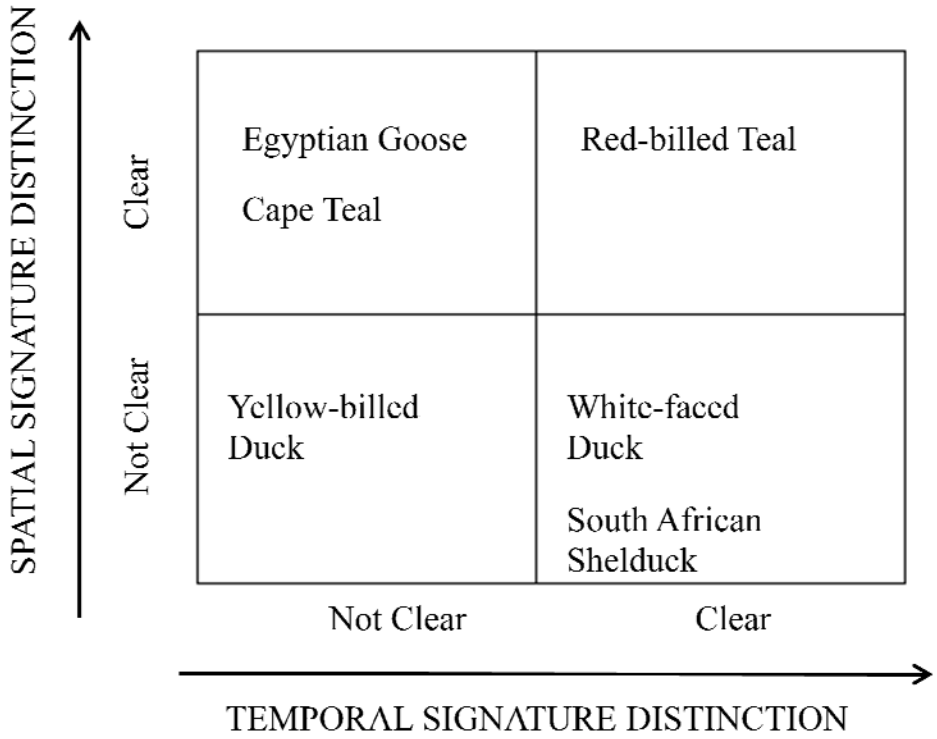


Figure 1.3: Classification of species depending on how clear their stable isotope distinctions were in space and in time (spatial and temporal signature distinction respectively). Some species could be separated both spatially and temporally (clear), others could not be distinguished (not clear) using feather isotope signatures δ^{15}N, δ^{13}C, and δD.

Geographic location

C_3/C_4 plant distribution varies with latitude. This is why $\delta^{13}C$ values display a strong latitudinal trend (Still et al. 2003). My study sites are separated in latitude by close to 10° making the existence of a $\delta^{13}C$ isotope gradient probable. As affirmed by Rubenstein and Hobson (2004), $\delta^{13}C$ decreases with increasing latitude, my findings alluded to this by showing Barberspan and Manyame birds with generally higher $\delta^{13}C$ values than Strandfontein birds.

According to Yohannes et al. (2007) longitudinal trends in the proportion of C_3/C_4 plants in Africa are not yet well documented. Using feathers of wintering Aquatic Warblers (*Acrocephalus paludicola*), Pain et al. (2004) found no significant pattern in mean $\delta^{13}C$ in relation to either longitude or latitude. Even though the highest concentrations of C_4 vegetation in African is in the tropical and subtropical grassland and savanna regions, there is significant coverage of C_3 vegetation in highland regions of Ethiopia (Yohannes et al. 2007). There is a chance that C_3 differences observed involved vegetation composition differences along a longitudinal axis.

Diet and foraging behaviour

Interspecies differences in isotope discrimination during diet-tissue nutrient assimilation processes play a role in shaping animal tissue isotope signatures. Metabolic rate variations have been reported to cause fluctuations in isotope uptake during diet-tissue assimilation processes (Bearhop et al. 2002). Element routing, metabolic rates and diet-tissue discrimination of stable isotopes vary with species (Gannes et al. 1997) compromising the technique's accuracy. Biological processes are species-specific and may vary with individuals in some species depending on physical competitiveness, especially in resource limited environments. Species-specific calibrations are necessary. However, this complicates use of the technique to study bird movements in southern Africa. Furthermore, some species may extensively use food reserves which can introduce unaccountable sources of variation. Fox et al. (2009) demonstrated that endogenous contributions may occur during times of food stress in the Greylag Goose (*Anser anser*). This can lead to inaccurate representation of isotopic ratios of diet in feathers at the time of tissue growth, reducing the reliability of new locally grown feathers as proxies to the moulting site's signature.

Foraging behaviour indirectly affects signature through diet choice, which is reliant upon various extrinsic factors (Ogilvie and Pearson 1994; Todd 1995). Intra and inter-specific competition for instance, depending on food availability and population

compositions at different moulting sites, determines which food a bird would take most cost-effectively; bird counts (appendix 2) at different study sites revealed high variability in abundance and diversity of species both spatially and temporally. Further research is necessary to investigate the influence of dietary processes and foraging behaviour on tissue isotope signatures in southern African ducks.

Seasonal differences in isotopic signatures

My species showed inter-individual variations in moult schedules (appendix 1 and 3), I therefore managed to get a sample of moulting birds in each season. Stable isotope differences between seasons probably reflect temporal isotope signature changes in a similar habitat (Yohannes et al. 2007). Only the White-faced Duck and South African Shelduck yielded significantly different signatures between summer and winter in $\delta^{13}C$. Egyptian Geese yielded a significantly different signature in only δD across seasons. This can be a consequence of deuterium's sensitivity to moisture levels in the atmosphere and because southern Africa has drastic changes in precipitation between summer and winter. δD isotope signature in Red-billed Teal feathers were not distinct between summer and winter as in Egyptian Geese. This might be due to variation in foraging behaviours and metabolic rates between the two species (Cabanellas-Reboredo 2009).

Red-billed Teals and Yellow-billed Ducks had a constant signature between the two seasons in all isotopes tested. Inter-seasonal isotope signature consistency implies that the species do not drastically change moulting habitat with season, or moulting site signatures do not change drastically between seasons. White-faced Ducks and South African Shelducks showed inter-seasonal changes in site signatures. These species are likely to be changing foraging habitat between seasons. Changes in abundance and diversity of food species due to changes in environmental factors such as temperature, light, water and humidity (Lipp et al. 1998; Yohannes et al. 2007) would account for moulting habitat changes.

Between year differences in isotopic signatures

Three of the species tested across different moulting years (Egyptian Goose, Yellow-billed Duck and Cape Teal) showed consistency for both feather $\delta^{13}C$ and $\delta^{15}N$ values. Red-billed Teals, South African Shelducks and White-faced Ducks did not. Red-billed Teals had significantly different isotope signatures across years in $\delta^{13}C$ and $\delta^{15}N$; South African

Shelduck in $\delta^{14}C$ and White-faced Ducks in $\delta^{15}N$. Similar feather isotope signatures across years indicate that ducks tended to return to, or to maintain the same moulting site and selected diets that generated similar isotopic signatures (Yohannes et al. 2007). Year to year $\delta^{15}N$ values suggest that ducks fed at a similar trophic level during moult across different years (Hobson 1999). Those species that did not show inter-annual consistency in signature pattern could be shifting moulting habitats and diets from year to year, possibly as a result of competition from other species at moulting sites. This is plausible because dramatic changes in abundance (and to some extent the diversity of ducks) are evident in the counts (appendix 2). There are noticeable population changes across seasons and years at each of the study sites. For example, in 2007 Barberspan recorded a total of 5.57 ducks/ha of South African Shelducks, the number went up to 32.36 ducks/ha in 2008.

Deuterium

Clark et al. (2006) demonstrated that precipitation isotopes can influence wetland signature despite the fact that wetlands receive and hold water from diverse sources in storage over long periods. A higher than normal fractionation (Table 1.5) between precipitation isotopes (D_p calculated from the online GNIP precipitation isotope calculator) and feather isotopes (D_f) is because water held in storage over long periods accumulates the heavier H at the expense of the lighter H which readily leaves on evaporation (Clark et al. 2006). The Hydrogen results (as expected) showed a higher than the average fractionation (~ -25‰) reported in other studies between feathers and precipitation (Wassenaar and Hobson 2000; Hobson et al. 2004), δD fractionation values ranged from -36 to -61‰ depending on the species.

Table 1.5: Annual average Deuterium isotopes in precipitation (δD_p) and average feather isotopes (δD_f) from three study sites, Strandfontein (STR), Barberspan (BAR) and Manyame catchment (MAN). Fractionation between precipitation and feather isotopes is also shown for each species at each site (δD_p to D_f). EG = Egyptian Goose, RBT = Red-billed Teal. δD_p values were derived from the online calculator (Bowen 2009, www.waterisotopes.org). The average yearly signature for each species feather was more depleted in relation to isotopes in precipitation.

		δD_p	δD_f EG	δD_f RBT
STR	Mean	-12±1	-70.21	-48.68
	Fractionation (D_p to D_f)		58	36
BAR	Mean	-21±6	-63.92	-53.31
	Fractionation (D_p to D_f)		42	32
MAN	Mean	-32±1	-93.44	-78.16
	Fractionation (D_p to D_f)		61	46

Conclusions

Duck species vary in their expression of spatial patterns of different stable isotope signatures. Independent variations in $\delta^{15}N$, $\delta^{13}C$, and δD (such that δD distinguished ducks from different moulting locations where $\delta^{15}N$ and $\delta^{13}C$ could not) demonstrate the effectiveness of multi-isotope approaches as in other studies (Clark et al. 2006 ; Ramos et al. 2009). However, even though the study was able to distinguish populations of ducks from different wetlands, the varying degrees of distinction by species were unexpected. This however proves that organismal biology can deviate from environmental isotope patterns at regional scales as also shown at continental scales by Rocque et al. (2006). Three out of four duck species tested across different sites showed distinction in at least one isotope. It is clear that not all southern African ducks are good candidates for stable isotope-based movement studies. Better species would be the more catchable ones which can be sampled across as many sites as possible and showing inter-seasonal and inter-annual consistency in isotope signatures e.g., Egyptian Geese and Red-billed Teals.

Literature cited:

Abdennadher, A., Ramirez, F., Salah, M., Ruiz, X., Jover, L., Sanpera, C. 2010. Biomonitoring of coastal areas in Tunisia: Stable isotope and trace element analysis in the Yellow-legged Gull. *Marine Pollution Bulletin*, 60, 440-447.

Ambrose, S. H. 1991. Effects of diet, climate and physiology on Nitrogen isotope abundance in terrestrial food webs. *Journal of Archaeology and Science,* 18, 293-317.

Baldassarre, G.A.R., Bolen, E.G. 2006. *Waterfowl ecology and management*, 2nd edn. Malabar: Krieger Publishing.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W. 2002. Factors that influence assimilation rates and fractionation of Nitrogen and Carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology*, 75, 451-458.

Bowen, G.J. 2009. The Online Isotopes in Precipitation Calculator, http://www.waterisotopes.org.

Bowen, G.J., Revenaugh, J. 2003. Interpolating the isotopic composition of modern meteoric precipitation. *Water Resources Research,* 39, 1299-1312.

Bowen, G.J., Wassenaar, L.I., Hobson, K.A. 2005. Global application of stable Hydrogen and Oxygen isotopes to wildlife forensics. *Oecologia,* 143, 337-348,

Cabanellas-Reboredo, M., Deudero, S., Blanco, A. 2009. Stable-isotope signatures (δ^{13}C and δ^{15}N) of different tissues of *Pinna nobilis* Linnaeus, 1758 (Bivalvia), isotopic variations among tissues and between seasons. *Journal of Molluscan Studies*, 75, 343-349.

Cerling, T.E., Wittemyer, G., Ehleringer, J.R., Remien, C.H., Douglas-Hamilton, I. 2009. History of animals using isotope records (HAIR): A 6-year dietary history of one family of African elephants. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 8093-8100.

Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W., Graves, G.R. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia*, 109, 132-141.

Cherel, Y., Phillips, R.A., Hobson, K.A., McGill, R. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters*, 2, 301-303.

Clark, R.G., Hobson, K.A., Wassenaar, L.I. 2006. Geographic variation in the isotopic (δD, δ^{13}C, δ^{15}N, δ^{34}S) composition of feathers and claws from Lesser Scaup and Northern

pintail: implications for studies of migratory connectivity. *Canadian Journal of Zoology*, 84, 1395-1401.

Das, K., Beans, C., Holsbeek, L., Mauger, G., Berrow, S.D., Rogan, E., Bouquegneau, J.M. 2003. Marine mammals from the southern North Sea: feeding ecology data from $\delta^{13}C$ and $\delta^{15}N$ measurements. *Marine Ecology Progress Series*, 263, 287-298.

Farmer, A., Rye, R., Landis, G., Bern, C., Kester, C., Ridleyet, I. 2003. Tracing the pathways of neotropical migratory shorebirds using stable isotopes: a pilot study. *Isotopes In Environmental And Health Studies*, 39, 169-177.

Food and Agriculture Organization of the United Nations (FAO). 2006. *Gridded livestock of the world.* Rome: FAO.

Forero, M.G., Hobson, K.A. 2003. Using stable isotopes of Nitrogen and Carbon to study seabird ecology: applications in the Mediterranean seabird community. *Scientia Marina*, 67, 23-32.

Fox, A.D., Hobson, K.A., Kahlert, J. 2009. Isotopic evidence for endogenous protein contributions to Greylag Goose *Anser anser* flight feathers. *Journal of Avian Biology*, 40, 108-112.

Fox, A.D., Kahlert, J. 1999. Adjustments to Nitrogen metabolism during wing moult in Greylag Geese *Anser anser*. *Functional Ecology*, 13, 661-669.

Gannes, L.Z., Obrien, D.M., Del Rio, C.M. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology,* 78, 1271-1276.

Girling, S.J. 1991. Feather growth, including nutritional and endocrine factors. Edinburgh: The Braid Veterinary Hospital.

Hebert, C.E., Wassenaar, L.I. 2001. Stable Nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environmental Science and Technology*, 35, 3482-3487.

Hobson, K.A. 1995. Reconstructing avian diets using stable Carbon and Nitrogen isotope analysis of egg components: Patterns of isotopic fractionation and turnover. *Condor*, 97, 752-762.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes. *Oecologia,* 120, 314-326.

Hobson, K.A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, 11, 157-164.

Hobson, K.A. 2008. Applying isotopic methods to tracking animal movements. In: Hobson K.A., and Wassenaar, L.I., (eds). 2008. *Tracking animal migration with stable isotopes*. pp. 45-78, London: Elsevier.

Hobson, K.A., Clark, R.G. 1992. Assessing Avian Diets Using Stable Isotopes: Turnover of $\delta^{13}C$ in Tissues. *Condor*, 94, 181.

Hobson, K.A., Wassenaar, L.I. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable Hydrogen isotopic analysis of feathers. *Oecologia,* 109, 142-148.

Hobson, K.A., Aubry, Y., Wassenaar, L.I. 2004. Migratory connectivity in Bicknell's Thrush: Locating missing populations with Hydrogen isotopes. *Condor,* 106, 905-909.

Hobson, K.A., Wassenaar L.I., 2008. (eds). *Applying isotopic methods to tracking animal movements*. London: Elsevier.

Hockey, P.A.R., Dean, W.R.J., Ryan, P.G., (eds). 2005. *Roberts' birds of southern Africa*: Cape Town: Trustees of the John Voelcker Bird Book Fund.

Inger, R., Bearhop, S. 2008. Applications of stable isotope analysis to avian ecology. *Ibis,* 150, 447-461.

Jaeger, A., Connan, M., Richard, P., Cherel, Y. 2009. Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Marine Ecology Progress Series,* 401, 269-277.

King, J.R. 1981. Energetics of avian moult. *17th International Ornithological Congress,* 1, 312-317.

Koch, P.L., Heisinger, J., Moss, C., Carlson, R., Fogel, M.L., Behrensmeyer, A.K. 1995. Isotopic tracking of change in diet and habitat use in African Elephants. *Science,* 267, 1340-1343.

Lipp, J., Trimborn, P., Payer, H.D. 1998. Influence of relative humidity on the $\delta^{13}C$ content in bean plants (*Vicia faber*): a model experiment in exposure chambers. In: International atomic energy agency (IAEA) proceedings series; isotope techniques in the study of environmental change; IAEA 14-18 April 1997, Vienna, pp. 878-881.

Marra, P.P., Hobson, K.A., Holmes, R.T. 1998. Linking winter and summer events in a migratory bird by using stable-Carbon isotopes. *Physiology*, 282, 1884-1886.

Nathan, R. 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19050-19051.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E., Cain, M.L. 2003. Methods for estimating long-distance dispersal. *Oikos*, 103, 261-273.

Nicholson, S.E. 2000. The nature of rainfall variability over Africa on time scales of decades to millennia. *Global and Planetary Change,* 26, 137-158

Ogilvie, M., Pearson, B. 1994. *Wildfowl Behaviour Guide*, Melbourne: Hamlyn.

Ramos, R., Ramirez, F., Sanpera, C., Jover, L., Ruiz, X. 2009. Feeding ecology of Yellow-legged Gulls *Larus michahellis* in the western Mediterranean: a comparative assessment using conventional and isotopic methods. *Marine Ecology Progress Series*, 377, 289-297

Ringelman, J.K. 1990. Habitat management for moulting waterfowl: Wildlife Damage Management, Internet Center for Waterfowl Management Handbook. Colorado: University of Nebraska.

Rocque, D.A., Ben-David, M., Barry, R.P., Winker, K. 2006. Assigning birds to wintering and breeding grounds using stable isotopes: lessons from two feather generations among three intercontinental migrants. *Journal of Ornithology*, 147, 395-404.

Rubenstein, D.R., Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution*, 19, 256-263.

Sinclair, M., Bruckner, G.K., and Kotze, J.J. 2005. Avian influenza in ostriches: epidemiological investigation in the Western Cape Province of South Africa. *Elsenburg Journal,* 2, 2-4.

Sokal, R.R., Rohlf, F.J. 1994. *Biometry: the principles and practice of statistics in biological research,* Freeman: New York.

Still, C.J., Berry, J.A., Collatz, G.J., DeFries, R.S. 2003. Global distribution of C_3 and C_4 vegetation: Carbon cycle implications. *Global Biogeochemical Cycles,* 17, 1006-1029.

Todd, F. 1996. *Natural history of the waterfowl*. California: San Diego Natural History Museum.

Wassenaar, L.I., Hobson, K.A. 2000. Improved method for determining the stable-Hydrogen isotopic compositon (δD) of complex organic materials of environmental interest. *Environmental Science and Technology,* 34, 2354-2360

West, J.B., Bowen, G.J., Cerling, T.E., Ehleringer, J.R. 2006. Stable isotopes as one of nature's recorders. *Trends in Ecology and Evolution,* 21, 408-414.

Yohannes, E. 2007. Feather stable-isotope profiles reveal stopover habitat selection and site fidelity in nine migratory species moving through sub-Saharan Africa. *Journal of Avian Biology,* 38, 347-355.

Yohannes, E., Hobson, K.A., Pearson, D.J., Wassenaar, L.I. 2005. Stable isotope analyses of feathers help identify autumn stopover sites of three long-distance migrants in north-eastern Africa. *Journal of Avian Biology,* 36, 235-241.

Yohannes, E., Hansson, B., Lee, R.W., Waldenstrom, J., Westerdahl, H., Akesson, M., Hasselquist, D., Bensch, S. 2008. Isotope signatures in winter moulted feathers predict malaria prevalence in a breeding avian host. *Oecologia*, 158, 299-306.

Zuur, A.F., Ieno, E.N., Elphick, C.S. 2009. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3-14

CHAPTER 2

CAN FEATHER STABLE ISOTOPES REVEAL DIFFERING MOBILITY AMONG SOUTHERN AFRICAN DUCKS?

Abstract

Duck feathers moderately reflect regions of distinct stable isotope proportion patterns within southern Africa. Use of diverse sites by ducks can be inferred from isotope signatures of feathers grown at different times of the year. This study investigated whether the stable isotope profiles of southern African duck feathers can reveal use of different sites and whether the technique can be used to determine differing mobility among ducks. Comparisons were carried within each population of ducks between flight (growing flight feathers from moulting ducks and fully grown flight feathers from non-moulting ducks) and body feathers of 7 southern African ducks (Egyptian Geese from Strandfontein and Barberspan, Spur-winged Geese from Strandfontein and Barberspan, Red-billed Teals from Lake Ngami; South African Shelducks, Cape Shovelers, Yellow-billed Ducks, and Cape Teals from Barberspan). I predicted that the more mobile species would show more and stronger signature distinctions between different feather types grown at different life phases: to test this, reference was made to mobility scores from other studies. Relative to body feathers, Barberspan Cape Shovelers' fully grown flight feathers were δ^{13}C depleted, Strandfontein Egyptian Geese flight feathers (both growing and fully grown) were δ^{15}N enriched, Barberspan South African Shelducks' growing flight feathers were δ^{15}N depleted and the Strandfontein Spur-winged Geese' fully grown flight feathers were δ^{13}C depleted. Body and flight feathers of Yellow-billed Ducks and Cape Teals from Barberspan were not distinct. However, these patterns could not be exactly related to the mobility of each of the species. Isotope signature distinctions between duck feathers grown at different life stages cannot be clearly underpinned to the use of different sites alone, neither can similar signatures depict that a species did not move; signature distinctions can be due to seasonal diet variations, whilst non-distinctions can be that the species moved during other times outside breeding and moulting phase. I therefore concluded that the method needs stringent calibration techniques for it to be usable in tracing dispersal pattern variations among

southern African ducks. Future studies should investigate duck diet and feeding ecology and how it influences results in isotope-based movement studies.

Introduction

To date, movement ecology of southern African ducks has largely depended on observation and ring recoveries. Despite long-term ringing schemes the information generated is not well detailed due to the low probability of ringing recoveries. Satellite tracking methods are expensive and ultimately limited to providing information on a few individual movements (Hobson 2003). Movement is a crucial component of ecology because it determines the rates of processes driving biological invasions, spread of pathogens and diseases, and persistence of local populations, especially in this world of ever increasing habitat fragmentation and global environmental changes (Nathan 2008; Lincoln et al. 1982, pp 25).

Mobility and movement patterns vary considerably among southern African ducks (Harrison et al. 1997; Underhill et al. 1999). Risk aversion, social dominance and seasonal dynamics of resources play important roles in shaping mobility (Baldassare and Bolen 2006; Roshier et al. 2006; 2008). Southern Africa is characterised by stochastic and resource poor environments which facilitate opportunism and nomadism in ducks (Roshier et al. 2008). Consequently movement patterns of ducks in southern Africa are difficult to predict (Cumming et al. 2008).

Decades of ringing have produced scant information on mobility of southern African ducks (Harrison et al. 1997). However, ring returns are the only available sources of information on mobility at present except for the work of Siegfried et al (1977) which investigated on the African Black Duck's distribution using radio transmitters. More movement studies using satellite telemetry are still yet unpublished. Ring recovery information shows variation in mobility of different ducks of southern Africa, and this allows for tests of the effectiveness of stable isotopes at detecting duck movements within the region. Species can be roughly classed according to length and frequency of distances travelled, with attention to the proportion of ringed to recovered number of individuals per species (Cumming et al. 2008). Logically, more mobile species have a higher chance of encountering geographically and isotopically distinct sites, and showing more signature distinctions among feathers grown at different phases of the annual cycle.

Stable isotope signature patterning originates from environmental drivers: geology, physiography, climatology, and biology. These drivers may influence different isotopes

uniquely but all resulting in either spatially continuous or spatially discrete isotopic patterns (isoscapes). Many researchers have managed to study dispersal, movements and habitat usage in birds using the existence of isoscapes of δD (e.g., Hobson et al. 2003) and δ^{13}C and δ^{15}N (e.g., Rubenstein et al. 2002, Yohannes et al. 2007; 2008). Isotopic patterns are passed from the environment to biological tissues through nutrition (Sorensen et al. 2009) and spatial patterns can be revealed in animal tissue. As a bonus, stable isotope techniques can offer a more affordable and high data yielding option for studying movements of animals; satellite telemetry is expensive and mark-recapture techniques are characterized by low rates of recovery.

Patterns of Carbon stable isotopes in the environment are determined by vegetation composition and geography. Ecosystems dominated with C_4 vegetation are ^{13}C enriched compared to C_3 vegetation types due to differences in how the enzymes used in the two pathways discriminate against ^{13}C (Bowen and West 2008). Additionally, in C_3 ecosystems, xeric areas are more ^{13}C enriched than mesic areas due to limited stomatal opening in plants under dry conditions which reduces the ^{13}C loss into the atmosphere (Bowen and West 2008). Geographically, there has been evidence of latitudinal patterns of δ^{13}C whereby higher latitudes get progressively depleted (Table 1 and 2; Bowen and West 2008).

Nitrogen isotope patterns in the environment vary with weather patterns at the site of interest. Weather drives root-mychorrizal reactions and Nitrogen cycling. Additionally, anthropogenic inputs to the environment also influence δ^{15}N patterns. Generally dry regions are more ^{15}N enriched than wet regions, and human influenced regions show variations depending on fertilizer application with agriculture and sewage effluent (Bowen and West 2008). ^{15}N is enriched close to marine environments (Table 1 and 2; Rubenstein and Hobson 2004).

Hydrogen isotope patterns in the environment are influenced by precipitation patterns. Precipitation processes discriminate against D in such a way that the heavy D composed rain molecules are released first. The resulting pattern is a progressive depletion in D with increase in altitude as well as latitude and distance from the water source (Table 1 and 2; Rubenstein and Hobson 2004; Bowen and West 2008).

Ducks moult body and flight feathers at differently timed phases of their annual cycle. Flight feathers are grown during the moulting phase and body feathers after the wintering phase, mostly during breeding (Scott and Rose 1996; Todd 1996; Hockey et al. 2005; Kear 2005). Secure and forage rich sites with plenty of water are particularly selected for the

flightless moult (Brickell 1988; Hockey et al. 2005; Baldassarre and Bolen 2006). Chapter one showed that the majority of ducks from different moulting locations had moderately distinct isotope signatures in growing flight feathers. This suggested the existence of isotope gradients in the southern African region meaning that different feathers grown during different life-stages can be compared to investigate whether isotopically and possibly geographically distinct sites were used.

This chapter tests whether stable isotopes detect the use of different sites (movements) by southern African ducks. In particular, I asked two questions: (1) Do local populations of more mobile species show greater signature variation in feathers grown during different life-stages? (2) Does variation of stable isotope signature patterns in feathers change across species and from one study site to another?

Methods

Feathers of 7 duck species from three wetlands in southern Africa (Strandfontein, Barberspan and Lake Ngami) were sampled and analysed for $\delta^{15}N$, $\delta^{13}C$ and δD. Growing flight feathers from moulting ducks and fully grown flight feathers from non-moulting ducks (second secondary feather; S2) were compared against body feathers (growing S2 versus back feather and fully grown S2 versus back feather). Non-moulting ducks with fully grown flight feathers might have moulted elsewhere. Fully grown flight feathers versus back feathers from the same bird can determine whether or not the previous unknown moulting location was the same as the breeding site. Growing flight feathers versus back feathers from the same individual can determine whether or not the current moulting location used is the same as the breeding site. Similar signatures between tissues under comparison imply similar diets and probably similar geographic locations being used.

Comparison of feathers grown at different life-phases was carried out by capture site; each site has its own unique climatic conditions as shown by vegetation compositions (Fig 1), bird population dynamics (appendix 2), and topographical characteristics. Duck foraging and movement ecology is likely to differ among sites. Ducks probably experience external pressures variably by site, meaning unique diet quality and selection by site. Combining sites in comparing different feathers would confound results.

I limited the analysis to one season (summer) and one year (2008) because the majority of back feathers were collected during the summer of 2008; chapter 1 proved that

isotope analysis needs to be time explicit. For mobility comparisons, mobility scores were taken from Cumming et al. (2008) in which six expert ornithologists were asked to score African duck species on the mobility criterion as part of seven *a priori* risk criteria (in avian influenza spread). They used a ranking system ranging from 1 to 5:

1 = largely sedentary

2 = some short-distance movement

3 = regular short-distance movement, some long-distance movement

4 = regular long-distance movement

5 = regular long- and short-distance movement

The ranking also considered maximum distance moved and proportion of ringed birds recovered. These data were compared to a hierarchical arrangement of species from those showing the strongest signature distinctions to those showing the weakest. Detailed methods on sample collection and isotope analysis were described in the general methods section.

Statistical Analysis

Data for each species were normally distributed (one sample Kolmogorov-Smirnov tests, all $P > 0.05$). Normality testing was carried out in Predictive Analysis Software (PASW) version 18. All other statistical tests (appendix 7) were carried out in Statistica version 8. Paired t-tests were carried out for each of the species with individuals from whom two feather types (flight and back feather) were sampled (a total of 224 individuals; appendix 5). Comparisons were site specific; my study sites were located in different vegetation biomes experiencing different climatic conditions. Since from some species, I had either a growing flight feather and a back feather or a fully grown flight feather and a back feather, I paired them up separately i.e., back feather versus growing flight feather and back feather versus fully grown flight feather. Fully grown feathers showed different results from growing flight feathers when compared to body feathers of the same species. This showed that the moult status affected results and feathers in different moult status had to be compared separately. Biologically it makes sense because a species may use isotopically distinct moulting sites or habitats for different moulting phases.

Paired t-tests had more power for drawing movement inferences because both feathers compared came from the same individual. I then used scatterplots (δ^{15}N against δ^{13}C to investigate individual tendencies. Since the scatter-plots for each species showed random and diverse patterns in flight feather - body feather relationships, I suggested there was high inter-

individual diet and possibly site change between different life phases and this could not be clearly and fully shown in paired t-test comparisons alone; average values were possibly masking the predominant individual patterns. I therefore calculated the individual differences between body and flight feather isotope signatures per individual, defined by the vector $\Delta\delta^{15}N \rightarrow \Delta\delta^{13}C$. I used the Pythagoras equation to calculate the distance: $\sqrt{[(\Delta\delta^{15}N)^2 + (\Delta\delta^{13}C)^2]}$. I compared these compounded individual signature distances/distinctions (between flight and back feathers) by plotting them against categories defined by species in a hierarchy according to each species' mobility score (Cumming et al. 2008; Fig 2.3).

Results

Distinction of signature between fully grown S2 and back, growing S2 and back feathers varied with site of capture, and species as shown in Fig 2.3 and appendix 7. Four duck species showed distinction between flight feather and back feather signatures. Cape Shoveler and Spur-winged Goose from Barberspan and Strandfontein respectively had distinct isotope signatures between fully grown flight and back feathers. South African Shelducks from Barberspan had isotopically distinct growing flight and body feathers in $\delta^{15}N$. Strandfontein Egyptian Geese' growing and fully grown flight feathers were both distinct from body feathers in $\delta^{15}N$. All the paired t-test results are displayed in appendix 7.

At Strandfontein, Egyptian Geese growing and fully grown flight feathers were enriched relative to body feathers in $\delta^{15}N$, yet Spur-winged Geese' fully grown flight feathers were depleted relative to body feathers in $\delta^{13}C$. Egyptian Geese population had birds that used two successive moulting diets and/or sites which were isotopically distinct from their breeding sites, where body feathers were grown. At Strandfontein, Spur-winged Geese population had ducks which used only one moulting phase diet and possibly site which was different from the breeding; more individuals possibly remained on the same site for one moulting and one breeding phase prior to the capture. Egyptian Geese here appeared to be more mobile than Spur-winged Geese and this agrees with mobility scores.

At Barberspan, South African Shelducks showed a stronger p value ($P < 0.01$) and had $\delta^{15}N$ depleted growing feathers relative to body feathers. Cape Shovelers at the same site had $\delta^{13}C$ depleted fully grown flight feathers relative to body feathers but with a weaker p value. South African Shelduck population had individuals possibly using more distinct diets

and/or sites than Cape Shovelers, implying they are more mobile than South African Shelducks. However, this does not exactly agree with the given mobility scores.

Yellow-billed Ducks and Cape Teals from both Strandfontein and Barberspan, as well as Red-billed Teals from Lake Ngami did not show signature distinctions between flight and back feathers yet mobility scores show them as highly mobile (3.8 for Cape Teals and 4.8 for Red-billed Teals). These species probably moved during other times outside the breeding and moulting phases.

Even though some species had statistically similar isotope signatures between body and flight feathers on the overall picture, scatter plots in Figs 2.1 and 2.2 demonstrate that there were random individual feather signature patterns within the same population of ducks. Comparing the Pythagoras distances $\sqrt{[(\Delta\delta^{15}N)^2 + (\Delta\delta^{13}C)^2]}$ between feather pairs with mobility scores did not show any clear relationship. Even though Barberspan birds had a near-positive increase in isotope distinctions with increase in mobility score (Fig 2.3), distinctions were highly variable across individuals. The general trend was that the more the birds sampled, the wider the variation of distinction distances across individuals within a population at a particular site (Fig 2.3).

A more detailed account of the results per species is presented in the following sections.

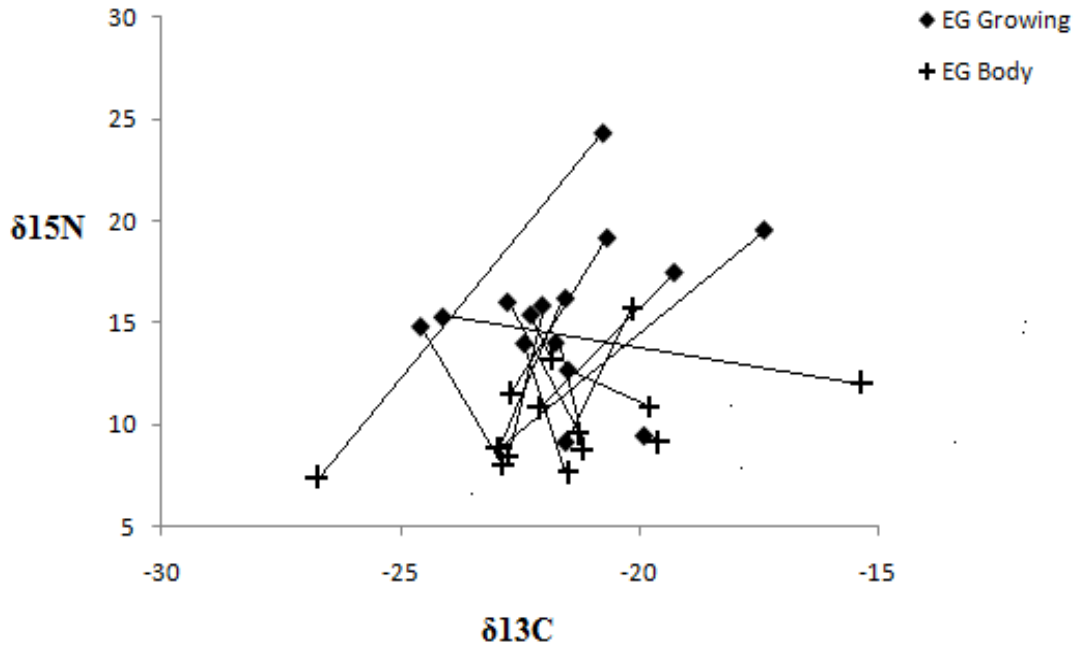


Figure 2.1: Carbon and Nitrogen isotopes (δ^{13}C and δ^{15}N) paired-scatter-plot for Strandfontein Egyptian Geese growing flight feathers (EG Growing) and body feathers (EG Body) from each individual bird (joined by a line).

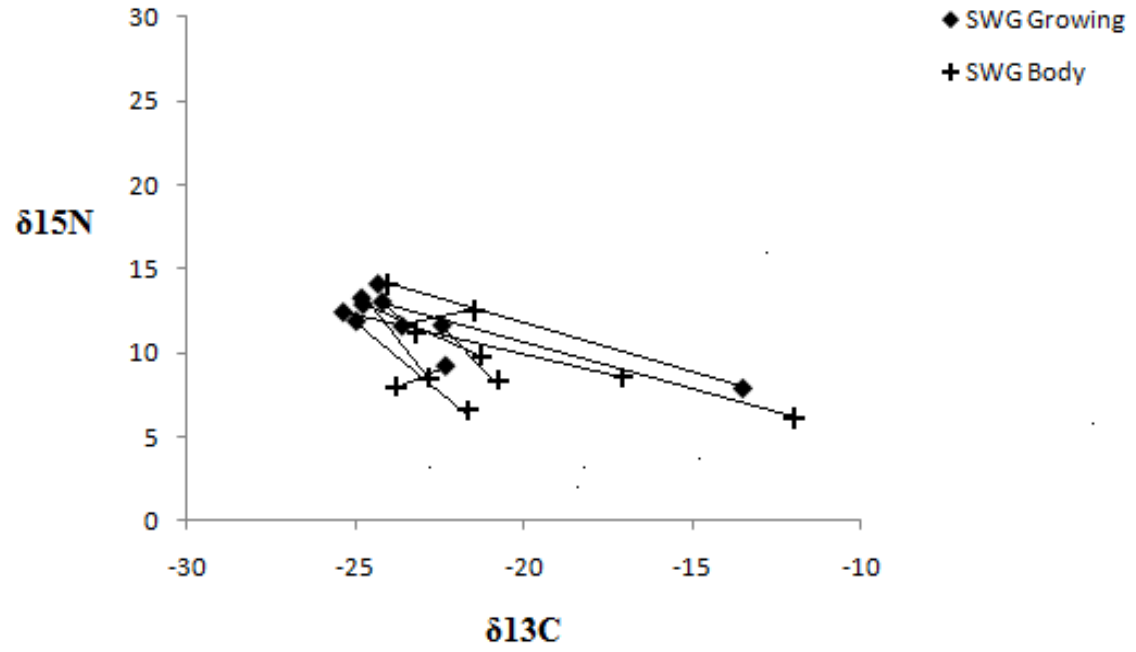


Figure 2.2: Carbon and Nitrogen isotopes (δ^{13}C and δ^{15}N) paired scatter-plot for Strandfontein Spur-winged Goose growing flight feathers (SWG Growing) and body feathers (SWG Body) from each individual bird (joined by a line).

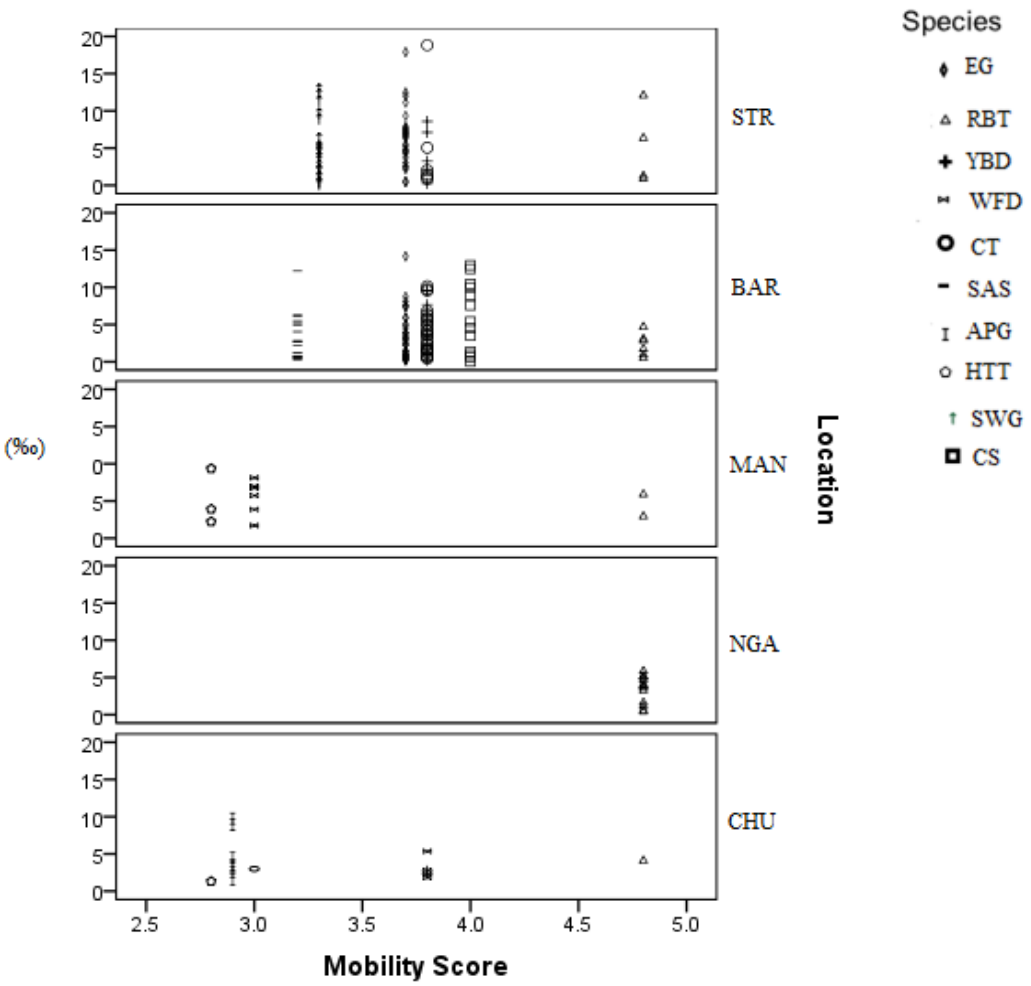


Figure 2.3: Stable isotope signature distinction $\Delta\delta^{15}N \rightarrow \Delta\delta^{13}C$ (compounded; ‰) between flight and body feathers from each duck plotted against categories of mobility score per species (mobility scores from Cumming et al. 2008). Species: EG = Egyptian Goose, RBT = Red-billed Teal, YBD = Yellow-billed Duck, WFD = White-faced Duck, CT = Cape Teal, SAS = South African Shelduck, APG = African Pygmy Goose, HTT = Hottentot Teal, SWG = Spur-winged Goose, CS = Cape Shoveler. **NB** – other species of small sample sizes (n < 10) have been included in this figure to give a clearer picture of signature differences between body and flight feathers across more sites.

Egyptian Goose

Egyptian Geese from Strandfontein showed distinction between growing flight and body feathers (n = 15) as well as between fully grown and body feathers (n = 13) in $\delta^{15}N$ (Fig 2.1). Barberspan Egyptian Geese flight (n = 24 for growing and n = 16 for fully grown feathers) and body feathers were not distinct in both $\delta^{15}N$ and $\delta^{13}C$. I did not have Egyptian Geese body feathers from the Manyame catchment, Lake Ngami and Lake Chuali (ref appendix 7 for paired t-test results).

South African Shelduck

Growing flight feathers and back feathers of South African Shelducks from Barberspan (n= 16) were distinct in $\delta^{15}N$ but similar in $\delta^{13}C$. (appendix 7).

Spur-winged Goose

Fully grown flight and back feathers of Spur-winged Geese from Strandfontein (n = 10) were distinct in $\delta^{13}C$; growing and back feathers (n = 10) were similar in both $\delta^{15}N$ and $\delta^{13}C$ (Fig 2.2). Fully grown and back feathers of Spur-winged Geese from Barberspan (n = 14) were similar in both $\delta^{13}C$ and $\delta^{15}N$ (ref appendix 7 for paired t-test results).

Cape Shoveler

Fully grown and back feathers of Cape Shovelers from Barberspan (n = 13) were distinct in $\delta^{13}C$; I did not have growing flight feathers (appendix 7).

Yellow-billed Duck

Fully grown flight feathers and back feathers of Yellow-billed Ducks from Barberspan (n = 12), were similar in both $\delta^{13}C$ and $\delta^{15}N$ (appendix 7).

Cape Teal

Barberspan Cape Teals were not distinct between fully grown and back feather isotope signatures (n = 20; appendix 7); there were no samples for growing flight feathers (ref appendix 7 for paired t-test results).

Red-billed Teal

Red-billed Teals from Lake Ngami (n = 14) did not show significant differences in isotope signatures between fully grown flight and back feathers (Ref appendix 7 for paired t-test results).

Discussion

Isotope signature distinctions did not occur as exactly expected. Some of the highly mobile species according mobility scores did not show stronger and more isotope distinctions than the less mobile species, between feathers grown during different life-phases (Fig 2.3; appendix 5). Additionally, isotope signature distinctions were not consistent per species but varied from site to site. These patterns have been grouped and explained according to spatial,

temporal, inter-species and inter-individual variations, with an overall discussion of implications on mobility at the end as follows.

Spatial variations in isotope signature distinctions

Ducks grow flight feathers at a large water body that offers security from predators; this may be located far from the breeding site. Ducks deliberately search for suitable moulting sites (Kear 2005). This accounts for the distinction of isotope signatures between flight and back feathers. It is probable that the ducks used different sites for breeding and moulting. Therefore, individuals of Cape Shoveler, Spur-Winged Goose, South African Shelduck and Egyptian Goose are likely to have taken different diets for breeding and moulting and possibly different sites; assuming that diets did not vary temporally at the same spatial scale.

These findings imply that environmental conditions vary across sites and this influences the bird's decision to either remain resident or to move to another patch in order to increase foraging profitability. Some of the factors a bird considers include presence of predators, competition levels and consistency of resource availability (Kamil and Sargent 1981; Hughes 1989). It could also be that birds not showing isotopically distinct tissues were moving during other times outside the moulting and breeding phases. Results from paired t-tests showed distinction of isotope signatures between flight and body feathers from Egyptian Geese and Spur-winged Geese from Strandfontein and South African Shelducks and Cape Shovelers from Barberspan, yet all the other ducks tested did not.

At different sites, the same species showed different distinction patterns. Site conditions (species composition, climate, season and food availability) influence breeding and moulting location selection, suggesting change of movement patterns as a function of conditions experienced at a site of origin. This demonstrates how varying site conditions influence movements as well as isotope signature patterns in bird tissues. It is plausible therefore to carry out site specific approaches when analysing and interpreting isotope data.

Temporal isotope signature variations

Of the ducks that showed distinctive isotopic signatures in at least one of the comparisons between feathers grown at different life-stages, distinctions did not occur consistently between fully grown flight versus body feathers and growing flight versus body feathers of

the same species. This suggests that some of the southern African ducks use diverse sites for different life-phases, and the use of these sites is inconsistent from season to season and year to year. There seems to be no clear deliberate site fidelity for breeding and moulting among southern African ducks.

These findings make sense in the light of the fact southern Africa exhibits unpredictable availability of resources owing to dynamic weather patterns (Mueller and Fagan 2008). Ducks therefore exhibit complex movements to find resources as and when they occur in a dynamic pattern. This is in agreement with other studies that southern African ducks' movements and their use of habitats are random, unpredictable, ranging and explosive (Brickell 1988; Hockey et al. 2005; Cumming et al. 2008).

Inter-species variations in feather isotope distinctions

If sites are distinct and ducks habitually use diverse sites for different life phases then each duck species occurring in a particular site ought to show distinctions of signatures between tissues grown at different times, if different diets and sites were used. This was the case with some of the species. However, at the same site whilst some species were showing distinction between different feathers, other species would remain constant. Duck species obviously differ in their movement patterns even to individual level as evidenced by variations in distances and directions moved by ducks in southern Africa (Underhill et al. 1999). Some species and individuals choose to remain sedentary at particular sites whilst others change sites. For example, Egyptian Geese and Spur-winged Geese from Strandfontein (Figs 2.1 & 2.2); some individuals occupied different areas from the rest of the sampled individuals on the scatter plots. There were some individuals within each population which used isotopically distinct diets and possibly different sites from the rest, even when the overall effect is not statistically significant.

Additionally, diets and foraging habits differ across duck species and this influences the rate and quantity of isotopes incorporated into feathers. The duck species tested belong to three different feeding guilds: Yellow-billed Duck, Cape Teal, Hottentot Teal, Red-billed Teal and Cape Shoveler are predominantly water surface feeders foraging by dabbling, sieving and up-ending (Owen and Black 1990; Baldassarre and Bolen 2006). The African Pygmy Goose forages by diving and feeding under water. Egyptian Goose, Spur-winged Goose, and White-faced Duck feed mostly on land by grazing. However, feeding habits can be flexible across guilds depending on the availability of resources (Ogilvie & Pearson 1994;

Todd 1996). For example, the predominantly grazing Egyptian Goose sometimes dabbles when the land is arid (Swap et al. 2004). Even though a species specific approach to analysing and interpreting isotope data is plausible, flexible foraging habits and diet plasticity among southern African ducks can further confound isotope results.

Inter-individual variations

Random inter-individual variations in isotope signature distinction between fully grown and body feathers shown in Figs 2.1, 2.2, and 2.3 imply diverse sources of duck populations converging on each study site (more so at Barberspan; Fig 2.3). Possibly Ducks are moving from various sites for moulting at the study sites chosen. However, these distinctions cannot be completely ascribed to movements because of the possibility of inter-individual dietary variations and habitat heterogeneity (both through natural and anthropogenic means). There is need for investigating on background isotope signature patterns to determine the extent to which isotope signature distinctions can be ascribed to movements (whilst paying attention to diet and feeding ecology).

Mobility

Comparing isotope distinction defined mobility with mobility scores from Cumming et al (2008; Fig. 2.3) showed the Egyptian Geese from Strandfontein and Cape Shovelers from Barberspan with both high mobility scores and isotope distinctions. All the other species' isotope signatures did not agree with mobility scores. Isotope signature distinctions between duck feathers grown at different life stages cannot be clearly underpinned to the use of different sites alone, neither can similar signatures depict that a species did not move; signature distinctions can be due to seasonal diet and habitat variations and, whilst non-distinctions can be that the species moved during other times outside breeding and moulting phase. More stringent calibration techniques are thus required to make isotope data more usable in movement ecology studies.

Within site habitat heterogeneity can bias results. Unfortunately, this means that isotope signature distinctions between tissues grown during different phases do not only imply the use of different sites but also temporally different diets within the same site. For example, an Egyptian Goose in Barberspan may solely forage from the water-body during moulting and then move to the neighbouring maize fields during the breeding period when it

has re-gained flight capacity. Agricultural crops are enriched in δ^{15}N through fertilizer application and will be significantly different from naturally occurring vegetation in stable isotope signatures. Furthermore, signature distinctions are influenced by diets, species, individual specific biological processes and anthropogenic influences; all of which affect the ingestion and assimilation of isotope signatures into animal tissue (Bearhop et al. 2002; Rubenstein and Hobson 2004; Britzke et al. 2009). Further research is recommended on diets and foraging behaviour of southern African ducks and how these influence isotope-based movement studies.

Anthropogenic inputs to the environment through sewage effluent and agriculture can cause species occupying more human influenced sites to have distorted signature patterns. Industrial effluent, sewerage and agricultural chemicals are usually enriched in isotope signatures hence modifying isotopic patterns in the environment by increasing spatial and temporal isotope pattern heterogeneity (Cadenasso et al. 2003; Hobson 2005). In comparative movement inferences, this confounds results (Rubenstein and Hobson 2004).

Another bias can be the coverage of vegetation biomes. They can be extensive (> 1000 km) like the savannah in southern Africa. Bird movement within such a biome might not be detectable in isotopes like δ^{13}C which mainly depend on vegetation composition. There is need for finer scale differentiation isotope techniques like increasing the number of isotopes and incorporating trace elements and heavy isotopes. Including heavy stable isotopes (Strontium and Rubidium) can be helpful because their proportions are conserved from diet to tissue with very negligible fractionation if any (Hobson et al. 2010; Sellick 2009; West et al. 2010).

In southern Africa Cerling et al. (2009) managed to trace seasonal changes in use of habitats by African Elephants (*Loxodonta africana)* using δ^{15}N and δ^{13}C. Elsewhere, Phillips et al. (2009) demonstrated a clear correspondence of δ^{15}N and δ^{13}C patterns in feathers and off-breeding distributions of seabirds using loggers. The isotope technique has been successfully used to trace movements and origins of different animals at various scales (Cherel et al. 2006).

It is important to also consider the shortfalls of comparing isotope data to mark-recapture-based mobility information; ring recovery distances are biased by regional differences in banding efforts and reporting rate (which for southern Africa are predominantly located in South Africa). It is difficult to give a conclusive judgement on the efficiency of the isotope technique without considering the biases inherent in the ringing technique as well. My isotope data for some of the species studied (Egyptian Goose and Cape

Shoveler) show that more mobile species (as determined from mobility scores) show stronger signature distinctions of feathers grown at different times (Fig 2.3). For the other species, isotope signature data were inconsistent with mobility scores. Future research can compare the results to satellite tracked movements of selected ducks as in Phillips et al (2009) and in Ramos et al (2009).

Collecting relevant tissue for isotope analysis as often as possible when animal ecology field studies are carried out can give more answers to several ecological questions being asked. Usually inert tissue is collected for isotope analysis; it can be stored over indefinite periods of time and then be used to answer questions over an extensive temporal scale. Additionally, Isotope techniques continue to advance as more research is being carried out; archived animal tissue can yield information of great value in the future (West et al. 2010).

Conclusions

Even though the stable isotope technique can reveal important clues on habitat usage and movement ecology of mobile organisms, my results showed that in tracing the movements of southern African ducks, it is unreliable. The technique needs stringent calibration techniques for it to be usable in tracing dispersal pattern variations among southern African ducks.

Dynamic weather patterns and stochastic environments impose random and unpredictable movement patterns among ducks. Background isotope signature patterns are affected in a similar way. This reduces the possibilities of developing a consistent background base against which tissue of unknown origin can be compared to draw inferences on movement. Even a case by case specific approach as demonstrated by my research incorporates a multitude of sources of variation which cannot be effectively accounted for during interpretation of tissue isotope patterns.

Habitat usage and movement patterns have implications for conservation and disease/pathogen spread and control, especially in this world of ever increasing fragmentation of habitats. If rigorous calibration techniques are devised to cater for the various sources of variation, and isotope maps (isoscapes) of $\delta^{13}C$ and $\delta^{15}N$ are developed, the isotope technique might contribute towards a useful archive of ecological information for present and future reference; the technique has a high data yielding capacity and stable isotope techniques continue to advance. Research has commenced on remote sensing for foliar and soil isotopes

which will provide a reliable background base for reference in movement studies (West et al 2010).

Literature cited:

Baldassarre, G.A., Bolen, E.G. 2006. *Waterfowl Ecology and Management.* Florida: Krieger.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W. 2002. Factors that influence assimilation rates and fractionation of Nitrogen and Carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology*, 75, 451-458.

Brickell, N. 1988. *Ducks, Geese and Swans of Africa*. Cape Town: Frandsen.

Britzke, E.R., Loeb, S.C., Hobson, K.A., Romanek, C.S., Vonhof, M.J. 2009. Using Hydrogen isotopes to assign origins of bats in the eastern United States. *Journal of Mammalogy*, 90, 743-751.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Bell, S.S., Benning, T.L. 2003. An Interdisciplinary and synthetic approach to ecological boundaries. *BioScience*, 53, 717-722.

Cerling, T.E., Wittemyer, G., Ehleringer J.R., Remiene, C.H., Douglas-Hamilton, I. 2009. History of Animals using Isotope Records (HAIR): a 6-year dietary history of one family of African elephants. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 8093-8100.

Cherel, Y. Phillips, R.A., Hobson, K.A., McGill, R. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters*, 2, 301-303.

Cumming, G.S., Hockey, P.A.R., Bruinzeel, L.W., Du Plessis, M.A. 2008. Wild bird movements and avian influenza risk mapping in southern Africa. *Ecology And Society*, 13, [online] URL:http://www.ecologyandsociety.org/vol13/iss2/art26/

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremens, M., Tree, A.J., Parker, V., Brown, C.J. (eds). 1997. *The atlas of southern African birds*. Johannesburg: BirdLife South Africa.

Hobson, K. A. 2003. Making migratory connections with stable isotopes. In: Berthold, P., Gwinner, E., Sonnenschein, E. (eds). *Avian migration*. pp 45. Springer-Verlag: New York.

Hobson, K.A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, 11, 157-164.

Hobson, K.A. 2008. Applying isotopic methods to tracking animal movements. In: K.A. Hobson and L.I. Wassenaar. (eds). Tracking animal migration with stable isotopes. pp. 45-78, London: Elsevier.

Hobson, K.A., Wassenaar, L.I., Mila, B., Lovette, I., Dingle, C., Smith, T.B. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia,* 136, 302-308.

Hobson, K.A., Johnson, R.B., Cerling, T. 2010. Using Isoscapes to track animal migration. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (eds). Isoscapes; Understanding movements, pattern and process on Earth through Isotope mapping. pp. 51-78, London: Springer.

Hockey, P.A.R., Dean, W.R.J., Ryan, P.G. (eds). 2005. *Roberts' birds of southern Africa*. Cape Town: Trustees of the John Voelcker Bird Book Fund.

Hughes, R.N. 1989. Behavioural mechanisms of food selection. London: Springer

Kear, J. 2005. Ducks, Geese, and Swans. Volume 1: General chapters and species accounts (*Anhima to Salvadorina*). Oxford: Oxford University Press.

Inger, R., Bearhop, S. 2008. Applications of stable isotope analyses to avian ecology. *Ibis*, 150, 447-461.

Kamil, A.C., Sargent, T.D. 1981. Foraging behavior: ecological, ethological, and psychological approaches. London: Garland.

Lincoln, R.J., Boxshall, G.A., Clark, P.F. 1982. *A dictionary of ecology, evolution and systematics*. London: Cambridge.

Mueller, T., Fagan, W.F. 2008. Search and navigation in dynamic environments - from individual behaviours to population distributions. *Oikos*, 117, 654-664.

Nathan, R. 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19050-19051.

Ogilvie, M., Pearson, B. 1994. *Wildfowl Behaviour Guide*, Melbourne: Hamlyn.

Phillips, R.A., Bearhop, S., McGill, R.A.R., Dawson, D.A. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the non-breeding period. *Oecologia*, 160, 795-806.

Ramos, R., Ramırez, F., Sanpera, C., Jover, L., Ruiz, X. 2009. Feeding ecology of Yellow-legged Gulls (*Larus michahellis*) in the Western Mediterranean: a comparative assessment using conventional and isotopic methods. *Marine Ecology Progress Series,* 377, 289-296.

Roshier, D., Klomp N.I., Asmus. M. 2006. Movements of a nomadic waterfowl, Grey Teal (*Anas gracilis*), across inland Australia: results from satellite telemetry spanning fifteen months. *Ardea,* 94, 461-475.

Roshier, D., Asmus, M. Klaassen, M. 2008. What drives long-distance movements in the nomadic Grey Teal (*Anas gracilis)* in Australia? *Ibis,* 150, 474-484.

Rubenstein, D.R., Chamberlain, C.P., Holmes, R.T., Ayres, M.P., Waldbauer, J.R., Graves, G.R., Tuross, N.C. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science,* 295, 1062-1065.

Rubenstein, D.R., Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution,* 19, 256-263.

Sellick, M.J., Kyser, T.K., Wunder, M.B., Chipley, D., Norris, D.R. 2009. Geographic variation of Strontium and Hydrogen isotopes in avian tissue: implications for tracking migration and dispersal. *PloS one*, 4, 4735-4746.

Siegfried, W.R., Frost, P.G.H., Ball, I.J., McKinney, D.F. 1977. Effects of radio packages on African black ducks. *South African Journal of Wildlife Research,* 7, 37-40.

Sorensen, M.C., Hipfner, J.M., Kyser, T.K., Noris, D.R. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology*, 78, 460-467

Todd, F., 1996. *Natural history of the waterfowl*. California: San Diego Natural History Museum.

Underhill, L.G., Tree, A.J., Oschadleus, H.D., Parker, V. 1999. *Review of ring recoveries of waterbirds in southern Africa*. Cape Town: Avian Demography Unit, University of Cape Town.

West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (eds). 2010. *Understanding movements, pattern and process on Earth through isotope mapping.* London: Springer.

Yohannes, E., Hobson, K.A., Pearson, D.J. 2007. Feather stable-isotope profiles reveal stopover habitat selection and site fidelity in nine migratory species moving through sub-Saharan Africa. *Journal of Avian Biology,* 38, 347-355.

Yohannes, E., Hansson, B., Lee, R.W., Waldenström, J., Westerdahl, H., Akesson, M., Hasselquist, D., Bensch, S. 2008. Isotope signatures in winter moulted feathers predict malaria prevalence in a breeding avian host. *Oecologia*, 158, 299-306.

CHAPTER 3

USING STABLE ISOTOPES TO STUDY THE FORAGING ECOLOGY OF DUCKS IN SOUTHERN AFRICA

Abstract

It has been established that different ducks in southern Africa vary in feather isotope signature patterns by species, year, season and environment. These variations are mainly due to diet, feeding habits, assimilation and environmental differences because signatures reflected in animal tissue derive from nutrition. Here, I investigated the utility of the isotope technique in dietary and foraging ecology studies of ducks in southern Africa. I also investigated how feather isotope-based movement inferences vary in resolution as a consequence of diet and foraging habits. New locally grown feathers of eight ducks, from five different wetlands, sampled across different seasons and years, were analysed for $\delta^{13}C$, $\delta^{15}N$, and δD. Isotope signatures were compared across species at each site to assess whether there was variation in diet and foraging habits among duck species at each study site. I compared inter-individual isotope variation across species at each site. Because ducks moult flight feathers synchronously, they become flightless and regrow feathers in one location. High inter-individual isotope proportion variances in growing flight feathers reflect dietary flexibility, and not movements. High dietary flexibility was common in the species which had isotope patterns diverging from ringing data movement information (Cape Teal and Yellow-billed Duck populations). Isotopic specialist foragers (Egyptian Goose, South African Shelduck and Spur-winged Goose) had low isotope signature variances and displayed clearer isotope patterns in chapters one and two. Stable isotopes can reveal important information on diet and foraging ecology of southern African ducks. Here ducks showed dynamic and inconsistent diet and foraging habits in space and time. Ultimately, diet and foraging habits of southern African ducks shown in this study compromise the isotope technique's resolution capacity in movement studies. Movement studies based on the isotope technique should be accompanied with conventional techniques to detect and counter dietary imposed variation. Further research on how assimilation biology affects tissue signatures in duck feathers is necessary.

Introduction

Accurate information on diet composition is important in several key areas of ecology, such as the management of problematic species and the use of a species to monitor the environmental impact of pollutants. The majority of dietary studies of southern African ducks are based on field observations and regurgitate assessments (see Hockey et al. 2005). The methods do not give accurate information on feeding habits due to biases caused by prey digestibility differences (Ramos et al. 2009). Field-observation-based diet studies are also biased toward conspicuous prey. Regurgitate assessment presents prey identification difficulties (prey is often partially digested). These methodologies provide only a 'snap shot' view of an individual's diet; each sample represents a specific feeding event meaning exhaustive monitoring over time is needed (Votier et al. 2001; Jordan 2005). Stable isotope analysis (SIA) in animal ecology is burgeoning in recent years (Hodum & Hobson 2000, Post 2002). Although SIA does not provide the taxonomic detail, it avoids prey digestibility biases by taking into account assimilated food, providing a ready-made integrated estimate because the assimilated diet for a certain period of time is summarised (Hobson 1999).

Stable isotopes in animal tissue are derived from diet and the environment from which the animal forages, but with a fractionation value that disallows exact similarity between diet and tissue (Focken and Becker 1998). Inter and intra species variation in metabolic rates, environmental conditions and diet, modify tissue signatures such that each species possesses a distinct isotopic composition. This is evidence that information on diet and foraging ecology can be inferred from stable isotope patterns in an organism's tissues (Bearhop et al. 2006; Codron et al. 2006; Cremona et al. 2010; Vanderklift and Wernberg 2010). Isotopic analysis of feathers can yield important insights in the ecology of birds including resource partitioning, migratory connectivity and seasonal interactions (Pain et al. 2004; Rubenstein and Hobson 2004).

In order to meet foraging demands cost effectively, southern hemisphere ducks use a different feeding ecology from northern hemisphere ducks (Todd 1996; Ndlovu et al 2010). The Egyptian Goose for example, has shown phenotypic flexibility to reduce wing loading thereby expediting the recovery of flight capacity after moulting (Ndlovu et al. 2010). Northern hemisphere ducks maintain their weight and use fat reserves to speed up feather growth instead of reducing wing loading (Ndlovu et al. 2010). Quick recovery of flight ensures easy access to rich forage. Such differences in foraging ecology between northern

and southern hemisphere ducks suggest that what is known in the northern hemisphere about stable isotopes in waterfowl may not apply equally to the southern hemisphere.

Stable isotopes of single feathers from each individual bird can answer questions on variations of niche breadth and inter-species interactions among duck populations, assuming that within bird variability is negligible. Variances in $\delta^{15}N$ and $\delta^{13}C$ can be used as proxies to niche width (Jaeger et al. 2009). Higher variances mean more generalist foraging behaviour and vice versa for low variances. Inter-species signature comparisons can tell whether and when different species resort to a common diet, as well as when different species overlap in habitat use (Newsome et al. 2007). Variance in δ space among individuals has been used as a proxy for niche width by Jaeger et al. (2009); Bearhop et al. (2004) and Newsome et al. (2007). Here I used inter-individual niche width commonly known as the between individual variance component (BIC; Cherel et al. 2006).

The ducks studied here exhibit a variety of feeding habits: (1) water surface feeding (dabbling, sieving and upending), (2) diving and feeding under water, and (3) feeding on land (grazing). Yellow-billed Duck, Cape Teal, Hottentot Teal, Red-billed Teal and Cape Shoveler are water surface feeders. Egyptian Goose, Spur-winged Goose, and White-faced Duck feed mostly on land by grazing. South African Shelduck feeds mainly on algae, aquatic invertebrates and occasionally on crops (Geldenhuys 1977; Ogilvie and Pearson 1994; Brickell 1988). According to Todd (1996); Ogilvie and Pearson (1994) and Brickell (1988), these feeding habits can be flexible depending on food availability. For example, the Egyptian Goose may resort to dabbling during times of aridity on land. Within each feeding guild, different species have different bill morphologies which further segregate the type of food exploited. Cape Teal for instance, have finer transverse lamellae lining the mandibles to filter out finer particulate material. As a result, waterbirds display a multitude of feeding techniques linked to bill, neck and body characteristics (Ogilvie and Pearson 1994).

In isotope-based movement studies, prior dietary knowledge is essential to calibrate results against dietary imposed isotope signature variation. In chapter two, only two duck species (Cape Shoveler from Barberspan and Egyptian Goose from Strandfontein) with high mobility scores also showed high isotope signature distinctions. The difference between isotope data and ring recovery information was attributed to different feeding ecologies across different species as well as absence of knowledge of the animal's more fine scale movements.

In this study, the main objective was to learn how much information on diet and foraging behaviour of southern African ducks can be inferred from feather stable isotopes.

I also aimed to verify how spatial and temporal variation in diet and foraging ecology of southern African ducks affects results in isotope-based movement studies (in chapter 1 and 2). Growing flight feathers of nine ducks from five sites within southern Africa were analysed for δ^{13}C, δ^{15}N and δD and comparisons were made across different species per study site. Inter-individual variances per species were graphically computed and compared. I tested whether (1) there was convergence in diet during moulting, (2) different individuals of the same species showed variation in isotopic signature, (3) whether intra and inter-species signature variations changed at different times of the year and (4) dietary and foraging behaviour was related to the isotope-based site distinctions and movement patterns derived in chapters one and two.

Methods

Isotope proportions of Nitrogen (δ^{15}N) and Carbon (δ^{13}C) define an organism's niche in two dimensions, trophic position and habitat breadth respectively (Jaeger et al. 2009). By inspection of variances of these signatures within individuals (within individual variance component –WIC, if multiple feathers are taken from each individual) or across different individuals (between individual variance component - BIC, if single feathers are taken from each individual), inferences of whether specialist or generalist foraging behaviours are practised can be drawn. BIC and WIC measures are usually summed up to give an overall measure of trophic niche width (TNW): BIC + WIC = TNW. BIC can be used as a proxy for TNW as in this research, when only single feathers are collected. Higher variances (high BIC or TNW) depict generalist foraging habits (Jaeger et al. 2009).

Comparisons of isotope signatures among different individuals or populations can reveal information on habitat and trophic overlaps among different species within a community. This can give ideas of habitat usage and species interactions at different moulting sites. I compared new feather stable isotope signatures using ANOVA and the Turkey-type variance test to investigate variation in habitat usage during moult across different species at each moulting site. I used inter-individual variances (BIC) to distinguish between generalist and specialist foraging populations.

I plotted bar-graphs of population isotope variances in δ^{15}N and δ^{13}C of each species per given site and season (Fig. 3.4). These graphical comparisons were used to segregate each of the species per site of origin into three relative classes of variance magnitudes (Fig. 3.5). Foraging behaviours were interpreted to population level (BIC) 'between individual variance

component' as a proxy to trophic niche width (Bearhop et al. 2004). I could not further depict the within individual variance component (WIC) which is used to tell type A from type B generalists as in Jaeger et al. (2009; 2010) because it requires several feathers from each individual bird. I only collected two feathers per individual.

δD comparisons were made between Egyptian Geese and Red-billed Teals only. Detailed methods on sample collection and isotope analysis are given in the general methods section.

Statistical Analysis

Data were tested by site for normality using a one sample Kolmogorov-Smirnov test in Predictive Analysis Software (PASW) version 18. Inter-species feather isotope signature comparisons were carried out per site using growing flight feathers. These comparisons were grouped by season and year of moulting. Each analysis was preceded by Levene's test for equality of variance. If variances were equal, Analysis of Variance (ANOVA) was used, otherwise the Kruskal-Wallis test. Finally, where species proved significantly different, post-hoc tests (Bonferroni for equal variance samples and Tamhane's for unequal variance samples) were carried out to distinguish between isotopically distinct and similar species (Zuur et al. 2009). Inter-individual variations were compared using the Turkey-type multiple comparison test for differences among variances to compare δ^{13}C and δ^{15}N variances across species per given site (appendix 8).

Results

A total of 371 freshly grown duck feathers were analysed from ten species as shown in Table 3.1. Inter-species and inter-individual signature comparisons showed signature overlaps and varying isotopic niche breadths; with season, year and site (Table 3.1) and this was further confirmed by statistical tests. Ducks were converging in diet at moulting sites especially during the dry seasons. Some species like the Egyptian Goose maintained a high trophic status (δ^{15}N) across different sites and seasons. These results are described in detail firstly through inter-species and secondly through inter-individual comparisons.

Table 3.1: Average Carbon and Nitrogen ($\delta^{13}C$ and $\delta^{15}N$) values in growing feathers of southern African ducks

	STR			BAR			MAN			NGA			CHU		
	N	$\delta^{15}N$	$\delta^{13}C$	N	$\delta^{15}N$	$\delta^{13}C$	N	$\delta^{15}N$	$\delta^{13}C$	N	$\delta^{15}N$	$\delta^{13}C$	N	$\delta^{15}N$	$\delta^{13}C$
EG	58	15.00	-21.45	55	9.97	-12.81	2	12.68	-16.41	3	15.71	-19.05			
RBT	4	12.21	-18.28	11	11.25	-14.12	50	9.35	-19.64	1	11.35	-13.62	3	6.65	-16.81
YBD	3	15.21	-22.25	28	10.19	-13.31									
WFD							70	12.10	-18.07				5	10.64	-18.60
CT	7	20.14	-18.27	11	13.79	-17.97									
SAS				44	10.03	-11.95									
APG													1	12.48	-13.51
HTT							3	9.77	-24.10				1	9.61	-23.11
SWG	11	11.68	-23.01												
T	83			149			125			4			10		

Egyptian Goose = EG, Red-billed Teal = RBT, Spur Winged Goose = SWG, South African Shelduck = SAS, African Pygmy Goose = APG, Hottentot Teal = HTT, Yellow-billed Duck = YBD, White-faced Duck = WFD and Cape Teal = CT. Study sites: CHU = Lake Chuali, MAN = Manyame catchment, NGA = Lake Ngami, BAR = Barberspan, STR = Strandfontein.

Inter-species Comparisons

Figures 3.1, 3.2 and 3.3 illustrate how different species separated in feather signature overall across the entire sampling period. Some species were distinct from each other and others overlapped. However, these patterns changed haphazardly at different sites, seasons and years.

Seasonal tendencies

Strandfontein birds, during summer (Egyptian Goose, Red-billed Teal, Yellow-billed Duck and Cape Teal) showed different signatures in growing flight feathers in all the three isotopes: δ^{15}N (ANOVA, $F_{3, 46} = 3.068$; $P < 0.05$), δ^{13}C (ANOVA, $F_{3, 46} = 4.061$; $P< 0.05$), δD (ANOVA, $F_{1, 9} = 13.62$; $P < 0.01$). During winter the three species captured (Egyptian Goose, Spur-winged Goose and Red-billed Teal) were distinct in both δ^{15}N and δ^{13}C [δ^{15}N (df = 2, 19 Kruskal-Wallis test, $P < 0.05$) δ^{13}C (df = 2, 19; Kruskal-Wallis test, $P < 0.05$)].

Barberspan species, during summer, were distinct in δ^{13}C and δ^{15}N but not in δD unlike Strandfontein species: δ^{15}N (df = 4, 74; Kruskal-Wallis test, $P < 0.01$), δ^{13}C (df = 4, 74; Kruskal-Wallis test, $P < 0.001$), δD (ANOVA, $F_{1, 1} = 6.120$; $P > 0.05$). During winter more overlaps were shown, the four species captured (Egyptian Goose, Cape Teal, Red-billed Teal and South African Shelduck) were similar in δ^{13}C and δ^{15}N and δD: δ^{15}N (df = 4, 65; Kruskal-Wallis test, $P > 0.05$), δ^{13}C (ANOVA, $F_{4, 65} = 2.316$; $P > 0.05$) δD (ANOVA, $F_{1, 14} = 2.400$; $P > 0.05$).

The Manyame birds showed relatively fewer distinctions during summer and only in δ^{15}N (df = 3, 58; Kruskal-Wallis test, $P < 0.001$) but not in δ^{13}C (ANOVA, $F_{3, 58} = 2.283$; $P > 0.05$) and in δD (ANOVA, $F_{1, 22} = 3.420$; $P > 0.05$). Additionally during winter, the two species captured (Egyptian Goose and Red-billed Teal) were similar in all isotopes tested: δ^{15}N (ANOVA, $F_{1, 64} = 1.273$; $P > 0.05$), δ^{13}C (ANOVA, $F_{1, 64} = 2.205$; $P > 0.05$).

Lake Ngami birds (Egyptian Goose and Red-billed Teal) and Lake Chuali birds (Red-billed Teal and White-faced Duck) were not distinct in terms of either Nitrogen or Carbon isotopes: δ^{15}N (ANOVA, $F_{1, 2} = 2.107$; $P > 0.05$), δ^{13}C (ANOVA, $F_{1, 2} = 1.632$; $P > 0.05$) for Lake Ngami and δ^{15}N (ANOVA, $F_{1, 6} = 3.581$ $P > 0.05$), δ^{13}C (ANOVA, $F_{1, 6} = 0.518$; $P > 0.05$) for Lake Chuali species (Red-billed Teal and White-faced Duck).

Post hoc test results mainly show that: (1) Cape Teal and Egyptian Goose had the most distinct signatures (Table 3.2). They were distinct in both δ^{13}C and δ^{15}N at both sites (Strandfontein and Barberspan) and during both seasons with only the exception of δ^{13}C

during summer, the two species became isotopically similar. (2) During dry seasons, different species became more isotopically similar (Table 3.2). For example, the pairs: Cape Teal and South African Shelduck, Red-billed Teal and South African Shelduck, were distinct in both $\delta^{13}C$ and $\delta^{15}N$ at Barberspan during summer but they became similar during winter.

Annual tendencies

In the year 2007 at Strandfontein, three species captured were significantly different in $\delta^{15}N$ (ANOVA, $F_{3, 36} = 18.73$; $P < 0.001$), $\delta^{13}C$ (ANOVA, $F_{3, 36} = 14.26$; $P < 0.001$, and δD (ANOVA, $F_{1, 10} = 17.37$; $P < 0.01$). During 2008, the species captured were distinct again in $\delta^{15}N$ (ANOVA, $F_{3, 20} = 18.42$; $P < 0.001$) and $\delta^{13}C$ (ANOVA, $F_{3, 20} = 6.63$; $P < 0.01$). In 2009, the ducks captured (Egyptian Goose, Spur-winged Goose and Yellow-billed Duck) were not distinct in both $\delta^{15}N$ and $\delta^{13}C$: $\delta^{15}N$ (ANOVA, $F_{2, 16} = 0.04$; $P > 0.05$), $\delta^{13}C$ (ANOVA, $F_{2, 16} = 0.23$; $P > 0.05$)

On the contrary, Barberspan birds in 2007 (Egyptian Goose, Red-billed Teal, Yellow-billed Duck and South African Shelduck) were similar in $\delta^{15}N$ (ANOVA, $F_{3, 72} = 0.47$; $P > 0.05$) and in $\delta^{13}C$ (df = 3, 72; Kruskal-Wallis test, $P > 0.05$). Additionally, Red-billed Teal and Egyptian Goose were similar in δD (ANOVA, $F_{1, 15} = 3.38$; $P > 0.05$). However, in 2008 ducks were distinct in $\delta^{15}N$ (df = 4, 46; Kruskal-Wallis test, $P < 0.01$) and in $\delta^{13}C$ (ANOVA, $F_{4, 45} = 16.09$; $P < 0.001$).

Manyame 2007 birds: White Faced Ducks were more enriched than Red-billed Teals in $\delta^{15}N$ (df = 1, 64; Kruskal-Wallis test, $P < 0.01$). The species were however similar in $\delta^{13}C$ (ANOVA, $F_{1, 64} = 3.60$; $P > 0.05$). In 2008 the species (Egyptian Goose, Red-billed Teal, White-faced Duck and Hottentot Teal) were similar in $\delta^{15}N$ (ANOVA, $F_{3, 48} = 0.62$; $P > 0.05$), $\delta^{13}C$ (df = 3, 48; Kruskal-Wallis test, $P > 0.05$). Egyptian Geese and Red-billed Teals were analysed for δD and were distinct: δD (ANOVA, $F_{1, 5} = 23.05$; $P < 0.01$).

Post hoc test comparisons in Table 3.2 show that across all the sampled sites, different species had more unique signatures during the year 2008 than in 2007.

Inter-individual Comparisons

Variance space

Figures 3.4a and 3.4b show the overall tendencies of variances in 'δ' space ($\delta^{15}N$ and $\delta^{13}C$) for the whole period of sampling. The highest variances (> 20) were shown by Red-billed Teals, in Strandfontein and Barberspan in $\delta^{13}C$. In $\delta^{15}N$, highest variances (> 20) were shown

by Yellow-billed Ducks, Cape Teals, and Hottentot Teals from Strandfontein, Barberspan and Manyame respectively.

Intermediate values (5-20) in $\delta^{13}C$ variances were shown by Yellow-billed Ducks and Spur-winged Geese from Strandfontein, Yellow-billed Ducks and Cape Teals from Barberspan, Red-billed Teals and White-faced Ducks from Manyame, Egyptian Geese from Lake Ngami and White-faced Ducks from Lake Chuali. In $\delta^{15}N$ intermediate values (5-20) were from Egyptian Geese, Cape Teals and White-faced Ducks from Strandfontein, Barberspan, and Manyame respectively; and White-faced Ducks from Lake Chuali.

The lowest values (< 5) in $\delta^{13}C$ variance were shown by Egyptian Geese and Cape Teals from Strandfontein, Egyptian Geese and South African Shelducks from Barberspan, and Red-billed Teals from Lake Chuali. In $\delta^{15}N$, smallest variances (< 5) were shown by Red-billed Teals and Spur-winged Geese from Strandfontein; Egyptian Geese, Yellow-billed Ducks and South African Shelducks from Barberspan, and Red-billed Teals from Manyame and Lake Chuali.

However, when considering seasonal and yearly tendencies, no predictable pattern could be deduced implying high variations of niche breadths per season, site and year (appendix 9). Figure 3.5 segregates the ducks into high, intermediate and low inter-species variance classes using relative comparisons (Fig. 3.4 and appendix 9). Each species was treated uniquely by site of origin and this identified the Yellow billed Duck from Strandfontein and Cape Teal from Barberspan with the highest isotopic variances.

Variance comparisons using Turkey-type F-ratio test

At Strandfontein, Red-billed Teals, Spur-winged Geese, Cape Teals, Egyptian Geese, and Yellow-billed Ducks were compared using the Turkey-type variance test (appendix 8). Yellow-billed Ducks had the highest variance and they were significantly different from Red-billed Teals. Egyptian Geese had the second highest variance and were significantly different from Red-billed Teals. The Yellow-billed Ducks were similar to Cape Teals and Egyptian Geese, Egyptian Geese were similar to Cape Teals and Spur-winged Geese, Cape Teals were similar to Spur-winged Geese and Red-billed Teals in $\delta^{15}N$.

In $\delta^{13}C$, Red-billed Teals had the highest variance and were significantly different from Egyptian Geese and Cape Teals. Red-billed Teals were similar to Spur-winged Geese and Yellow-billed Ducks. Yellow-billed Ducks were similar to all species; Spur-winged Geese were also similar to all species.

At Barberspan, Cape Teals and South African Shelducks, Cape Teals and Yellow-billed Ducks, Cape Teals and Egyptian Geese had distinct variances from each other in δ^{15}N. Cape Teals and Red-billed Teals, Red-billed Teals and Egyptian Geese, Red-billed Teals and Yellow-billed Ducks, Red-billed Teals and South African Shelducks, Egyptian Geese and South African Shelducks, Egyptian Geese and Yellow-billed Ducks, Yellow-billed Ducks and South African Shelducks were similar in δ^{15}N.

In δ^{13}C, Red-billed Teals and South African Shelducks, Red-billed Teals and Egyptian Geese, Yellow-billed Ducks and South African Shelducks, Cape Teals and South African Shelducks, Egyptian Geese and South African Shelducks were distinct. Red-billed Teals and Cape Teals, Red-billed Teals and Yellow-billed Ducks, Yellow-billed Ducks and Cape Teals and Egyptian Geese were similar; Cape Teals and Egyptian Geese were similar.

At Manyame catchment, Hottentot Teals and Egyptian Geese, White-faced Ducks and Red-billed Teals, White-faced Ducks and Egyptian Geese, Red-billed Teals and Egyptian Geese were distinct in δ^{15}N. Hottentot Teals, White-faced Ducks and Red-billed Teals were all similar.

White-faced Ducks and Egyptian Geese, Red-billed Teals and Egyptian Geese, Hottentot Teals and Egyptian Geese were distinct in δ^{13}C; Red-billed Teals and Hottentot Teals; White-faced Ducks, Red-billed Teals and Hottentot Teals were similar.

At Lake Chuali Red-billed Teals and White-faced Ducks were similar in both δ^{13}C and δ^{15}N.

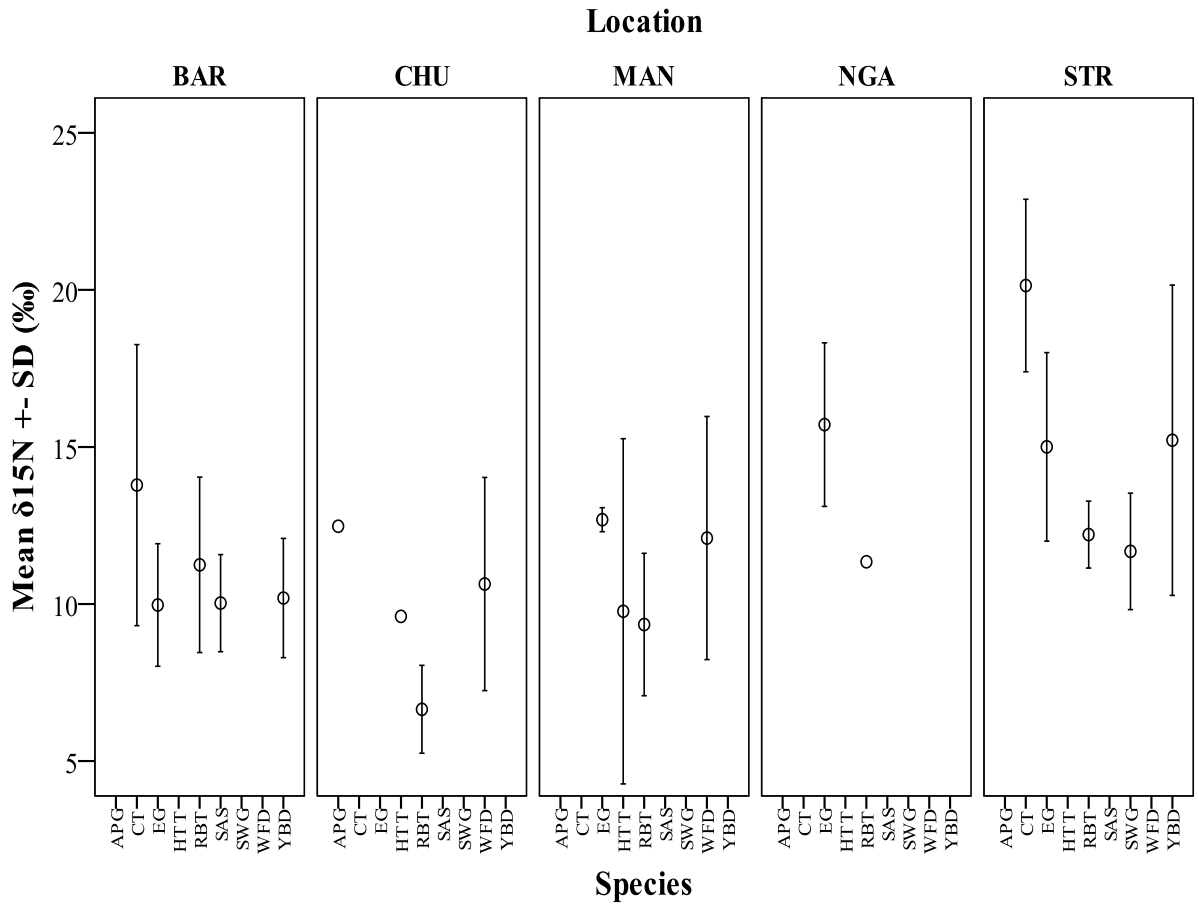


Figure 3.1: Mean stable isotope proportions of Nitrogen (δ^{15}N) ± SD from growing flight feathers of Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), African Pygmy Goose (APG), Spur-winged Goose (SWG), and Cape Shoveler (CS) from study sites Strandfontein (STR), Barberspan (BAR), Lake Ngami (NGA), Manyame catchment (MAN), and Lake Chuali (CHU). Generally most of the ducks were feeding from similar trophic levels. The Yellow-billed duck in Strandfontein, Cape Teal in Barberspan and Hottentot Teal in Manyame site exploited wide trophic niches.

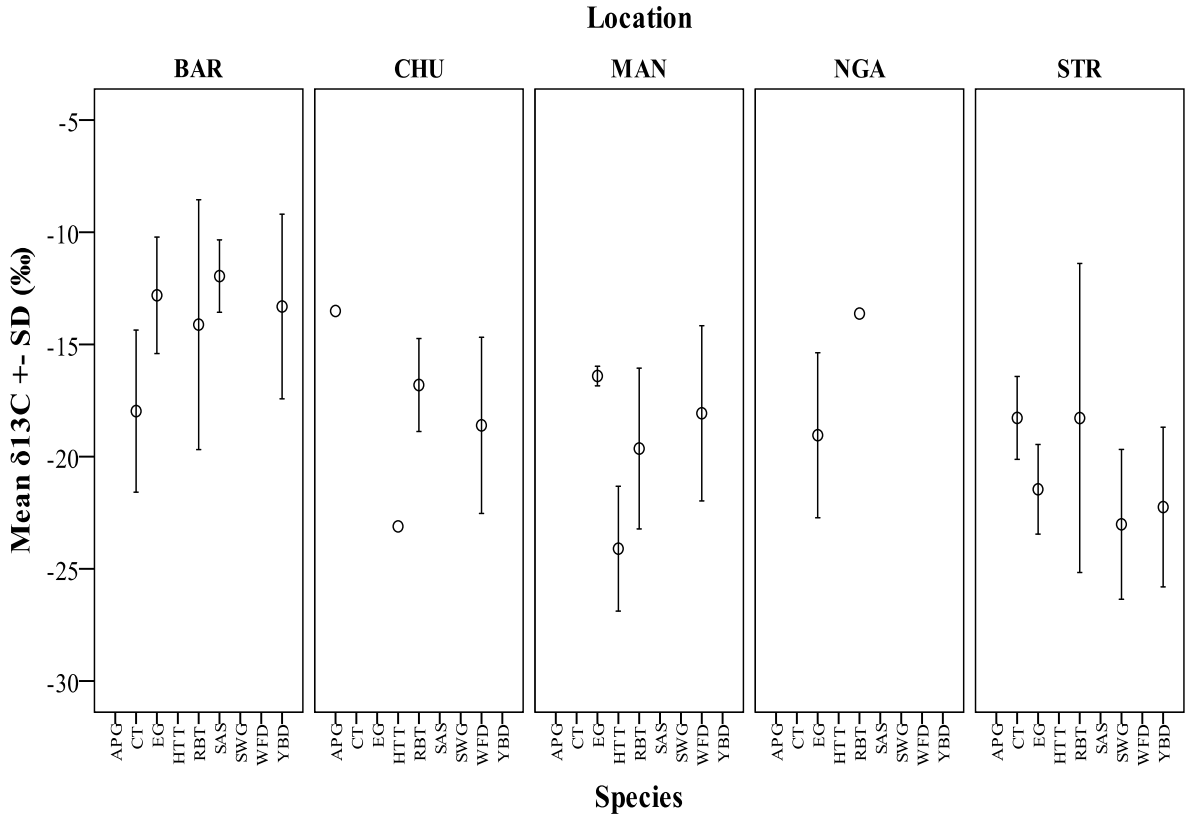


Figure 3.2: Mean stable isotope proportion of Carbon ($\delta^{13}C$) ± SD of growing flight feathers of Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), African Pygmy Goose (APG), Spur-winged Goose (SWG), and Cape Shoveler (CS) from study sites Strandfontein (STR), Barberspan (BAR), Lake Ngami (NGA), Manyame catchment (MAN), and Lake Chuali (CHU).

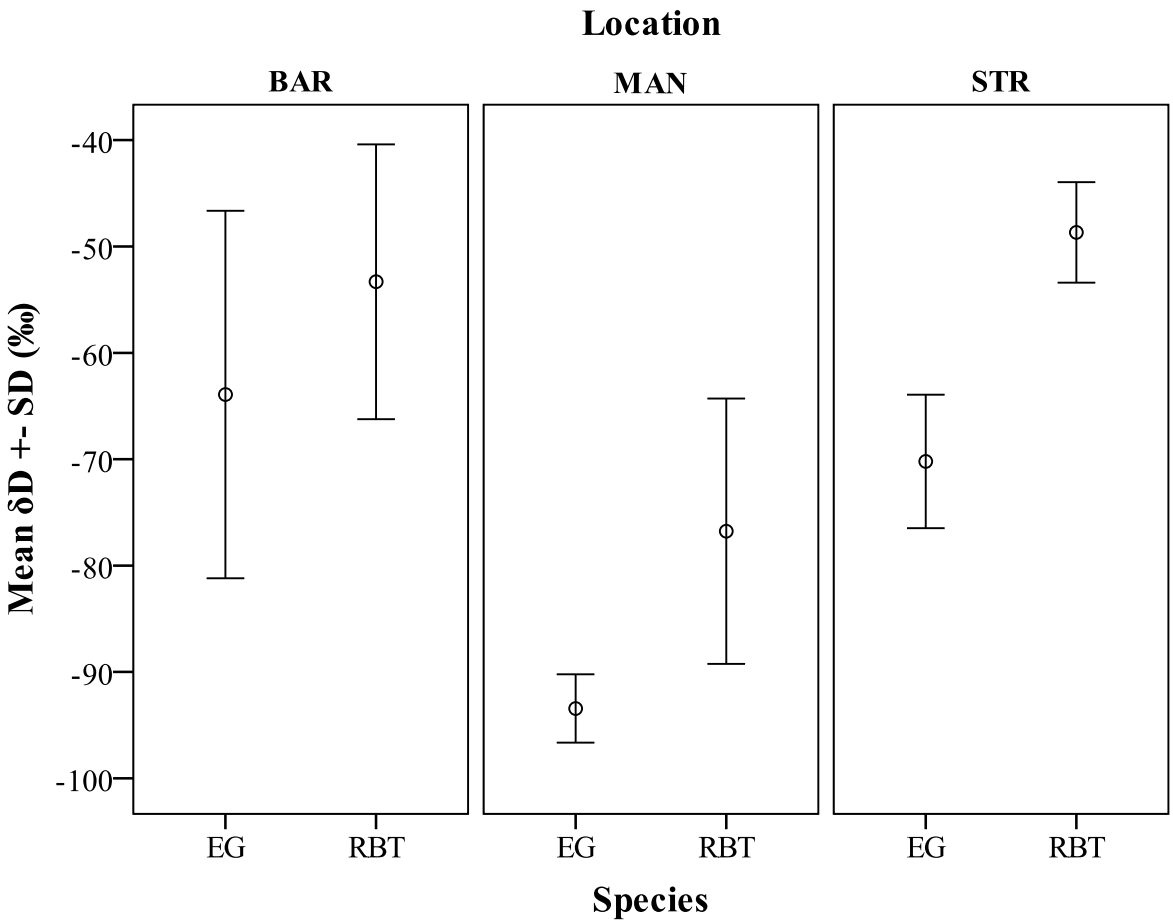


Figure 3.3: Mean stable isotope proportions of Hydrogen (δD) ± SD of growing flight feathers of Egyptian Goose (EG) and Red-billed Teal (RBT) from study sites Strandfontein (STR), Barberspan (BAR), and Manyame catchment (MAN).

(a)

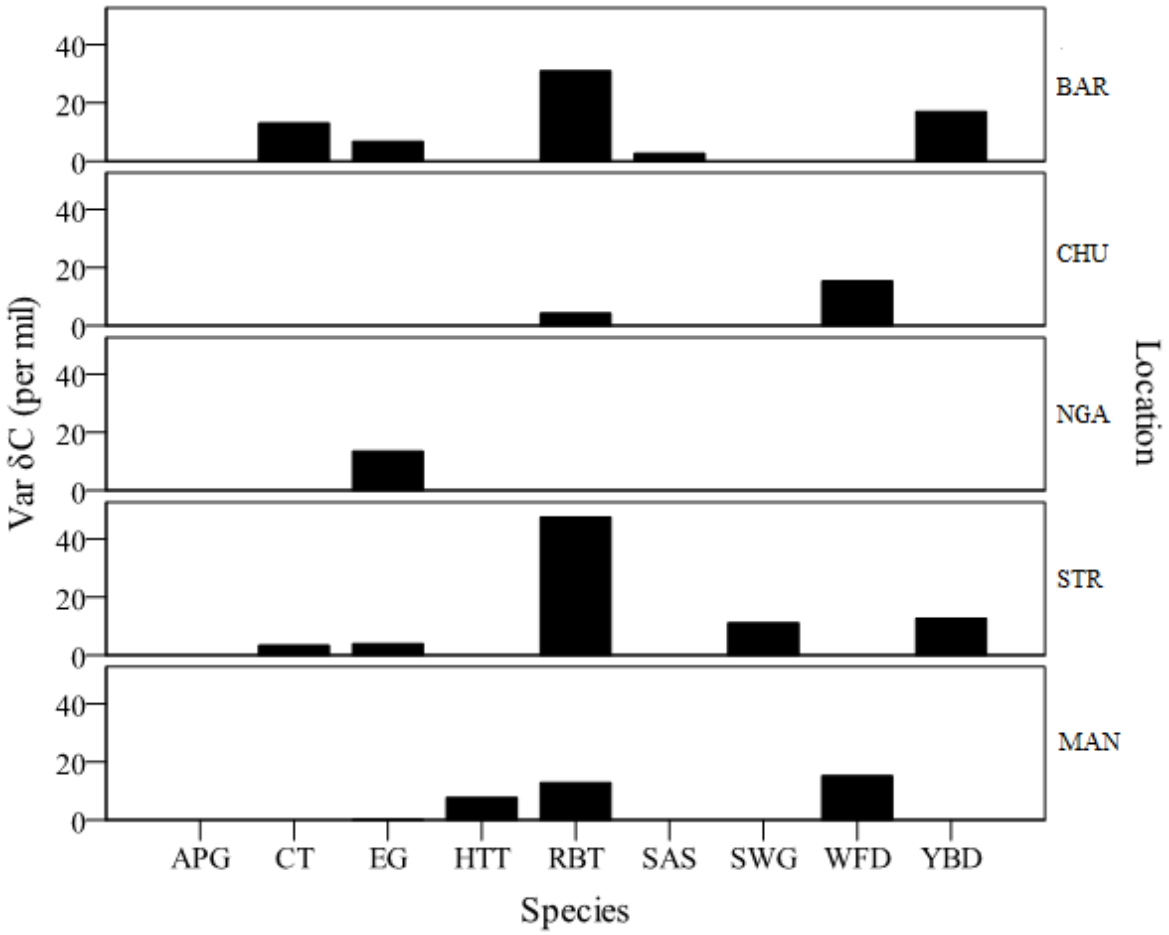


Fig. 3.4 (a): Inter-individual isotope proportion variances of Carbon (Var δ^{13}C) for Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), African Pygmy Goose (APG), Hottentot Teal (HTT) and Spur-winged Goose (SWG); from Strandfontein (STR), Barberspan (BAR), Lake Ngami (NGA), Manyame catchment (MAN), and Lake Chuali (CHU). Blanks mean no analysis was carried out for the species.

(b)

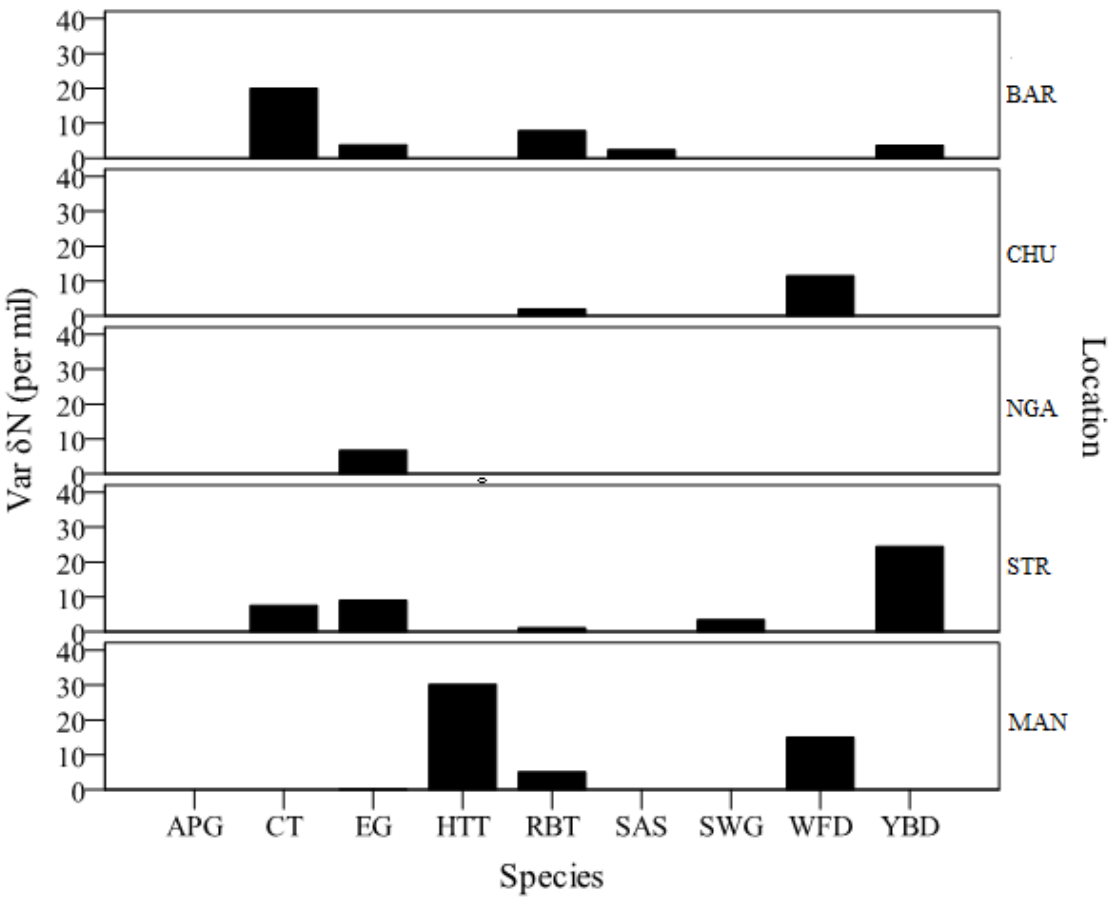


Fig. 3.4 (b): Inter-individual Isotope proportion variances of Nitrogen (Var δN) for Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), African Pygmy Goose (APG), Hottentot Teal (HTT) and Spur-winged Goose (SWG); from Strandfontein (STR), Barberspan (BAR), Lake Ngami (NGA), Manyame catchment (MAN), and Lake Chuali (CHU). Blanks mean no analysis was carried out for the species.

Table 3.2: Inter-species comparisons (rows against columns) of stable isotope proportions of Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) in growing flight feathers. The isotope distinguishing species is indicated, e.g. $\delta^{13}C$. 'No comparisons made' is represented by dots, 'comparisons made and species found similar' is represented by '='. Above and below the diagonal show comparisons of the same pair of species made at different time scales (either different years or different seasons as indicated by arrows).

Barberspan

	EG	RBT	YBD	CT	SAS	
EG		=	….	$\delta^{15}N$, $\delta^{13}C$	=	
RBT	=		….	=	$\delta^{15}N$, $\delta^{13}C$	
YBD	=	=		$\delta^{15}N$	=	
CT	$\delta^{15}N$	=	….		$\delta^{15}N$, $\delta^{13}C$	↑
SAS	=	$\delta^{13}C$	….	=		Summer

← Winter

	EG	RBT	YBD	SAS	CT	
EG		=	=	=	….	
RBT	$\delta^{13}C$		=	=	….	
YBD	=	$\delta^{13}C$		=	….	
SAS	=	$\delta^{15}N$, $\delta^{13}C$	=		….	↑
CT	=	=	=	$\delta^{13}C$ ←		2007

2008

Strandfontein

	EG	RBT	YBD	CT	SWG	
EG		=	=	$\delta^{15}N$, $\delta^{13}C$	….	
RBT	$\delta^{15}N$, $\delta^{13}C$		=	$\delta^{13}C$	….	
YBD	….	….		=	….	↑
CT	….	….	….		….	
SWG	$\delta^{15}N$, $\delta^{13}C$	$\delta^{13}C$	….	..		Summer

← Winter

	EG	RBT	CT	SWG	
EG		δ^{15}N, δ^{13}C	….	δ^{15}N	
RBT	=		….	=	
CT	δ^{15}N, δ^{13}C	δ^{15}N, δ^{13}C		….	↑
SWG	….	….	…. ←		2007
				2008	

	EG	YBD	SWG	
EG		=	=	
YBD	….		=	
SWG	….	….		↑
				2009

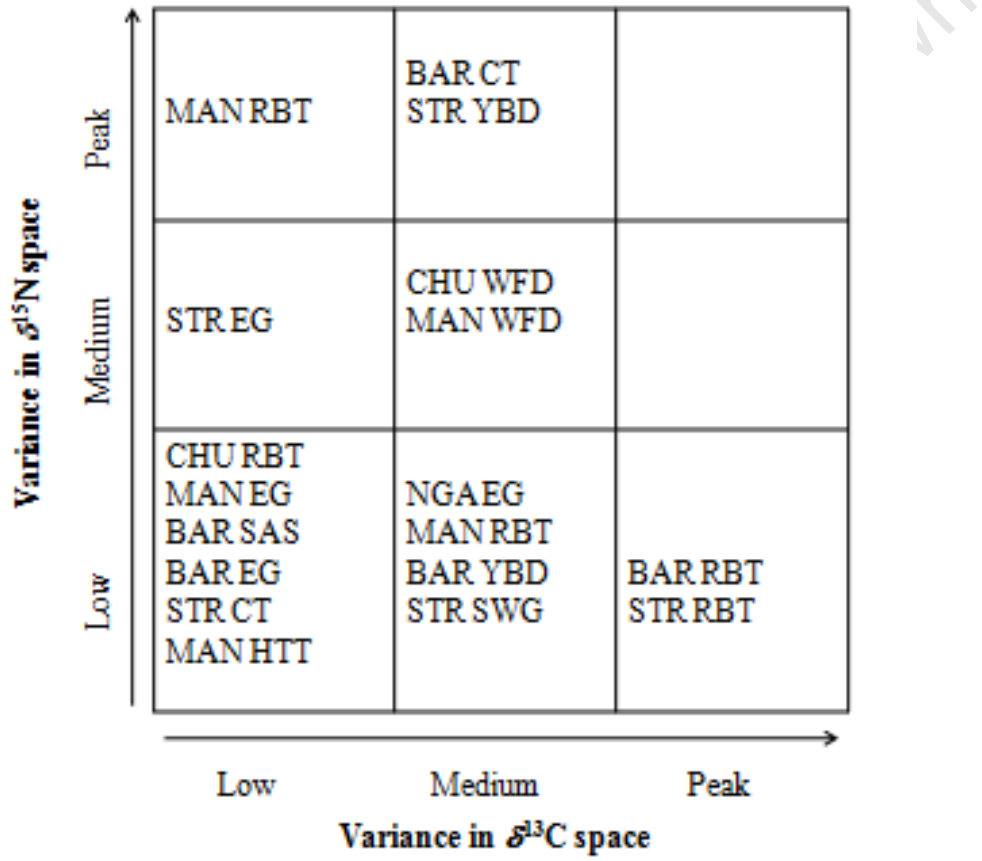
Manyame catchment

	EG	RBT	WFD	HTT	
EG		δ^{15}N	=	=	
RBT	=		δ^{15}N	=	↑
WFD	….	….		….	
HTT	….	….	….		Summer
			←		
				Winter	

	EG	RBT	WFD	HTT	
EG		….	….	….	
RBT	δD		δ^{15}N	….	↑
WFD	=	=		….	
HTT	=	=	=		2007
				← 2008	

Species compared: Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), Hottentot Teal (HTT), and Spur-winged Goose (SWG). '=' means similar signatures, '….' Means no comparisons made.

Table 3.3: Relative classification of ducks (low, medium, peak variances) according to the magnitude of Inter-individual variance in feather stable isotope proportions of Carbon and Nitrogen (Variance in δ^{13}C and δ^{15}N space) using comparisons from Fig. 3.4 and Appendices 9 and 10. Bird species: Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), African Pygmy Goose (APG), Hottentot Teal (HTT) and Spur-winged Goose (SWG). Study sites: Strandfontein (STR), Barberspan (BAR), Lake Ngami (NGA), Manyame catchment (MAN), and Lake Chuali (CHU).



Discussion

Isotope patterns showed variation in space and time implying dynamic foraging behaviours at different sites and across different seasons and years. There were more signature overlaps between different species during the dry season and within the more remote sites (Lake Chuali and Lake Ngami). For instance, Egyptian Goose and Red-billed Teal, from Lake

Ngami and White-faced Duck and Red-billed Teal from Lake Chuali were not distinct in δ^{15}N and δ^{13}C. More distinctions were displayed in δ^{13}C than in δ^{15}N meaning more habitat separations through resource partitioning among species (Adams et al. 2004; Forero et al. 2002). Diet and foraging behaviour manifested mainly through inter-species, inter-individual and temporal isotope signature patterns.

Inter-species isotope signature patterns

Species within the same feeding guild did not necessarily show similarity of signatures as expected (appendix 9). Bill morphologies, neck lengths and body structures further govern related species' access to forage or parts of forage in a given environment (Ogilvie and Pearson 1994). During moulting, species of the same feeding guild may use similar food but at different depths, in different sizes and from different parts of the same food item (Brickell 1988; Ogilvie and Pearson 1994; Todd 1996). My results imply that southern African ducks have highly plastic diets. Their choice of food is guided more by availability than choice. They feed on whatever is available and in times of shortages, they may cross guilds exploiting what they do not normally feed on. Such foraging behaviours make their stable isotope signature patterns highly unpredictable and less useable in movement ecology studies.

However, many dietary studies have adopted the stable isotope technique owing to the ease with which samples (< I mg) can be handled (in large numbers) meaning information can be obtained from large samples non-destructively (Newsome et al. 2007). Jaeger et al. (2009) showed resource partitioning, migratory connectivity, seasonal interactions, seasonal niche variations, and moulting isotopic niches in birds using stable isotopes δ^{13}C and δ^{15}N. Generalist and specialist foragers have been determined using variance in 'δ' space in several studies (Newsome et al. 2007; Jaeger et al. 2010).

Inter-individual Isotope signature patterns

Because tests in this chapter were limited to growing flight feathers and the bird was foraging in one limited location, inter-individual variations in isotope signatures imply dietary and foraging behaviour variations, not movements. Inter-individual isotope proportion variance of Carbon and Nitrogen (Var δ^{13}C and δ^{15}N respectively) showed two foraging behaviours: specialist and generalist. Small isotopic variances imply feeding on a narrow range of food items (Matthews and Mazumder 2004; Del Rio et al. 2009; Jaeger et al. 2010). However, a

population of isotopic specialists can include dietary specialists and dietary generalists that feed on the same mixture of resources at all times (Del Rio et al. 2009). This means the technique is not a hundred percent reliable.

However, higher variance implies high foraging plasticity. Hence, scoring each species according to the number of appearances in the low versus high variance zones showed the Egyptian Goose, South African Shelduck and Spur-winged Goose, with predominant appearances in the low variance zone (Fig. 3.4). These species are mostly primary grazers; populations of these species forage on a narrower range of food items in space, type and time (Baldassarre and Bolen 2006). In contrast, Red-billed Teal, Cape Teal, Yellow-billed Duck, White-faced Duck, and Hottentot Teal, exhibited relatively greater variances, suggesting they have more flexible diets. During moulting, when ducks cannot fly, they are forced to feed locally on whatever is available. For instance, grazing ducks may have more of a dabbling diet (Ogilvie and Pearson 1994; Todd 1996). The majority of ducks did not show a particular dietary preference during moulting in this study, but probably were maximising the usage of what was available (owing to the high isotopic variances).

Egyptian Goose and Cape Teal seemed to have fed at a higher trophic level in Strandfontein (Fig. 3.1). The site is on the coast and the sea is characteristically enriched in $\delta^{15}N$ isotopes (Rubenstein and Hobson 2004). This elevates the site's flora and fauna $\delta^{15}N$ isotope signatures, which are then transferred into duck tissues through nutrition. Additionally, Strandfontein is the most human influenced among my study sites; it is a sewage works site surrounded by suburban areas and a landfill site, this causes spatial and temporal isotope pattern heterogeneity (Rubenstein and Hobson 2004). It is for this reason that ducks from the site had high isotope variances.

When comparing dietary information generated from feather stable isotopes to movement inferences drawn earlier in chapter 1 and 2, it was evident that species with more flexible foraging habits also fell far from expected spatial isotope patterns. The Yellow-billed Duck did not show isotopic distinction between feathers grown during different life-phases; here they exhibited the highest variance, mainly being imposed by the Strandfontein Yellow-billed Duck population (Table 3.3). This observation probably implies that the greater the flexibility of foraging habit for a particular species, the lesser resolvable its movements is through the isotope technique. These dietary-imposed shortfalls limit the isotope technique's capacity to trace movements of ducks in southern Africa.

Overall figures 3.1 and 3.2 show that Egyptian Goose, Yellow-billed Duck and South African Shelduck in Barberspan predominantly used C_4 (-11 to -14‰; Cerling et al. 2009)

based diets during moulting as opposed to ducks from across the other sites. This makes sense because the site is dominated by grassy vegetation which is C_4 based. Additionally, the site is surrounded by vast fields of maize (a C_4 based crop), some of which are within walking distances from a few points of the pan and can be exploited during moulting. Moulting Egyptian Geese have been observed walking to and from maize fields closest to the pan (personal observation). Ducks from other sites had intermediate values (-15 to 24‰) between C_4 and C_3 vegetation (C_3 plants range between -25 to -29‰; Cerling et al. 2009).

Temporal signature patterns

During the dry seasons (winter in Barberspan, Manyame catchment, Lake Ngami, and Lake Chuali and summer in Strandfontein) more signature overlaps were shown. This makes sense because during dryer seasons there is less forage, habitats shrink and different species are forced into restricted foraging areas (Baldassarre and Bolen 2006; Ogilvie and Pearson 1994). This results in diet convergence and possibly competition among duck species at moulting locations. Seasonal and species interaction imposed changes in foraging ecology imply seasonal signature variation and a 'species interaction driven' diet to tissue signature variation. Isotope-based movement studies need to be season specific and to some degree, factor in species-interaction effects at different sites.

Conclusions

Feather stable isotopes can reveal diverse pieces of information on the diet and foraging ecology of ducks in southern Africa. Diet and foraging behaviour compromise the resolution capacity of stable isotopes in movement studies within the region. Even though foraging habits and diet influence isotope results, isotope patterns can also be distorted by biological processes during assimilation of isotopes into tissue (Bearhop et al. 2002). It is difficult to judge conclusively whether predominantly diet and foraging habit or intrinsic biology of the species affects the usefulness of the isotope technique. Further research is needed to distinguish between intrinsic biology and feeding ecology effects on isotope signatures in feathers.

It is imperative to carry out a dietary analysis with all movement studies based on the isotope technique in order to verify how reliable the results and inferences drawn are. Here my results show that dietary inherent differences in tissue signatures greatly compromise

isotope results. A better but more costly method would be to generate isotope base maps from vegetation and soil of $\delta^{15}N$, $\delta^{13}C$ patterns as recommended by other studies (Yohannes 2007). These can serve as unequivocal references in tracing movements and origins of animals.

Literature cited:

Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73, 1007-1012.

Baldassarre, G.A.R., Bolen, E.G. 2006. *Waterfowl ecology and management*, 2nd edn. Malabar: Krieger.

Bearhop, S., Waldron, S., Votier, S.C., Furness, R.W. 2002. Factors that influence assimilation rates and fractionation of Nitrogen and Carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology*, 75, 451-458.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology,* 73, 1007-1012

Bearhop, S., Phillips, R., McGill, R., Cherel, Y., Dawson, D., Croxall, J. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Marine Ecology Progress Series*, 311, 157-164.

Brickell, N. 1988. *Ducks, Geese and Swans of Africa*, Sandton: Frandsen.

Cerling, T.E., Wittemyer, G., Ehleringer, J.R., Remien, C.H., Douglas-Hamilton, I. 2009. History of Animals using Isotope Records (HAIR): a 6-year dietary history of one family of African elephants. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 8093-8100.

Cherel, Y., Phillips, R.A., Hobson, K.A., McGill, R. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters*, 2, 301-303.

Codron, D., Lee-Thorp, J.A., Sponheimer, M., Ruiter, D.D., Codron, J. 2006. Inter- and intra-habitat dietary variability of Chacma Baboons *(Papio ursinus)* in South African Savannas based on faecal $\delta^{13}C$, $\delta^{15}N$, and % N. *American Journal of Physical Anthropology*, 214, 204-214.

Cremona, F., Planas, D., Lucotte, M. 2010. Influence of functional feeding groups and spatiotemporal variables on the δ^{15}N signature of littoral macro-invertebrates. *Hydrobiologia*, 247, 51-61.

Del Rio, C.M., Sabat, P., Anderson-Sprecher, R., Gonzalez, S.P. 2009. Dietary and isotopic specialization: the isotopic niche of three *Cinclodes* ovenbirds. *Oecologia*, 161, 149-159.

Focken, U., Becker, K. 1998. Metabolic fractionation of stable Carbon isotopes: implications of different proximate compositions for studies of the aquatic food webs using δ^{13}C data. *Oecologia*, 115, 337-343.

Forero, M., Hobson, K., Bortolotti, G., Donázar, J., Bertellotti, M., Blanco, G. 2002. Food resource utilisation by the Magellanic Penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. *Marine Ecology Progress Series*, 234, 289-299.

Geldenhuys, J.N. 1977. Feeding habits of South African Shelduck. *South African Journal of Wildlife Research,* 7, 5-9.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, 120, 314-326.

Hodum, P.J., Hobson, K.A. 2000. Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope (δ^{15}N and δ^{13}C) analyses. *Marine Ecology Progress Series*, 198, 273-281

Jaeger, A., Connan, M., Richard, P., Cherel, Y. 2009. Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Marine Ecology Progress Series,* 401, 269-277.

Jordan, M.J.R. 2005. Dietary analysis for mammals and birds: a review of field techniques and animal-management applications. *International Zoology Yearbook,* 39, 108-116

Matthews, B., Mazumder, A. 2004. A critical evaluation of intra-population variation of δ^{13}C and isotopic evidence of individual specialization. *Oecologia*, 140, 361-71.

Ndlovu, M., Cumming, G.S., Hockey, P.A.R. 2010. Phenotypic flexibility of a southern African Duck during moult: Do northern hemisphere paradigms apply? *Journal of Avian Biology*, 41, 1-7.

Newsome, S., Del Rio, M.C., Phillips, D.L., Bearhop, S. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment,* 5, 429-436.

Ogilvie, M., Pearson, B. 1994. *Wildfowl Behaviour Guide.* Melbourne: Hamlyn.

Pain, D.J., Green, R.E., Giebetaing, B., Kozulin, A., Poluda, A., Ottosson, U., Flade, M., Hilton, G.M. 2004. Using stable isotopes to investigate migratory connectivity of the globally threatened Aquatic Warbler (*Acrocephalus paludicola)*. *Oecologia*, 138, 168-74.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology,* 83, 703-718

Rubenstein, D.R., Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution,* 19, 256-63.

Swap, R.J., Aranibar, J.N., Dowty, P.R., Gilhooly, W.P., Macko, S.A. 2004. Natural abundance of $\delta^{13}C$ and $\delta^{15}N$ in C_3 and C_4 vegetation of southern Africa: patterns and implications. *Global Change Biology*, 10, 350-358.

Todd, F. 1996. *Natural history of the waterfowl.* California: San Diego Natural History Museum.

Vanderklift, M., Wernberg, T. 2010. Stable isotopes reveal a consistent consumer-diet relationship across hundreds of kilometres. *Marine Ecology Progress Series*, 403, 53-61.

Votier, S.C., Bearhop, S., Ratcliffe, N., Furness, R.W. 2001. Pellets as indicators of diet in Great Skuas (*Catharacta skua)*. *Bird Study,* 48, 373-376.

Yohannes, E. 2007. Feather stable-isotope profiles reveal stopover habitat selection and site fidelity in nine migratory species moving through sub-Saharan Africa. *Journal of Avian Biology,* 38, 347-355.

Zar, J.H. 2010. *Biostatistical Analysis,* 5th edition. New Jersey: Prentice Hall.

SYNTHESIS

The primary aim of this research was to test the usefulness of stable isotopes in tracing the movement patterns of ducks in southern Africa. The technique depends on the existence of distinct isotopic regions and the efficiency with which chosen reference materials reflect isotope patterns in the environment through diet (Hobson 2005). I therefore compared isotope signatures, (1) of growing flight feathers from known origins across different sites to verify if different sites had unique isotope signatures, (2) between feathers grown during different life phases to see if isotopically and possibly geographically distinct sites were used; and if more mobile species showed more and stronger distinctions, (3) of growing feathers of different species occupying the same site to draw inferences of diet and foraging behaviour, and verify if these can influence the resolution capacity of isotopes in movement studies.

Within the capacity of an MSc, it was not possible to obtain 'state-of-the-art' results from each of the examinations. The intention was to rather explore the utility of the isotope technique under southern African stochastic environments. This study attended to many hypotheses, answered several questions, provided suggestions for refining isotope techniques, and indicated areas of future research needs.

The existence of distinct isotopic regions within southern Africa was tested by comparing new feather isotope signatures of ducks across three different wetlands (Strandfontein, Barberspan and Zimbabwe). The proposed hypothesis was that study sites chosen were isotopically distinct because they belong to different vegetation biomes and they are far apart (~1000km). Feather stable isotope proportions (δ^{13}C, δ^{15}N and δD) variably distinguished the study sites depending on season and year of sampling. I therefore concluded that moderately distinct isotopic regions exist in southern Africa and can be resolved using multi-isotope and time specific approaches.

Because different sites were isotopically distinct (in at least one isotope) for some of the ducks tested, and ducks habitually use different sites for different life phases, movement between sites was hypothesised to be distinguishable through comparing signatures of tissues grown during different life phases. Logically, more mobile species should show more and stronger distinctions between tissues grown during different life phases. In chapter two, I compared flight feathers (grown during the moulting phase) against body feathers (grown during the breeding phase). Some species showed distinctions in isotope signatures between

flight and body feathers, and this changed with site. Feather signature distinctions were higher and stronger in more mobile species (based on ring- recovery-based mobility scores) in only two of the species tested. I therefore concluded that the isotope technique is unreliable in detecting mobility and in determining whether different sites have been used for different life phases.

Because different species have different foraging behaviours across and within different feeding guilds, they take up unique dietary items potentially having different isotopic signatures. I hypothesised (in chapter three) that the isotope technique cannot reliably trace all duck species' movements because of dietary imposed isotope signature biases. In stochastic environments, foraging plasticity tends to increase; more sources of variation which cannot be controlled and accounted for are introduced. This compromises isotope-based comparative movement inferences. To test this hypothesis, chapter three compared different species' dietary behaviour inferred from isotope signatures of growing flight feathers at moulting locations. I verified if different feeding behaviours were related to the isotope signature divergence from mobility in chapter two. Specialist foragers as implied by low isotope variances showed clearer distinctions. I therefore concluded that foraging behaviour and diet has a profound impact on interpretability of isotope results through comparative analysis in southern African ducks. After ingestion, dietary signature further goes through assimilation processes which potentially contribute to environment-tissue signature differences (Bearhop et al. 2002). More research is needed to verify how assimilation biology in different southern African ducks influences tissue isotope signatures.

Southern Africa presents a challenging location for isotope application owing to its dynamic weather patterns (Tyson and Preston-Whyte 2000). Besides ecologically and intrinsically imposed isotope variations in tissues, the organism takes up diet exposed to dynamic environmental conditions. This introduces a multitude of sources of variation, as presented in the three chapters.

As implied by classical foraging theory, movement can be influenced by food availability, distribution, and accessibility (Kohlman and Risenhoover 1998). Ducks maximise forage uptake from profitable sources, i.e. with fewer predators, less competition and more nutritive value (Kohlman and Risenhoover 1998). Feeding guilds are evident among southern African ducks, but the flexibility and overlap of feeding within guilds seems very high as shown by isotope signature overlaps. Additionally, minimal overlap in diet across guilds reported in Anatids elsewhere was opposed by my results (Todd 1996; Scott & Rose 1996). Isotope signature and possibly dietary overlaps were unpredictable and variable

with season and site. The region is fairly arid and experiences droughts (Harsch 1992); times of forage scarcity enforce more flexible feeding behaviours (Owen & Black 1990; Ogilvie & Pearson 1994). This makes foraging behaviour a significant determinant of resolution in isotope-based movement studies in southern Africa.

Given southern Africa's stochastic environments, three pre-requisites have to be met in order for a species to be considered resolvable in movement investigations using stable isotopes. The species has to have a consistent diet and foraging behaviour, it has to move across distinct isotopic regions, and the study area has to be made of distinct isotopic regions. The research showed that the Egyptian Geese gave the most reliable results. Cape Teals, Spur-winged Geese, South African Shelducks and White-faced Ducks' results could be questioned; they did not meet the expected pattern when referring to mobility scores. The Yellow-billed Ducks were non-responsive to all the tests; it showed no distinction of isotope signatures between feathers grown during different life-stages implying that they possibly have very conservative foraging habits, finding similar foods in all habitats where they occur. The Yellow-billed Ducks also had highly flexible foraging habits as shown by their high inter-individual variances. Hottentot Teal, Cape Shoveler and African Pygmy Goose had too small sample sizes for tests other than foraging behaviour.

However, the research showed complex and fragmentary results. This was mainly a result of low catchability in some ducks during particular seasons at some of the study sites. Generally the results showed that there is weak to moderate evidence that different regions within southern Africa have different dietary signatures, and that there is a general trend for more mobile species to have more signature distinctions than more sedentary species. Beyond this, I found that ducks within the southern African region are not good candidates for use of isotopic signatures in studying movement ecology.

Nothing has been published on isotope proportions of ducks in southern Africa and very little if anything at all is known about $\delta^{13}C$, δD and $\delta^{15}N$ of the species therein. Additionally, we lack detailed information on the movements of most southern African Anatids (Cumming et al. 2008). Hence the level of information this research contributes is potentially important. The results are however exploratory and can help to direct future isotope research in southern African towards seeking refinement to cater for as many sources of variation as possible. As long as erroneous diverse sources of variation are not catered for and addressed, the method remains of little use in southern African conditions, at least in movement studies.

Ecologists should be wary about basing management strategies or building theory about movement patterns of species based on the technique at least in stochastic environments such as southern Africa. Even though this technique is useful for understanding movements and can provide more data in a smaller time frame than ringing, it is flawed with sources of exaggerated isotopic diversity that are not related to movement patterns. Until these sources of extraneous variation in isotope signals can be properly identified and accounted for, the technique is of little use in comparing duck mobility and tracing the movement patterns of ducks under southern African conditions.

Literature cited:

Baldassarre, G.A.R., Bolen, E.G. 2006. *Waterfowl ecology and management*, 2nd edn. Malabar: Krieger.

Cumming, G.S., Hockey, P.A.R., Bruinzeel, L.W., Du Plessis, M.A. 2008. Wild bird movements and avian influenza risk mapping in southern Africa. *Ecology And Society*, 13, 26 [online] URL: http://www.ecologyandsociety.org/vol13/iss2/art26/.

Harsch, E. 1992. Drought devastates Southern Africa. *Drought New York Times*, 2, 17-19

Hobson, K.A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, 11, 157-164.

Kohlmann, S.G., Risenhoover, K.L. 1998. Effects of resource distribution, patch spacing, and pre-harvest information on foraging decisions of Northern Bobwhites. *Behavioural Ecology*, 9, 177-186.

Ndlovu, M., Cumming, G.S., Hockey, P.A.R. 2010. Phenotypic flexibility of a southern African Duck during moult: Do northern hemisphere paradigms apply? *Journal of Avian Biology,* 41, 1-7.

Ogilvie, M., Pearson, B. 1994. *Wildfowl Behaviour Guide*, Melbourne: Hamlyn.

Owen, M., Black, J.B. 1990. *Waterfowl Ecology*, London: Chapman and Hall.

Scott, D.A., Rose, P.M. 1996. *Atlas of Anatidae populations in Africa and western Eurasia*, Wegeningen: Wetlands International.

Todd, F. 1996. *Natural history of the waterfowl*, California: San Diego Natural History Museum.

Tyson, P.B., Preston-Whyte, R.A. 2000. *The weather and climate of Southern Africa*. Oxford: Oxford University Press.

AKNOWLEDGEMENTS

Firstly I would like to thank my supervisor, Graeme Cumming at the Percy Fitzpatrick Institute of African Ornithology (PFPIAO) for his guidance and support in the project. This venture would never have been achievable without his contribution.

The GAINS-SA and Percy Fitzpatrick Institute of African Ornithology are greatly acknowledged for funding.

For fieldwork, I would like to acknowledge the following crew who went out of their way in providing help with capturing and sampling birds: Mduduzi Ndlovu, David Nkosi, Barberspan Bird Sanctuary Staff and the Manager (Sampi Van de Merwe), Mapula Kagodi, Felix Nchu and Sharon Okanga.

Pre-treatment of samples for isotope analysis was actively supported by the following crew: Portia Mutumi, Sharon Mudzimuirema, and Caroline Mushayi. A great thank you goes to the UCT archeology lab staff including Ian Newton and John Lanham for assistance in running the analyses, and to Stephan Woodbor (CSIR- Pretoria) for running the Hydrogen analyses.

For advice on statistical procedure and interpretation of results, I would like to thank Viviane Barquette, Rowan Martin, Timothee Cook, Susan Cunningham and Pardon Masuka.

To all the Percy Fitzpatrick staff, I would like to extend a special thank you for all forms of support. I would like to say PFPIAO was my home away from home!

Last but not least, I want to thank my Mum and Dad who have taught me to appreciate the beauty of nature. I acknowledge the strong encouragement they have given towards my career in natural science.

"I know the meaning of plagiarism and declare that all the work in this document, save for that which is properly acknowledged, is my own".

Appendix 1: Ecology of some of the study species (based on information from Hockey et al. 2005)

	Egyptian Goose	Yellow-billed Duck	White-faced Duck	Cape Teal	Red-billed Teal
Distribution	Sub-Saharan Africa and Nile river valley. Introduced in parts of Europe. Extensive range in southern Africa especially western cape, KZN and Zimbabwe	Ethiopia south, west Angola, Southern Africa. Largely absent from arid areas	Throughout most of sub Saharan Africa except in arid areas. Also in Madagascar, Comoro island and in Tropical America.	A population exists in Sudan and S. Ethiopia to Tanzania. The disjunct southern Africa population is from s Angolan coast and s Zambia to s S Africa. Localised and in small numbers in w and c Zimbabwe	Afro tropics including Madagascar. Recorded over most of southern Africa.
Population and demography	Pairs fully grown hold a territory of up to 1hactare in suitable fresh water. Reach sexual maturity at 2 years. They live up to 10-15 years. Estimated population between 200000-500000 in east and southern parts of south Africa	Population estimated at 52000-65000 in south Africa. Survival rate of about 79.5% for males and 72.2% for females. Male longevity 4.4 and female longevity 3.1	Population estimated at 1-2million in south and east Africa. It became the second most abundant species in 3 972 monthly counts at 133 farms in Zimbabwe 1972-1978. 8 years longevity. Susceptible to botulism. Parasitized by 3 feather lice, 1 nasal mite, and 1 leach (Theromyzon cooperi) causing paralysis and death.	100 000-250 000 in south Africa including Angola and Zambia. Western Cape (1088-2386 in 1964) affected by summer out breaks of botulism, preyed on by African marsh harrier, and possibly cape eagle owl (a ring recovered in pellet).	Estimated population at 500000 to 1million in southern Africa including Angola Zambia and Malawi. Infested by African Duck leech (*Theromyzon cooperi*) causing paralysis and death. Also affected by a cloacal tape worm (*Cloacotaenia megalops*) and schistosomes.
Movements	Wide spread movement 70 to 800km. some can go more than 1000km. annual post breeding moults taken in early winter. No traditional attachment to moulting sites. Recently built large dams often chosen as new destinations. Yearlings frequently exhibit natal phylopatry	Mostly nomadic, though some are sedentary on permanent waters like Barberspan (S.A north west province). Disperse from permanent waters after 100mm rainfall. Some have been recovered more than 1000km from a ringing site South Africa. Most have been recovered over much shorter distances.	Moult at permanent wetlands in winter but movements are irregular. Large annual fluctuations in numbers. Disperse to breed, mainly nomadic but has the most restricted movement based on genetics and meridian displacements of 99km. 76 recoveries from 1616 birds ringed. Longest traveller made 1125km to Zimbabwe from S.A	Nomadic, long distance Congregates on permanent water-bodies to moult and disperses to ephemeral ones to breed. Influx of breeding birds in June to October in Zimbabwe. No convincing evidence of migration or movement outside the region. Dispersal distance range from 54km to 2 171	Mostly nomadic favouring ephemeral wetlands for breeding. Make large seasonal movements to large permanent wetlands to moult. Dispersive/partial migration. Rapidly locates freshly flooded vleis and pans. Most leave Botswana in the dry season especially if lake Ngami is dry. 2 ringed in Barberspan recovered 2129 -2190 km to Tanzania.
Habitat	Dams, rivers, pans, lakes marshes, sewerage work and even estuaries, harbours and off shore islands. Waterbodies with open shorelines, rich aquatic plant growth and close to cereal fields. Forages mainly in crop fields and at wetland edges. Will enter ocean occasionally foraging along the shoreline.	Open water estuaries, sluggish and still waters of rivers and streams, lakes and endorheic pans, swamps, marshes and manmade impoundments including irrigation dams and sewage works. Avoids saline and highly acidic water bodies as well as fast flowing water.	Various inland waters, mainly in savannah and grassland, extensive shallows with short emergent vegetation especially for brood rearing. Man made water bodies favoured. Prefers ephemeral wetlands for breeding, moving to more permanent water bodies for winter flightless moult. Can breed while on herbivorous diet, hence can breed on wetlands with few macro-invertebrates	Open saline or brackish water especially salt pans, estuaries and coastal lagoons in w cape, temporary and permanent vleis, sewage and effluent ponds, dams, bare and grassy pans for breeding, deep open water for moulting. Aggressive even outside breeding (19% of 112 inter-specific attacks at Barberspan outside breeding period)	Most inland wetlands both natural and artificial. Breeds at shallow ephemeral pans and dams in dry season, assembles in large water bodies to moult and form pairs.

Foraging and food	Dabbles and probes in shallow water, perches on or follows hippopotamuses feeding on disturbed material mainly plants but primarily a grazer and seed stripper. Seeds, grasses, grains, shoots, leaves, aquatic plants and young crops. When moulting, relies solely on aquatic algae	Forages by swimming immersing and upending and filtering, sometimes diving or grazing new green growth of aquatic plants. Adults and juveniles fledged at Barberspan ate a mix of 83% plant material mainly pond weed and 17% animal matter.	Dabbles with head immersed, also upending and diving. Strips seeds from plants on land. In winter, forages day and night. Congregates to feed. Diet dominated by plant matter- 99.2 to 100% with slight increases in small vertebrates during breeding and moulting. Pondweed, sedge seed, maize are foraged	Shallow open waters foraging throughout the day. Also at night. Surface Filtering, picking animals off submerged material and water surfaces, Grazing on shore. Also dives into deep water for 30 seconds. Stomach contents of 39 birds collected summer-autumn had 83% animal matter mainly insects and 17% plant matter. 13 adult birds in winter at Baberspan had 99% animal matter and 1% plant material	Filtering on surface and mixed mode. Diet dominated by seeds of land grass (*Panicum Schnizii*) 73-97% of aggregate dry mass upper digestive tract contents. Other grasses like water grass, cow grass are favoured. Pondweed and insects
Breeding	Monogamous solitary nester, territorial. Copulation generally in shallow water and brief. Nest built by female on ground dug by feet and overlayed with grass reeds, leaves. 1-22 eggs laid at 22hour intervals. Incubation after clutch complete. Young precocial leaves nest before 6 days after hatch. Single brooded, or double under optimal conditions	Monogamous solitary nester. Nest= shallow depression in ground lined with fine grass or water reeds and down lining at the start of egg laying. Smallest nest built if conditions are dry and largest if in water logged conditions. Among reeds, rushes, dense grass which are rarely exposed, with funnel from outside. Lays throughout the year except in August 2-10 eggs	Monogamous solitary nester with long term pair bond. Nests are spaced at more than 75m. Copulates on water, forced copulation common. Both sexes build a well concealed nest in grass together or above water in reeds. Lays in January – March in S.A December to Feb in Kwazulu Natal, single brooded clutch of 5. Preyed on by African fish eagle.	Monogamous, bigamy recorded in captivity, long term pair bond possibly allowing pair to capitalise on unpredictable breeding opportunities. Breeding is opportunistic in response to rainfall.	Monogamous with breed pair dissolved before brood fledges usually earlier. Solitary nester, nests are 10m apart. Nest= shallow depression in dry ground lined with grass, down feathers. Laying dates vary widely. 5 to 12 eggs in W. Cape 25 to 27 days incubation. 97 % hatched.
Moult	Wing moult in south Africa occurs in March to October (in Barberspan), April to August in W.Cape. 40days flightless. Capable divers when moulting. Moulting areas usually open and undisturbed by human beings, with cropfields & grassland nearby	Becomes flightless at 4- 8 days before flight feathers are dropped. 32 to 50 days flightless period	Wing moult occurs year round in order to spread protein requirements but is suspended during egg laying and incubation. Wing moult extended from post breeding to spring with peaks in early winter and spring. Bird begins to fly before the feather is fully grown	Complete post breeding moult. Few records from Barberspan and Zimbabwe suggest summer moulting peak. Become flightless 2 days before flight feathers are dropped, replacement takes 23-24 days.	Body and tail moulted continuously but remiges during and after breeding season. Capable of flying when feather is 70- 80% grown. About 24- 28 days taken to regrow flight feathers

Appendix 2: Ducks present at each site during the research

Numbers shown are a sum of all counts done at each site i.e., bi-monthly at Strandfontein, Barberspan and Lakes Manyame and Chivero, four monthly at Lake Chuali and Lake Ngami. Relative abundance is expressed as an average per hectare per count (ducks/ha). Species EG= Egyptian Goose, RBT= Red-billed Teal, YBD= Yellow-billed Duck, WFD= White-faced Duck, CT= Cape Teal, SAS= South African Shelduck, APG= African Pygmy Goose. Sites BAR= Barberspan, STR= Strandfontein, MAN= Lake Manyame, CHI= Lake Chivero, NGA= Lake Ngami, CHU= Lake Chuali. Seasons Smr= summer and Wint= winter

Species _Year _Season		STR Count	STR ducks/ha	BAR Count	BAR ducks/ha	MAN Count	MAN ducks/ha	NGA Count	NGA ducks/ha	CHU Count	CHU ducks/ha
EG		**3400**	**77.05**	**19051**	**431.74**	**1398**	**31.68**	**1214**	**55.02**	**3**	**0.07**
	2007	2941	199.95	14893	1012.54	771	52.42	33	2.24	3	0.20
	Smr	2373	322.67	4388	596.66	130	17.68	33	4.49	3	0.41
	Wint	568	77.23	10505	1428.42	641	87.16		0.00		0.00
	2008	269	18.29	2348	159.63	77	5.24	105	7.14		0.00
	Smr	66	8.97	422	57.38	46	6.25	105	14.28		0.00
	Wint	203	27.60	1926	261.89	31	4.22		0.00		0.00
	2009	190	12.92	1810	123.06	550	37.39	1076	73.15		0.00
	Smr	190	25.84	690	93.82	515	70.03	432	58.74		0.00
	Wint		0.00	1120	152.29	35	4.76	644	87.57		0.00
RBT		**3679**	**83.38**	**1110**	**25.16**	**15308**	**346.92**	**16277**	**368.88**	**328**	**7.43**
	2007	3030	206.00	581	39.50	6634	451.03	10072	684.77	240	16.32
	Smr	1936	263.25	444	60.37	5043	685.72	10072	1369.54	214	29.10
	Wint	1094	148.76	137	18.63	1591	216.34		0.00	26	3.54
	2008	481	32.70	468	31.82	3762	255.77	3560	242.04	88	5.98
	Smr	48	6.53	46	6.25	534	72.61	3560	484.07		0.00
	Wint	433	58.88	422	57.38	3228	438.93		0.00	88	11.97
	2009	168	11.42	61	4.15	4912	333.95	2645	179.83		0.00
	Smr	144	19.58		0.00	3897	529.90	229	31.14		0.00

	Wint	24	3.26	61	8.29	1015	138.01	2416	328.52		0.00
YBD		**2621**	**59.40**	**8438**	**191.23**	**2**	**0.05**	**50**	**1.13**	**130**	**2.95**
	2007	515	35.01	2863	194.65		0.00	2	0.14	34	2.31
	Smr	487	66.22	2510	341.30		0.00	2	0.27	34	4.62
	Wint	28	3.81	353	48.00		0.00		0.00		0.00
	2008	2084	141.69	4544	308.94	2	0.14	48	3.26	96	6.53
	Smr	1345	182.89	1914	260.26	2	0.27	48	6.53	73	9.93
	Wint	739	100.49	2630	357.61		0.00		0.00	23	3.13
	2009	22	1.50	1031	70.10		0.00		0.00		0.00
	Wint	22	2.99	1031	140.19		0.00		0.00		0.00
WFD		**22**	**0.50**	**311**	**7.05**	**12977**	**294.09**	**2188**	**49.59**	**1300**	**29.46**
	2007		0.00		0.00	13	0.88	106	7.21		0.00
	Smr		0.00		0.00	13	1.77	106	14.41		0.00
	2008	18	1.22	176	11.97	9349	635.62	1147	77.98	1300	88.38
	Smr		0.00	131	17.81	3019	410.51	1147	155.96	334	45.42
	Wint	18	2.45	45	6.12	6330	860.72		0.00	966	131.35
	2009	4	0.27	135	9.18	3615	245.78	935	63.57		0.00
	Smr	4	0.54	13	1.77	3037	412.96	935	127.14		0.00
	Wint		0.00	122	16.59	578	78.59		0.00		0.00
CT		**6795**	**153.99**	**1163**	**26.36**	**46**	**1.04**	**12**	**0.27**		**0.00**
	2007	86	5.85	8	0.54		0.00		0.00		0.00
	Smr	86	11.69	8	1.09		0.00		0.00		0.00
	2008	3230	219.60	466	31.68	46	3.13	8	0.54		0.00
	Smr	2786	378.83	333	45.28		0.00	8	1.09		0.00
	Wint	444	60.37	133	18.08	46	6.25		0.00		0.00
	2009	3479	236.53	689	46.84		0.00	4	0.27		0.00
	Smr	2266	308.12	245	33.31		0.00	4	0.54		0.00
	Wint	1213	164.94	444	60.37		0.00		0.00		0.00
SAS		**494**	**11.20**	**1724**	**39.07**		**0.00**		**0.00**		**0.00**
	2007		0.00	82	5.57		0.00		0.00		0.00

	Smr		0.00	82	11.15		0.00		0.00	0.00
	2008	217	14.75	476	32.36		0.00		0.00	0.00
	Smr	215	29.23	456	62.00		0.00		0.00	0.00
	Wint	2	0.27	20	2.72		0.00		0.00	0.00
	2009	277	18.83	1166	79.27		0.00		0.00	0.00
	Smr	260	35.35	1115	151.61		0.00		0.00	0.00
	Wint	17	2.31	51	6.93		0.00		0.00	0.00
APG			**0.00**		**0.00**	**146**	**3.31**	**226**	**5.12**	**66**	**1.50**
	2007		0.00		0.00	3	0.20		0.00	26	1.77
	Wint		0.00		0.00	3	0.41		0.00	26	3.54
	2008		0.00		0.00	86	5.85	99	6.73		0.00
	Smr		0.00		0.00	86	11.69	99	13.46		0.00
	2009		0.00		0.00	57	3.88	127	8.63	40	2.72
	Smr		0.00		0.00	54	7.34	127	17.27	32	4.35
	Wint		0.00		0.00	3	0.41		0.00	8	1.09
HTT		**23**	**0.52**	**24**	**0.54**	**146**	**3.31**	**268**	**6.07**	**332**	**7.52**
	2007		0.00		0.00		0.00		0.00		0.00
	Smr		0.00		0.00	5	0.68	15	2.04		0.00
	Wint		0.00	3	0.41	29	3.94		0.00	82	11.15
	2008	7	0.48		0.00	35	2.38	89	6.05		0.00
	Smr		0.00		0.00	31	4.22	52	7.07		0.00
	Wint	7	0.95		0.00	4	0.54	37	5.03		0.00
	2009	16	1.09	21	1.43	77	5.24	164	11.15	250	17.00
	Smr	12	1.63	10	1.36	77	10.47	164	22.30	250	33.99
	Wint	4	0.54	11	1.50		0.00		0.00		0.00
SWG		**1122**	**25.43**	**2142**	**48.54**	**269**	**6.10**	**10**	**0.23**	**176**	**3.99**
	2007	114	7.75	435	29.57	216	14.69		0.00	53	3.60
	Smr	53	7.21	327	44.46	3	0.41		0.00		0.00
	Wint	61	8.29	108	14.69	213	28.96		0.00	53	7.21
	2008	321	21.82	292	19.85	46	3.13	1	0.07	26	1.77

	Smr	226	30.73	59	8.02	27	3.67	1	0.14	26	3.54
	Wint	95	12.92	233	31.68	19	2.58		0.00		0.00
	2009	687	46.71	1415	96.20	7	0.48	9	0.61	97	6.59
	Smr	615	83.62	423	57.52	7	0.95	9	1.22	82	11.15
	Wint	72	9.79	992	134.89		0.00		0.00	15	2.04
CS		**19241**	**436.05**	**1042**	**23.61**	**111**	**2.52**		**0.00**	**15**	**0.34**
	2007	2260	153.65	86	5.85	99	6.73		0.00	11	0.75
	Wint	2260	307.30	86	11.69	99	13.46		0.00	11	1.50
	2008	4804	326.61	246	16.72	12	0.82		0.00		0.00
	Smr	4506	612.70	122	16.59	8	1.09		0.00		0.00
	Wint	298	40.52	124	16.86	4	0.54		0.00		0.00
	2009	12177	827.88	710	48.27		0.00		0.00	4	0.27
	Smr	9204	1251.52	411	55.89		0.00		0.00	4	0.54
	Wint	2973	404.25	299	40.66		0.00		0.00		0.00
Grand Total		**37397**	**847.51**	**35005**	**793.30**	**30403**	**689.01**	**20245**	**458.80**	**2350**	**53.26**

Appendix 3: Capture across the five study sites during different years (2007 to 2009) and seasons (summer and winter)

Species EG= Egyptian Goose, RBT= Red-billed Teal, YBD= Yellow-billed Duck, WFD= White-faced Duck, CT= Cape Teal, SAS= South African Shelduck, APG= African Pygmy Goose. Sites BAR= Barberspan, STR= Strandfontein, MAN= Lake Manyame, CHI= Lake Chivero, NGA= Lake Ngami, CHU= Lake Chuali. Feathers Gr= Growing, Pn= Pin (Moult status 1), Mtr= Mature (Moult status 5), NQ= not quantified, Fully grown= worn out (Moult status 0)

Mean and SD= Standard deviation, Var= variance of isotopes of Nitrogen (δ^{15}N), Carbon (δ^{13}C) and Hydrogen (δD). T represents Totals, Smr= summer, Wint= winter

Species _Year _Season _feather	BAR	CHI	CHU	MAN	NGA	STR	Grand Total
EG	**191**				**5**	**558**	**754**
2007	82					219	301
Smr	5					144	149
Gr	2					30	32
Pn						25	25
Mtr	1					12	13
NQ	1					1	2
Fully grown	1					76	77
Wint	77					75	152
Gr	27					41	68
Pn	5					10	15
Mtr	20					3	23
NQ	2					3	5
Fully grown	23					18	41
2008	54				5	231	290
Smr	16					176	192
Gr	3					95	98
Pn						18	18
Mtr	1					14	15
NQ						4	4
Fully grown	12					45	57
Wint	38					55	98
Gr	31					36	67
Pn						7	7
Mtr	2					5	10
Fully grown	5					7	14
2009	55					108	163
Smr	54					108	162
Gr	17					58	75
Pn	3					10	13
Mtr	1					10	11
Fully grown	33					30	63
Wint	1						1
Mtr	1						1
RBT	**1**	**42**	**1**	**5**	**306**	**45**	**37**	**437**
2009					1			1
Smr					1			1

NQ				1			1
2007	1	12	1	305	4	5	328
Smr				188	4	2	194
Mtr				63			63
NQ				35			35
Fully grown				90	4	2	96
Wint	1	12	1	117		3	134
Gr		1					1
Mtr		6	1	6		2	15
NQ		1		11			12
Fully grown	1	4		100		1	106
2008		23	5		41	27	96
Smr		13	2		19	13	47
Gr					1		1
Mtr		1	1			3	5
Fully grown		12	1		18	10	41
Wint		10	3		22	14	49
Gr						1	1
Mtr		1	2		1	1	5
Fully grown		9	1		21	12	43
2009		7				5	12
Smr		7				5	12
Mtr		1					1
Fully grown		6				5	11
YBD		**279**	**4**			**36**	**321**
2007		206				2	210
Smr		6					8
Pn		1					1
Fully grown		5					7
Wint		200				2	202
Gr		12					12
Pn		2					2
Mtr		39					39
Fully grown		147				2	149
2008		62	4			29	95
Smr		25	3			23	51
Mtr		2				1	3
Fully grown		23	3			22	48
Wint		37	1			6	44
Gr		3					3
Mtr		4					4
Fully grown		30	1			6	37
2009		11				5	16
Smr		9				5	14
Mtr						2	2
Fully grown		9				3	12
Wint		2					2
Fully grown		2					2
WFD		7	59	12	38	6	123
2007		7	59		38		105
Wint		1			2		3
Mtr					1		1
NQ					1		1

Fully grown	1				1
Smr	6	59	36		102
Gr	1	7	1		9
Mtr		32	10		42
NQ		10	4		14
Fully grown	5	10	21		37
2008		12		6	18
Smr		4			4
Fully grown		4			4
Wint		8		6	14
Gr		1			1
Mtr		4			4
Fully grown		3		6	9
CT	89			24	113
2007	1			2	3
Wint	1			2	3
Pin				1	1
NQ	1				1
Fully grown				1	1
2008	65			20	85
Smr	20			16	36
Gr	1				1
Mtr	5			6	11
NQ	1				1
Fully grown	13			10	23
Wint	45			4	49
Mtr	4				4
Fully grown	41			4	45
2009	23			2	25
Smr	22			2	24
Mtr	1			1	2
Fully grown	21			1	22
Wint	1				1
Fully grown	1				1
SAS	86				86
2007	46				46
Smr	33				33
Gr	27				27
Pn	4				4
Fully grown	2				2
Wint	13				13
Mtr	2				2
NQ	1				1
Fully grown	10				10
2008	40				40
Smr	38				38
Gr	13				13
Pn	1				1
Mtr	8				8
Fully grown	16				16
Wint	2				2
Fully grown	2				2

APG		11			11
2008		11			11
Smr		10			10
Fully grown		10			10
Wint		1			1
Mtr		1			1
HTT		5	14		19
2007			1		1
Smr			1		1
Mtr			1		1
2008		5	13		18
Smr		4	4		8
Mtr		1			1
Fully grown		3	4		7
Wint		1	9		10
Mtr			1		1
Fully grown		1	8		9
SWG	9			29	38
2007	9				9
Wint	9				9
Gr	7				7
Pn	1				1
Mtr	1				1
2008				1	1
Wint				1	1
Fully grown				1	1
2009				28	28
Smr				28	28
Gr				5	5
Pn				1	1
Mtr				5	5
Fully grown				17	17
CS		31		6	38
2007		1			2
Smr					1
Fully grown					1
Wint		1			1
NQ		1			1
2008		13		5	18
Smr		4		3	7
Mtr		2			2
Fully grown		2		3	5
Wint		9		2	11
Mtr		1			1
Fully grown		8		2	10
2009		17		1	18
Smr		16		1	17
Fully grown		16		1	17
Wint		1			1
Fully grown		1			1
Grand Total	1	725	69	37	344	70	690	1940

Appendix 4: Descriptive statistics for chapter 1

Species EG= Egyptian Goose, RBT= Red-billed Teal, YBD= Yellow-billed Duck, WFD= White-faced Duck, CT= Cape Teal, SAS= South African Shelduck, APG= African Pygmy Goose. Sites BAR= Barberspan, STR= Strandfontein, MAN= Lakes Chivero and Manyame, NGA= Lake Ngami, CHU= Lake Chuali.
Mean and SD= Standard deviation, Var= variance of isotopes of Nitrogen (δ^{15}N), Carbon (δ^{13}C) and Hydrogen (δD). T represents Totals, Smr= Summer, Wint= Winter

(δ^{15}N)

Species _Year _Season	N			δ^{15}N			SD δ^{15}N			Var δ^{15}N			Total N	T Mean δ^{15}N	T SD δ^{15}N	T Var δ^{15}N
	STR	BAR	MAN	STR	BAR	MAN	STR	BAR	MAN	STR	BAR	MAN				
EG	**56**	**44**	**2**	**15.26**	**9.66**	**12.68**	**2.70**	**1.38**	**0.38**	**7.28**	**1.90**	**0.15**	**102**	**12.79**	**3.53**	**12.43**
2007	26	20		15.90	9.44		2.16	1.70		4.65	2.88		46	13.09	3.78	14.29
S	15	3		16.25	11.91		2.56	2.83		6.57	7.99		18	15.53	3.02	9.12
W	11	17		15.43	9.00		1.41	1.04		2.00	1.07		28	11.53	3.40	11.59
2008	16	11	2	13.02	10.39	12.68	1.90	1.17	0.38	3.61	1.37	0.15	29	12.00	2.02	4.07
S	8	3	2	12.85	9.40	12.68	2.44	1.30	0.38	5.98	1.69	0.15	13	12.03	2.45	6.03
W	8	8		13.19	10.76		1.30	0.95		1.70	0.89		16	11.98	1.67	2.78
2009	14	13		16.63	9.38		2.94	0.69		8.67	0.47		27	13.14	4.26	18.17
S	14	12		16.63	9.40		2.94	0.71		8.67	0.51		26	13.29	4.27	18.23
W		1			9.14			-			-		1	9.14	-	-
RBT	**4**	**11**	**48**	**12.21**	**11.25**	**9.41**	**1.06**	**2.79**	**2.29**	**1.13**	**7.80**	**5.24**	**63**	**9.91**	**2.48**	**6.14**
2007	2	7	21	11.51	10.02	8.61	0.19	1.90	1.78	0.03	3.61	3.18	30	9.14	1.93	3.72
S			21			8.61			1.78			3.18	21	8.61	1.78	3.18
W	2	7		11.51	10.02		0.19	1.90		0.03	3.61		9	10.35	1.77	3.14
2008	2	3	27	12.91	14.53	10.03	1.18	2.45	2.47	1.40	5.99	6.11	32	10.63	2.77	7.68
S	2	3	15	12.91	14.53	9.19	1.18	2.45	2.36	1.40	5.99	5.57	20	10.36	3.05	9.31

W			12			11.07			2.28			5.22	12	11.07	2.28	5.22
2009		1			9.99			-			-		1	9.99	-	-
S		1			9.99			-			-		1	9.99	-	-
YBD	**3**	**14**		**15.68**	**10.60**		**5.60**	**1.91**		**31.40**	**3.65**		**17**	**11.50**	**3.30**	**10.86**
2007		10			10.27			2.08			4.32		10	10.27	2.08	4.32
W		10			10.27			2.08			4.32		10	10.27	2.08	4.32
2008	1	4		15.89	11.44		-	1.26		-	1.58		5	12.33	2.27	5.15
S	1	1		15.89	10.46		-	-		-	-		2	13.17	3.84	14.74
W		3			11.76			1.31			1.73		3	11.76	1.31	1.73
2009	2			15.57			7.92			62.73			2	15.57	7.92	62.73
S	2			15.57			7.92			62.73			2	15.57	7.92	62.73
WFD			**41**			**12.10**			**4.37**			**19.08**	**41**	**12.10**	**4.37**	**19.08**
2007			15			14.93			4.87			23.68	15	14.93	4.87	23.68
S			4			12.37			0.73			0.53	4	12.37	0.73	0.53
W			11			15.86			5.43			29.43	11	15.86	5.43	29.43
2008			19			10.60			3.40			11.55	19	10.60	3.40	11.55
S			9			12.65			3.36			11.28	9	12.65	3.36	11.28
W			10			8.77			2.27			5.17	10	8.77	2.27	5.17
2009			7			10.11			2.35			5.51	7	10.11	2.35	5.51
S			7			10.11			2.35			5.51	7	10.11	2.35	5.51
CT	**7**	**8**		**20.14**	**12.99**		**2.75**	**4.77**		**7.54**	**22.74**		**15**	**16.33**	**5.31**	**28.23**
2007	1			24.84			-			-			1	24.84	-	-
W	1			24.84			-			-			1	24.84	-	-
2008	5	8		19.86	12.99		1.70	4.77		2.91	22.74		13	15.63	5.13	26.35
S	5	5		19.86	13.75		1.70	5.82		2.91	33.91		10	16.81	5.17	26.73
W		3			11.71			2.80			7.87		3	11.71	2.80	7.87
2009	1			16.81			-			-			1	16.81	-	-
W	1			16.81			-			-			1	16.81	-	-
SAS		**21**			**10.04**			**1.88**			**3.52**		**21**	**10.04**	**1.88**	**3.52**
2007		11			10.21			2.40			5.76		11	10.21	2.40	5.76

S		9			9.75			0.83			0.70		9	9.75	0.83	0.70
W		2			12.30			6.43			41.30		2	12.30	6.43	41.30
2008		10			9.84			1.16			1.34		10	9.84	1.16	1.34
S		10			9.84			1.16			1.34		10	9.84	1.16	1.34
Grand Total	70	98	91	15.59	10.33	10.69	3.20	2.33	3.62	10.27	5.42	13.09	259	11.88	3.81	14.50

(δ^{13}C)

Species _Year _Season	N			Mean δ^{13}C			SD δ^{13}C			Var δ^{13}C			T N	T Mean δ^{13}C	T SD δ^{13}C	T Var δ^{13}C
	STR	BAR	MAN	STR	BAR	MAN	STR	BAR	MAN	STR	BAR	MAN				
EG	**56**	**44**	**2**	**-21.44**	**-12.54**	**-16.41**	**2.03**	**2.38**	**0.44**	**4.12**	**5.67**	**0.19**	**102**	**-17.51**	**4.90**	**24.00**
2007	26	20		-21.33	-11.85		1.95	3.01		3.80	9.05		46	-17.21	5.34	28.51
S	15	3		-21.37	-13.34		2.33	1.94		5.43	3.76		18	-20.03	3.80	14.41
W	11	17		-21.28	-11.59		1.37	3.13		1.88	9.80		28	-15.40	5.45	29.72
2008	16	11	2	-21.84	-13.45	-16.41	2.29	1.80	0.44	5.23	3.26	0.19	29	-18.28	4.54	20.63
S	8	3	2	-22.39	-12.44	-16.41	2.56	1.30	0.44	6.53	1.68	0.19	13	-19.17	4.86	23.61
W	8	8		-21.28	-13.82		1.99	1.89		3.97	3.58		16	-17.55	4.28	18.36
2009	14	13		-21.20	-12.85		1.96	1.28		3.84	1.63		27	-17.18	4.56	20.75
S	14	12		-21.20	-13.00		1.96	1.21		3.84	1.45		26	-17.41	4.47	20.01
W		1			-11.02			-			-		1	-11.02	-	-
RBT	**4**	**11**	**48**	**-18.28**	**-14.12**	**-19.53**	**6.89**	**5.57**	**3.58**	**47.43**	**30.98**	**12.82**	**63**	**-18.50**	**4.61**	**21.25**
2007	2	7	21	-12.74	-10.47	-19.80	4.40	2.30	3.69	19.39	5.29	13.61	30	-17.15	5.32	28.32
S			21			-19.80			3.69			13.61	21	-19.80	3.69	13.61
W	2	7		-12.74	-10.47		4.40	2.30		19.39	5.29		9	-10.98	2.72	7.39
2008	2	3	27	-23.82	-20.55	-19.32	0.17	3.38	3.55	0.03	11.42	12.60	32	-19.72	3.55	12.60
S	2	3	15	-23.82	-20.55	-19.68	0.17	3.38	3.41	0.03	11.42	11.60	20	-20.23	3.37	11.36
W			12			-18.87			3.82			14.63	12	-18.87	3.82	14.63

2009		1			-20.30			-			-		1	-20.30	-	-
S		1			-20.30			-			-		1	-20.30	-	-
YBD	**3**	**14**		**-21.70**	**-13.92**		**4.44**	**4.30**		**19.69**	**18.49**		**17**	**-15.29**	**5.18**	**26.84**
2007		10			-13.55			4.96			24.58		10	-13.55	4.96	24.58
W		10			-13.55			4.96			24.58		10	-13.55	4.96	24.58
2008	1	4		-25.58	-14.82		-	2.20		-	4.84		5	-16.97	5.17	26.75
S	1	1		-25.58	-14.96		-	-		-	-		2	-20.27	7.51	56.39
W		3			-14.78			2.69			7.25		3	-14.78	2.69	7.25
2009	2			-19.77			4.11			16.88			2	-19.77	4.11	16.88
S	2			-19.77			4.11			16.88			2	-19.77	4.11	16.88
WFD			**41**			**-18.47**			**4.42**			**19.55**	**41**	**-18.47**	**4.42**	**19.55**
2007			15			-19.17			5.21			27.18	15	-19.17	5.21	27.18
S			4			-22.20			1.43			2.03	4	-22.20	1.43	2.03
W			11			-18.06			5.69			32.41	11	-18.06	5.69	32.41
2008			19			-17.98			4.45			19.82	19	-17.98	4.45	19.82
S			9			-21.04			3.50			12.24	9	-21.04	3.50	12.24
W			10			-15.23			3.32			11.03	10	-15.23	3.32	11.03
2009			7			-18.29			2.33			5.44	7	-18.29	2.33	5.44
S			7			-18.29			2.33			5.44	7	-18.29	2.33	5.44
CT	**7**	**8**		**-18.27**	**-17.81**		**1.85**	**3.84**		**3.41**	**14.77**		**15**	**-18.03**	**2.98**	**8.90**
2007	1			-15.61			-			-			1	-15.61	-	-
W	1			-15.61			-			-			1	-15.61	-	-
2008	5	8		-18.22	-17.81		1.09	3.84		1.19	14.77		13	-17.97	3.01	9.06
S	5	5		-18.22	-18.92		1.09	3.83		1.19	14.66		10	-18.57	2.68	7.18
W		3			-15.96			3.76			14.16		3	-15.96	3.76	14.16
2009	1			-21.20			-			-			1	-21.20	-	-
S	1			-21.20			-			-			1	-21.20	-	-
SAS		**21**			**-12.14**			**1.67**			**2.80**		**21**	**-12.14**	**1.67**	**2.80**
2007		11			-13.04			1.64			2.70		11	-13.04	1.64	2.70
S		9			-12.48			1.15			1.33		9	-12.48	1.15	1.33

W		2			-15.57			0.87			0.76		2	-15.57	0.87	0.76
2008		10			-11.15			1.07			1.15		10	-11.15	1.07	1.15
S		10			-11.15			1.07			1.15		10	-11.15	1.07	1.15
Grand Total	70	98	91	-20.96	-13.26	-18.98	2.75	3.49	3.98	7.58	12.18	15.81	259	-17.35	4.79	22.94

(*δ*D)

	STR				BAR				MAN				T N	T Mean *δ*D	TSD *δ*D	T Var *δ*D
Species _Year _Season	N	Mean *δ*D	SD *δ*D	Var *δ*D	N	Mean *δ*D	SD *δ*D	Var *δ*D	N	Mean *δ*D	SD *δ*D	Var *δ*D				
EG	**10**	**-70.21**	**6.27**	**39.35**	**10**	**-63.92**	**17.27**	**298.21**	**2**	**-93.44**	**3.21**	**10.33**	**22**	**-69.46**	**14.66**	**214.79**
2007	10	-70.21	6.27	39.35	10	-63.92	17.27	298.21					20	-67.06	13.05	170.31
S	10	-70.21	6.27	39.35	1	-89.40	-	-					11	-71.95	8.30	68.91
W					9	-61.09	15.66	245.28					9	-61.09	15.66	245.28
2008									2	-93.44	3.21	10.33	2	-93.44	3.21	10.33
S									2	-93.44	3.21	10.33	2	-93.44	3.21	10.33
RBT	**3**	**-48.68**	**4.72**	**22.30**	**9**	**-53.31**	**12.92**	**166.84**	**22**	**-76.77**	**12.47**	**155.53**	**34**	**-68.08**	**16.88**	**284.78**
2007	2	-50.17	5.60	31.39	7	-49.91	12.29	151.10	17	-77.92	13.80	190.42	26	-68.24	18.53	343.25
S									17	-77.92	13.80	190.42	17	-77.92	13.80	190.42
W	2	-50.17	5.60	31.39	7	-49.91	12.29	151.10					9	-49.97	10.83	117.26
2008	1	-45.71	-	-	2	-65.22	7.98	63.73	5	-72.87	5.50	30.20	8	-67.56	10.78	116.22
S	1	-45.71	-	-	2	-65.22	7.98	63.73	5	-72.87	5.50	30.20	8	-67.56	10.78	116.22
Grand T	13	-65.24	11.06	122.35	19	-58.90	15.90	252.86	24	-78.16	12.83	164.60	56	-68.62	15.92	253.34

Appendix 5: Descriptive statistics for chapter 2

Average values of $\delta^{13}C$ and $\delta^{15}N$ isotopes in flight (F) [either growing (Gr), or fully grown (Fully grown)] and body feathers (B) of southern African ducks from five study sites, Strandfontein (STR), Barberspan (BAR), Manyame catchment (MAN), Lake Ngami (NGA) and Lake Chuali (CHU). Comparisons were made between flight (Growing;Gr or Fully grown; FG) and body feathers only; and not between fully grown and growing flight feathers. * = P < 0.05 and ** = P < 0.01 between flight and back feather.

		Strandfontein					Barberspan				
		N	F$\delta^{15}N$	B$\delta^{15}N$	F$\delta^{13}C$	B$\delta^{13}C$	N	F$\delta^{15}N$	B$\delta^{15}N$	F$\delta^{13}C$	B$\delta^{13}C$
EG		28	14.67	9.59	-21.75	-21.79	40	10.43	9.95	-13.60	-14.35
	Gr	15	15.50*	10.05	-21.50	-21.58	24	10.07	9.43	-13.44	-14.66
	FG	13	13.71*	9.05	-22.03	-22.03	16	10.97	10.73	-13.83	-13.88
RBT		4	12.71	14.94	-20.51	-16.73	6	11.11	9.70	-16.99	-16.17
	Gr						1	12.03	9.09	-17.27	-13.61
	FG	4	12.71	14.94	-20.51	-16.73	5	10.93	9.82	-16.94	-16.69
YBD		5	16.39	14.48	-20.52	-21.11	13	10.69	10.64	-14.98	-15.71
	Gr	1	9.97	10.15	-22.67	-22.87	1	12.78	9.42	-14.37	-12.57
	FG	4	18.00	15.56	-19.99	-20.67	12	10.51	10.74	-15.03	-15.97
WFD											
	Gr										
	FG										
CT		6	20.16	17.10	-18.11	-19.83	24	13.95	14.06	-17.18	-17.54
	Gr	6	20.16	17.10	-18.11	-19.83	4	14.87	13.53	-17.82	-20.59
	FG						20	13.77	14.16	-17.06	-16.93
SAS							20	10.27	11.08	-12.48	-12.43
	Gr						16	9.84**	10.95	-11.49	-12.01
	FG						4	11.99	11.58	-16.20	-14.10
SWG		24	10.74	9.37	-22.67	-20.49					
	Gr	10	11.80	9.35	-23.04	-20.79					
	FG	14	9.98	9.39	-22.41*	-20.27					

CS						13	15.81	13.63	-23.66	-19.20	
	FG					13	15.81	13.63	-23.66*	-19.20	
Grand Total		67	13.76	10.87	-21.59	-20.80	116	11.80	11.47	-15.63	-15.47

Appendix 5 continued.

		Manyame					Ngami					Chuali					Total N
		N	Fδ^{15}N	Bδ^{15}N	Fδ^{13}C	Bδ^{13}C	N	Fδ^{15}N	Bδ^{15}N	Fδ^{13}C	Bδ^{13}C	N	FδN	Bδ^{15}N	Fδ^{13}C	Bδ^{13}C	
EG																	68
	Gr																39
	FG																29
RBT		2	8.81	8.95	-18.32	-19.81	14	9.81	9.25	-16.25	-15.34	1	9.62	7.74	-14.82	-18.45	27
	Gr	2	8.81	8.95	-18.32	-19.81											3
	FG						14	9.81	9.25	-16.25	-15.34	1	9.62	7.74	-14.82	-18.45	24
YBD												2	7.49	8.15	-21.19	-21.05	20
	Gr																2
	FG											2	7.49	8.15	-21.19	-21.05	18
WFD		6	10.81	9.54	-18.39	-17.73						4	10.21	10.13	-17.38	-16.84	10
	Gr	6	10.81	9.54	-18.39	-17.73											6
	FG											4	10.21	10.13	-17.38	-16.84	4
CT																	30
	Gr																10
	FG																20
SAS																	20
	Gr																16
	FG																4
APG												7	9.49	8.58	-20.22	-16.97	7
	FG											7	9.49	8.58	-20.22	-16.97	7
HTT		3	9.77	10.01	-24.10	-21.63						1	7.44	6.65	-19.76	-18.71	4

	Gr	3	9.77	10.01	-24.10	-21.63										3
	FG										1	7.44	6.65	-19.76	-18.71	1
WBD											1	10.00	7.41	-20.94	-19.46	1
	FG										1	10.00	7.41	-20.94	-19.46	1
SWG																24
	Gr															10
	FG															14
CS																13
	FG															13
Grand Total		11	10.16	9.56	-19.94	-19.18	14	9.81	9.25	-16.25	-15.34	16	9.33	8.67	-19.31	-17.81	224

F- represents flight feather isotope signatures e.g Fδ15N, B - represents body-feather isotope signatures e.g Bδ15N. * = $P < 0.05$ and ** = $P < 0.01$ between body and flight feather (GR = Growing, FG = Fully grown) isotope signatures. Body feathers were taken from the bird's back. Egyptian Goose = EG, Red-billed Teal = RBT, Spur Winged Goose = SWG, South African Shelduck = SAS, African Pygmy Goose = APG, Hottentot Teal = HTT, Yellow-billed Duck = YBD, White-faced Duck = WFD, Cape Shoveler = CS and Cape Teal = CT. Study sites: CHU = Lake Chuali, MAN= Manyame catchment, NGA= Lake Ngami, BAR= Barberspan, STR= Strandfontein.

Appendix 6: Descriptive statistics for chapter 3

Isotope signatures in growing flight feathers of moulting Duck Species: EG = Egyptian Goose, RBT = Red-billed Teal, YBD = Yellow-billed Duck, WFD = White-faced Duck, CT = Cape Teal, Cape CS = Shoveler, HTT = Hottentot Teal, SAS = South African Shelduck, APG = African Pygmy Goose. Per study site: BAR = Barberspan, STR = Strandfontein, MAN = Lakes Chivero and Manyame, NGA = Lake Ngami, CHU = Lake Chuali. Across the years 2007, 2008, 2009. SD = Standard deviation, Var = variance, Mn = mean, T represents Totals, SMR = summer, WNTR = winter,

Species	Year	Season	Site	N	Av δ^{15}N	SD δ^{15}N	Var δ^{15}N	Av δ^{13}C	SD δ^{13}C	Var δ^{13}C	N δD	Mn δD	SD δD	Var δD
EG	2007	SMR	STR	15	16.25	2.56	6.57	-21.37	2.33	5.43	10	-70.21	6.27	39.35
			STR T	15	16.25	2.56	6.57	-21.37	2.33	5.43	10	-70.21	6.27	39.35
			BAR	3	11.91	2.83	7.99	-13.34	1.94	3.76	1	-89.40		
			BAR T	3	11.91	2.83	7.99	-13.34	1.94	3.76	1	-89.40		
		SMR T		18	15.53	3.02	9.12	-20.03	3.80	14.41	11	-71.95	8.30	68.91
		WNTR	STR	11	15.43	1.41	2.00	-21.28	1.37	1.88				
			STR T	11	15.43	1.41	2.00	-21.28	1.37	1.88				
			BAR	17	9.00	1.04	1.07	-11.59	3.13	9.80	9	-61.09	15.66	245.28
			BAR T	17	9.00	1.04	1.07	-11.59	3.13	9.80	9	-61.09	15.66	245.28
		WNTR T		28	11.53	3.40	11.59	-15.40	5.45	29.72	9	-61.09	15.66	245.28
	2007 T			46	13.09	3.78	14.29	-17.21	5.34	28.51	20	-67.06	13.05	170.31
	2008	SMR	STR	8	12.85	2.44	5.98	-22.39	2.56	6.53				
			STR T	8	12.85	2.44	5.98	-22.39	2.56	6.53				
			BAR	3	9.40	1.30	1.69	-12.44	1.30	1.68				
			BAR T	3	9.40	1.30	1.69	-12.44	1.30	1.68				
			MAN	2	12.68	0.38	0.15	-16.41	0.44	0.19	2	-93.44	3.21	10.33
			MAN T	2	12.68	0.38	0.15	-16.41	0.44	0.19	2	-93.44	3.21	10.33
		SMR T		13	12.03	2.45	6.03	-19.17	4.86	23.61	2	-93.44	3.21	10.33
		WNTR	STR	8	13.19	1.30	1.70	-21.28	1.99	3.97				

			STR T	8	13.19	1.30	1.70	-21.28	1.99	3.97				
			BAR	12	10.53	0.94	0.88	-14.24	2.32	5.36				
			BAR T	12	10.53	0.94	0.88	-14.24	2.32	5.36				
			NGA	3	15.71	2.60	6.79	-19.05	3.68	13.51				
			NGA T	3	15.71	2.60	6.79	-19.05	3.68	13.51				
		WNTR T		23	12.13	2.27	5.14	-17.32	4.06	16.46				
	2008 T			36	12.09	2.30	5.30	-17.99	4.39	19.26	2	-93.44	3.21	10.33
	2009	SMR	STR	16	15.52	4.12	16.95	-21.27	1.84	3.37				
			STR T	16	15.52	4.12	16.95	-21.27	1.84	3.37				
			BAR	19	10.30	2.63	6.93	-13.06	2.13	4.55				
			BAR T	19	10.30	2.63	6.93	-13.06	2.13	4.55				
		SMR T		35	12.69	4.25	18.10	-16.81	4.59	21.11				
		WNTR	BAR	1	9.14			-11.02						
			BAR T	1	9.14			-11.02						
		WNTR T		1	9.14			-11.02						
	2009 T			36	12.59	4.23	17.93	-16.65	4.63	21.44				
EG T				118	12.63	3.55	12.62	-17.28	4.84	23.42	22	-69.46	14.66	214.79
RBT	2007	SMR	MAN	22	8.55	1.77	3.13	-20.02	3.75	14.09	17	-77.92	13.80	190.42
			MAN T	22	8.55	1.77	3.13	-20.02	3.75	14.09	17	-77.92	13.80	190.42
		SMR T		22	8.55	1.77	3.13	-20.02	3.75	14.09	17	-77.92	13.80	190.42
		WNTR	STR	2	11.51	0.19	0.03	-12.74	4.40	19.39	2	-50.17	5.60	31.39
			STR T	2	11.51	0.19	0.03	-12.74	4.40	19.39	2	-50.17	5.60	31.39
			BAR	7	10.02	1.90	3.61	-10.47	2.30	5.29	7	-49.91	12.29	151.10
			BAR T	7	10.02	1.90	3.61	-10.47	2.30	5.29	7	-49.91	12.29	151.10
			MAN	1	8.58			-19.73						
			MAN T	1	8.58			-19.73						
		WNTR T		10	10.18	1.76	3.11	-11.85	3.77	14.23	9	-49.97	10.83	117.26
	2007 T			32	9.06	1.90	3.61	-17.47	5.34	28.49	26	-68.24	18.53	343.25
	2008	SMR	STR	2	12.91	1.18	1.40	-23.82	0.17	0.03	1	-45.71		
			STR T	2	12.91	1.18	1.40	-23.82	0.17	0.03	1	-45.71		

			BAR	3	14.53	2.45	5.99	-20.55	3.38	11.42	2	-65.22	7.98	63.73
			BAR T	3	14.53	2.45	5.99	-20.55	3.38	11.42	2	-65.22	7.98	63.73
			MAN	15	9.19	2.36	5.57	-19.68	3.41	11.60	5	-72.87	5.50	30.20
			MAN T	15	9.19	2.36	5.57	-19.68	3.41	11.60	5	-72.87	5.50	30.20
			CHU	1	7.44			-18.08						
			CHU T	1	7.44			-18.08						
		SMR T		21	10.23	3.04	9.25	-20.12	3.32	11.01	8	-67.56	10.78	116.22
		WNTR	MAN	12	11.07	2.28	5.22	-18.87	3.82	14.63				
			MAN T	12	11.07	2.28	5.22	-18.87	3.82	14.63				
			NGA	1	11.35			-13.62						
			NGA T	1	11.35			-13.62						
			CHU	2	6.25	1.72	2.97	-16.17	2.48	6.15				
			CHU T	2	6.25	1.72	2.97	-16.17	2.48	6.15				
		WNTR T		15	10.45	2.69	7.22	-18.16	3.79	14.40				
	2008 T			36	10.32	2.86	8.19	-19.31	3.61	13.02	8	-67.56	10.78	116.22
	2009	SMR	BAR	1	9.99			-20.30						
			BAR T	1	9.99			-20.30						
		SMR T		1	9.99			-20.30						
	2009 T			1	9.99			-20.30						
RBT T				69	9.73	2.50	6.26	-18.47	4.54	20.58	34	-68.08	16.88	284.78
YBD	2007	WNTR	BAR	24	9.98	1.93	3.71	-13.06	4.33	18.78				
			BAR T	24	9.98	1.93	3.71	-13.06	4.33	18.78				
		WNTR T		24	9.98	1.93	3.71	-13.06	4.33	18.78				
	2007 T			24	9.98	1.93	3.71	-13.06	4.33	18.78				
	2008	SMR	STR	1	15.89			-25.58						
			STR T	1	15.89			-25.58						
			BAR	1	10.46			-14.96						
			BAR T	1	10.46			-14.96						
		SMR T		2	13.17	3.84	14.74	-20.27	7.51	56.39				
		WNTR	BAR	3	11.76	1.31	1.73	-14.78	2.69	7.25				

			BAR T	3	11.76	1.31	1.73	-14.78	2.69	7.25
		WNTR T		3	11.76	1.31	1.73	-14.78	2.69	7.25
	2008 T			5	12.33	2.27	5.15	-16.97	5.17	26.75
	2009	SMR	STR	2	14.88	6.94	48.13	-20.58	2.95	8.73
			STR T	2	14.88	6.94	48.13	-20.58	2.95	8.73
		SMR T		2	14.88	6.94	48.13	-20.58	2.95	8.73
	2009 T			2	14.88	6.94	48.13	-20.58	2.95	8.73
YBD T				31	10.68	2.67	7.15	-14.17	4.83	23.30
WFD	2007	SMR	MAN	4	12.37	0.73	0.53	-22.20	1.43	2.03
			MAN T	4	12.37	0.73	0.53	-22.20	1.43	2.03
		SMR T		4	12.37	0.73	0.53	-22.20	1.43	2.03
		WNTR	MAN	39	13.17	4.22	17.78	-17.70	3.90	15.19
			MAN T	39	13.17	4.22	17.78	-17.70	3.90	15.19
		WNTR T		39	13.17	4.22	17.78	-17.70	3.90	15.19
	2007 T			43	13.09	4.02	16.18	-18.12	3.96	15.64
	2008	SMR	MAN	9	12.65	3.36	11.28	-21.04	3.50	12.24
			MAN T	9	12.65	3.36	11.28	-21.04	3.50	12.24
		SMR T		9	12.65	3.36	11.28	-21.04	3.50	12.24
		WNTR	MAN	11	9.04	2.34	5.48	-15.29	3.16	9.96
			MAN T	11	9.04	2.34	5.48	-15.29	3.16	9.96
			CHU	5	10.64	3.39	11.52	-18.60	3.93	15.42
			CHU T	5	10.64	3.39	11.52	-18.60	3.93	15.42
		WNTR T		16	9.54	2.70	7.31	-16.33	3.64	13.27
	2008 T			25	10.66	3.26	10.64	-18.02	4.21	17.70
	2009	SMR	MAN	7	10.11	2.35	5.51	-18.29	2.33	5.44
			MAN T	7	10.11	2.35	5.51	-18.29	2.33	5.44
		SMR T		7	10.11	2.35	5.51	-18.29	2.33	5.44
	2009 T			7	10.11	2.35	5.51	-18.29	2.33	5.44
WFD T				75	12.00	3.84	14.72	-18.10	3.88	15.07
CT	2007	WNTR	STR	1	24.84			-15.61		

			STR T	1	24.84			-15.61		
		WNTR T		1	24.84			-15.61		
	2007 T			1	24.84			-15.61		
	2008	SMR	STR	5	19.86	1.70	2.91	-18.22	1.09	1.19
			STR T	5	19.86	1.70	2.91	-18.22	1.09	1.19
			BAR	6	13.60	5.22	27.28	-18.26	3.79	14.34
			BAR T	6	13.60	5.22	27.28	-18.26	3.79	14.34
		SMR T		11	16.45	5.05	25.51	-18.24	2.77	7.65
		WNTR	BAR	4	13.64	4.49	20.13	-16.48	3.25	10.55
			BAR T	4	13.64	4.49	20.13	-16.48	3.25	10.55
		WNTR T		4	13.64	4.49	20.13	-16.48	3.25	10.55
	2008 T			15	15.70	4.92	24.18	-17.77	2.89	8.37
	2009	SMR	STR	1	16.81			-21.20		
			STR T	1	16.81			-21.20		
			BAR	1	15.51			-22.17		
			BAR T	1	15.51			-22.17		
		SMR T		2	16.16	0.92	0.84	-21.69	0.69	0.47
	2009 T			2	16.16	0.92	0.84	-21.69	0.69	0.47
CT T				18	16.26	4.96	24.58	-18.09	2.98	8.89
SAS	2007	SMR	BAR	23	9.78	0.77	0.60	-12.19	0.86	0.74
			BAR T	23	9.78	0.77	0.60	-12.19	0.86	0.74
		SMR T		23	9.78	0.77	0.60	-12.19	0.86	0.74
		WNTR	BAR	2	12.30	6.43	41.30	-15.57	0.87	0.76
			BAR T	2	12.30	6.43	41.30	-15.57	0.87	0.76
		WNTR T		2	12.30	6.43	41.30	-15.57	0.87	0.76
	2007 T			25	9.98	1.66	2.76	-12.46	1.26	1.59
	2008	SMR	BAR	19	10.09	1.42	2.03	-11.26	1.81	3.28
			BAR T	19	10.09	1.42	2.03	-11.26	1.81	3.28
		SMR T		19	10.09	1.42	2.03	-11.26	1.81	3.28
	2008 T			19	10.09	1.42	2.03	-11.26	1.81	3.28

SAS T				44	10.03	1.55	2.39	-11.95	1.61	2.59				
APG	2008	WNTR	CHU	1	12.48			-13.51						
			CHU T	1	12.48			-13.51						
		WNTR T		1	12.48			-13.51						
	2008 T			1	12.48			-13.51						
APG T				1	12.48			-13.51						
HTT	2008	SMR	MAN	3	9.77	5.50	30.20	-24.10	2.78	7.73				
			MAN T	3	9.77	5.50	30.20	-24.10	2.78	7.73				
			CHU	1	9.61			-23.11						
			CHU T	1	9.61			-23.11						
		SMR T		4	9.73	4.49	20.14	-23.85	2.32	5.40				
	2008 T			4	9.73	4.49	20.14	-23.85	2.32	5.40				
HTT T				4	9.73	4.49	20.14	-23.85	2.32	5.40				
SWG	2007	SMR	STR	1	10.39			-22.79						
			STR T	1	10.39			-22.79						
		SMR T		1	10.39			-22.79						
	2007 T			1	10.39			-22.79						
	2009	SMR	STR	10	11.80	1.90	3.61	-23.04	3.52	12.39				
			STR T	10	11.80	1.90	3.61	-23.04	3.52	12.39				
		SMR T		10	11.80	1.90	3.61	-23.04	3.52	12.39				
	2009 T			10	11.80	1.90	3.61	-23.04	3.52	12.39				
SWG T				11	11.68	1.85	3.43	-23.01	3.34	11.15				
Grand T				371	11.61	3.58	12.81	-17.06	4.81	23.17	56	-68.62	15.92	253.34

Appendix 7: Paired t-test comparisons of back and flight feather signatures from each individual bird.

All back feather (B) comparisons against growing flight feathers (Gr) or fully grown flight feathers (FG) were limited to Summer 2008 captures from Study sites, Barberspan = BAR, Strandfontein = STR, Lakes Chivero and Manyame= MAN, Lake Chuali = CHU and Species, Egyptian Goose= EG, Red-billed Teal= RBT, Yellow-billed Duck = YBD, Cape Teal = CT, Cape Shoveler = CS, South African Shelduck = SAS, Spur-winged Goose= SWG, Hottentot Teal = HTT, African Pygmy-Goose = APG, White-faced Duck = WFD.
Underlined figures show significant results at 5% significant level

		STR					BAR					MAN					NGA					CHU				
EG		N	t	df	err	P	N	t	df	err	P	N	t	df	err	P	N	t	df	err	P	N	t	df	err	P
Gr vs. B	N	15	4.07	14	1.34	<u>0.001</u>	24	0.97	23	0.67	0.344															
	C	15	0.09	14	0.90	0.928	24	1.65	23	0.74	0.113															
	D																									
FG vs. B	N	13	4.23	12	1.10	<u>0.001</u>	16	0.50	15	0.47	0.622															
	C	13	0.00	12	0.62	0.999	16	0.07	15	0.72	0.943															
	D																									
RBT																										
FG vs. B	N																14	0.85	13	0.66	0.412					
	C																14	-1.14	13	0.80	0.277					
	D																									
YBD																										
Gr vs. B	N																									
	C																									
FG vs. B	N						12	-0.30	11	0.76	0.769															
	C						12	0.60	11	1.56	0.561															
CT																										
Gr vs. B	N	6	1.01	5	3.02	0.357	4	0.90	3	1.50	0.434															
	C	6	1.47	5	1.17	0.203	4	1.32	3	2.09	0.278															
FG vs. B	N						20	-0.44	19	0.92	0.669															
	C						20	-0.20	19	0.62	0.841															

SAS											
Gr vs. B	N						16	-2.40	15	0.46	0.03
	C						15	0.97	14	0.53	0.349
SWG											
Gr vs. B	N	10	2.17	9	1.13	0.058					
	C	10	-1.26	9	1.79	0.240					
FG vs. B	N	14	0.77	13	0.77	0.457	14	0.77	13	0.77	0.457
	C	14	-2.23	13	0.96	0.044	14	-2.23	13	0.96	0.44
CS											
Gr vs. B	N										
	C										
FG vs. B	N						13	1.96	12	1.11	0.074
	C						13	-3.74	12	1.19	0.003

Appendix 8: Turkey-type multiple comparisons test for differences among variances.

N= sample size, Var= variance, Ln= natural logarithm, A represents the larger variance, B represents the smaller variance, test statistic q= ($LnVar_A$-$LnVar_B$)/SE, where SE=√($1/N_A$+$1/N_B$). Critical values for α= 0.05 and k and ∞ degrees of freedom ($q_{0.05,\infty,k}$) were obtained from statistical tables (Zar 2010). Study sites: Barberspan= BAR, Strandfontein= STR, Lakes Chivero and Manyame= MAN, Lake Chuali= CHU and Species, Egyptian Goose= EG, Red-billed Teal= RBT, Yellow-billed Duck= YBD, Cape Teal= CT, Cape Shoveler= CS, South African Shelduck= SAS, Spur-winged Goose= SWG, Hottentot Teal= HTT, African Pygmy-Goose= APG, White-faced Duck= WFD

STR

	N	Var δ^{15}N	Ln		$LnVar_A$-$LnVar_B$	SE	q	$q_{0.05,\infty,k}$	
RBT	4	1.13	0.12	YBD vs. RBT	3.07	0.76	4.02	3.858	YBD≠RBT
SWG	11	3.43	1.23	YBD vs. SWG	1.96	0.65	3.01	3.858	YBD=SWG
CT	7	7.54	2.02	YBD vs. CT	1.17	0.69	1.70	3.858	YBD=CT
EG	58	9.00	2.20	YBD vs. EG	1.00	0.59	1.68	3.858	YBD=EG
YBD	3	24.40	3.19	EG vs. CT	0.18	0.40	0.44	3.858	EG=CT
				EG vs. SWG	0.96	0.33	2.93	3.858	EG=SWG
				EG vs. RBT	2.08	0.52	4.01	3.858	EG≠RBT
				CT vs. SWG	0.79	0.48	1.63	3.858	CT=SWG
				CT vs. RBT	1.90	0.63	3.03	3.858	CT=RBT
				SWG vs. RBT	1.11	0.58	1.90	3.858	SWG=RBT
		Var δ^{13}C							
CT	7	3.41	1.23	RBT vs. CT	2.63	0.63	4.20	3.858	RBT≠CT
EG	58	3.99	1.38	RBT vs. EG	2.48	0.52	4.79	3.858	RBT≠EG
SWG	11	11.15	2.41	RBT vs. SWG	1.45	0.58	2.48	3.858	RBT=SWG
YBD	3	12.68	2.54	RBT vs. YBD	1.32	0.76	1.73	3.858	RBT=YBD
RBT	4	47.43	3.86	YBD vs. SWG	0.13	0.65	0.20	3.858	YBD=SWG
				YBD vs. EG	1.16	0.59	1.95	3.858	YBD=EG
				YBD vs. CT	1.31	0.69	1.90	3.858	YBD=CT
				SWG vs. EG	1.03	0.33	3.13	3.858	SWG=EG

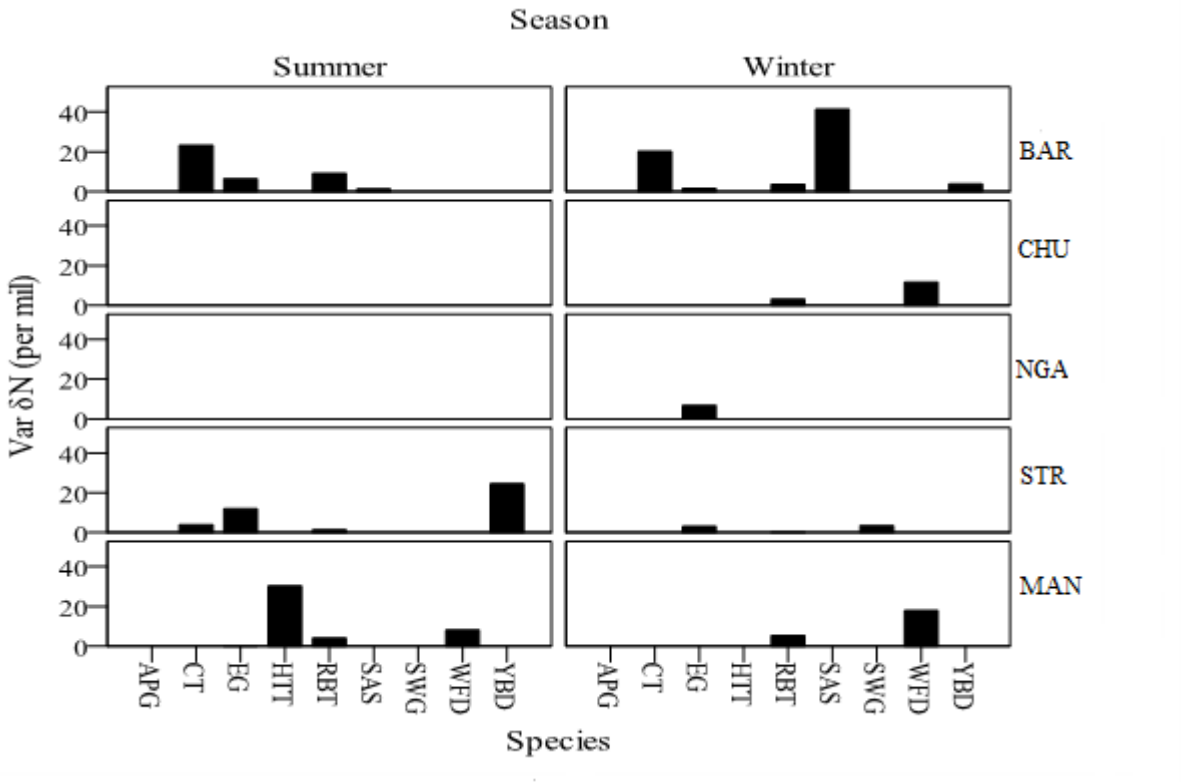
				SWG vs. CT	1.19	0.48	2.45	3.858	SWG=CT
				EG vs. CT	0.16	0.40	0.39	3.858	EG=CT
BAR		Var δ^{15}N							
SAS	44	2.39	0.87	CT vs. SAS	2.13	0.34	6.30	3.858	CT≠SAS
YBD	28	3.60	1.28	CT vs. YBD	1.71	0.36	4.82	3.858	CT≠YBD
EG	55	3.81	1.34	CT vs. EG	1.66	0.33	5.02	3.858	CT≠G
RBT	11	7.80	2.05	CT vs. RBT	0.94	0.43	2.21	3.858	CT=RBT
CT	11	20.01	3.00	RBT vs. EG	0.72	0.33	2.17	3.858	RBT=EG
				RBT vs. YBD	0.77	0.36	2.17	3.858	RBT=YBD
				RBT vs. SAS	1.18	0.34	3.51	3.858	RBT=SAS
				EG vs. YBD	0.06	0.23	0.24	3.858	EG=YBD
				EG vs. SAS	0.47	0.20	2.30	3.858	EG=SAS
				YBD vs. SAS	0.41	0.24	1.70	3.858	YBD=SAS
BAR		Var δ^{13}C							
SAS	44	2.59	0.95	RBT vs. SAS	2.48	0.34	7.36	3.858	RBT≠SAS
EG	55	6.74	1.91	RBT vs. EG	1.53	0.33	4.62	3.858	RBT≠EG
CT	11	13.04	2.57	RBT vs. CT	0.87	0.43	2.03	3.858	RBT=CT
YBD	28	16.93	2.83	RBT vs. YBD	0.60	0.36	1.70	3.858	RBT=YBD
RBT	11	30.98	3.43	YBD vs. CT	0.26	0.36	0.73	3.858	YBD=CT
				YBD vs. EG	0.92	0.23	3.97	3.858	YBD=EG
				YBD vs. SAS	1.88	0.24	7.76	3.858	YBD≠SAS
				CT vs. EG	0.66	0.33	2.00	3.858	CT=EG
				CT vs. SAS	1.61	0.34	4.79	3.858	CT≠SAS
				EG vs. SAS	0.95	0.20	4.72	3.858	EG≠SAS
MAN		Var δ^{15}N							
EG	2	0.15	-1.92	HTT vs. EG	5.33	0.91	5.84	3.633	HTT≠EG
RBT	50	5.14	1.64	HTT vs. RBT	1.77	0.59	2.98	3.633	HTT=RBT
WFD	70	14.97	2.71	HTT vs. WFD	0.70	0.59	1.19	3.633	HTT=WFD

HTT	3	30.20	3.41	WFD vs. RBT	1.07	0.19	5.78	3.633	WFD≠RBT
				WFD vs. EG	4.63	0.72	6.45	3.633	WFD≠EG
				RBT vs. EG	3.56	0.72	4.93	3.633	RBT≠EG
MAN		Var $\delta^{13}C$							
EG	2	0.19	-1.64	WFD vs. EG	4.37	0.72	6.09	3.633	WFD≠EG
HTT	3	7.73	2.04	WFD vs. HTT	0.68	0.59	1.15	3.633	WFD=HTT
RBT	50	12.85	2.55	WFD vs. RBT	0.17	0.19	0.92	3.633	WFD=RBT
WFD	70	15.24	2.72	RBT vs. HTT	0.51	0.59	0.86	3.633	RBT=HTT
				RBT vs. EG	4.20	0.72	5.82	3.633	RBT≠EG
				HTT vs. EG	3.69	0.91	4.04	3.633	HTT≠EG
CHU		Var $\delta^{15}N$							
RBT	3	1.96	0.67	WFD vs. RBT	1.77	0.73	2.43	2.772	WFD=RBT
WFD	5	11.52	2.44						
CHU		Var $\delta^{13}C$							
RBT	3	4.28	1.46	WFD vs. RBT	1.28	0.73	1.75	2.772	WFD=RBT
WFD	5	15.42	2.74						

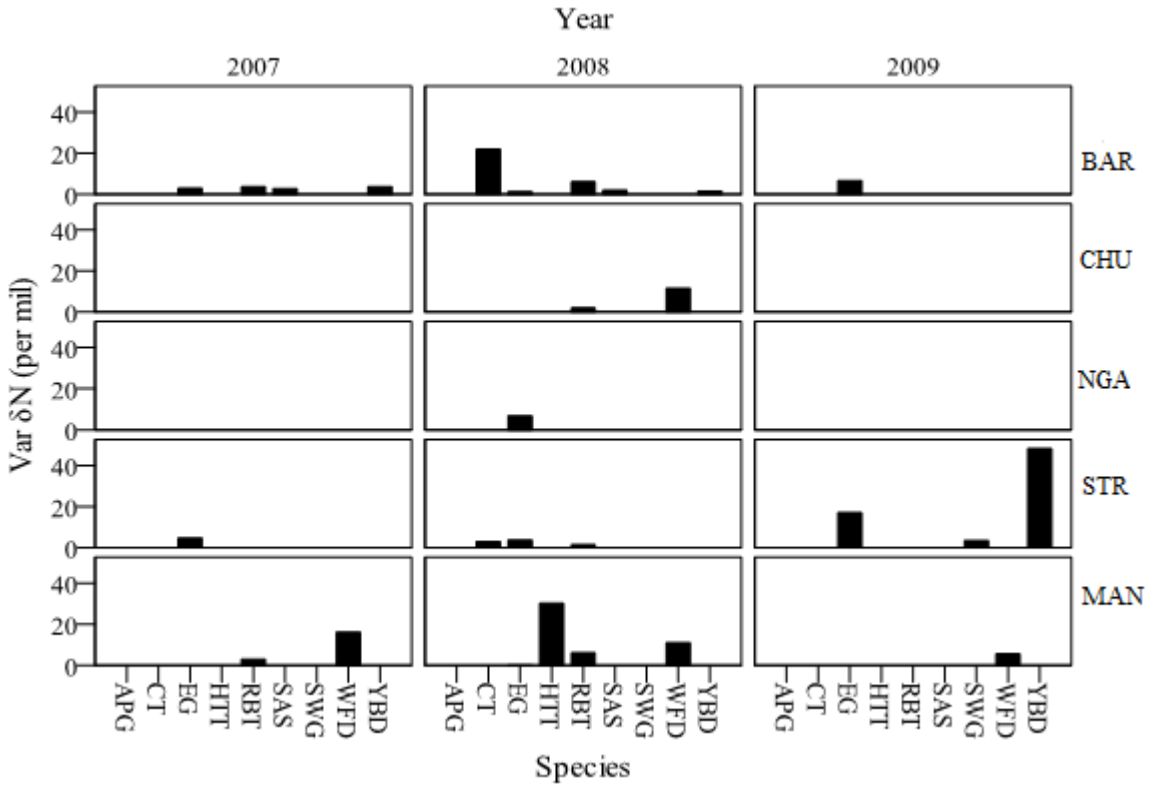
Appendix 9: Inter-individual isotopic variances per species, site, season and year.

Inter-individual variances of feather isotope proportions: of Nitrogen (Var δ^{15}N) by season (a) and by year (b), of Carbon (Var δ^{13}C) by season (c) and by year (d). Species: Egyptian Goose (EG), Red-billed Teal (RBT), Yellow-billed Duck (YBD), White-faced Duck (WFD), Cape Teal (CT), South African Shelduck (SAS), African Pygmy Goose (APG), Hottentot Teal (HTT) and Spur-winged Goose (SWG) from study sites Strandfontein (STR), Barberspan (BAR), Lake Ngami (NGA), Lakes Chivero and Manyame (MAN), and Lake Chuali (CHU). The species are using niches that are highly variable with location, season, and year.

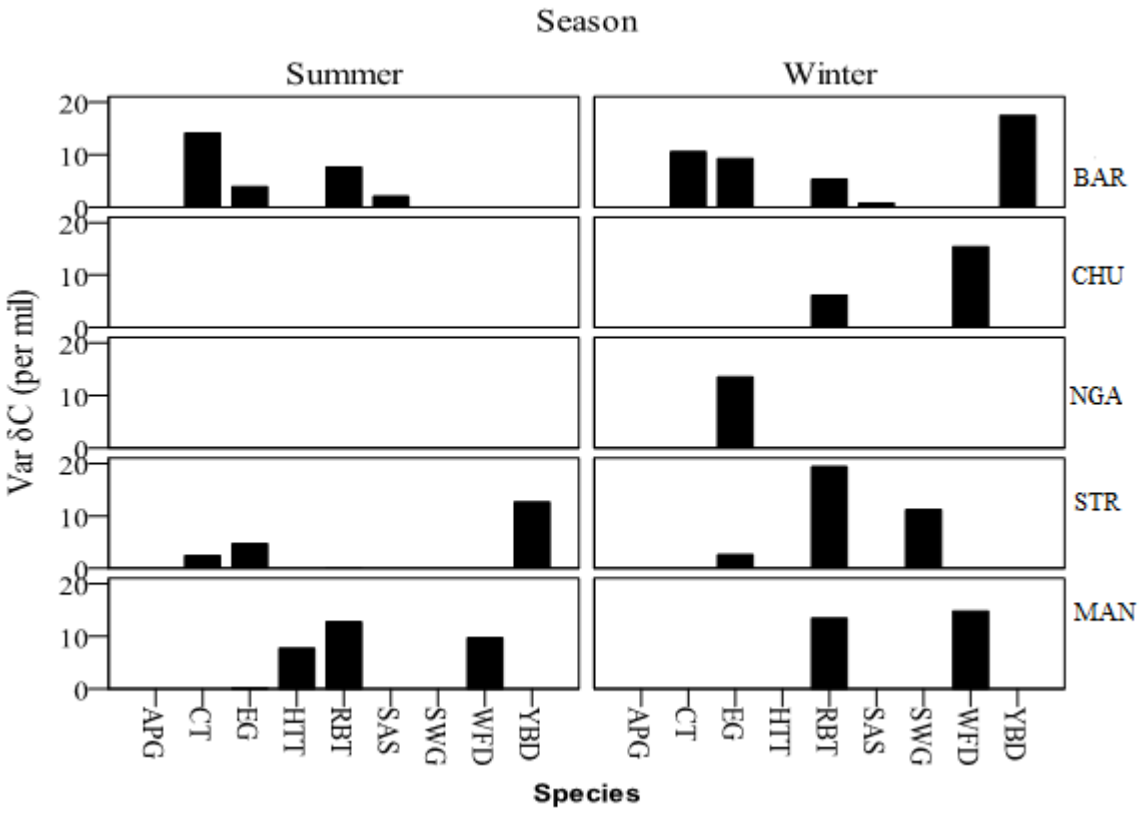
(a)



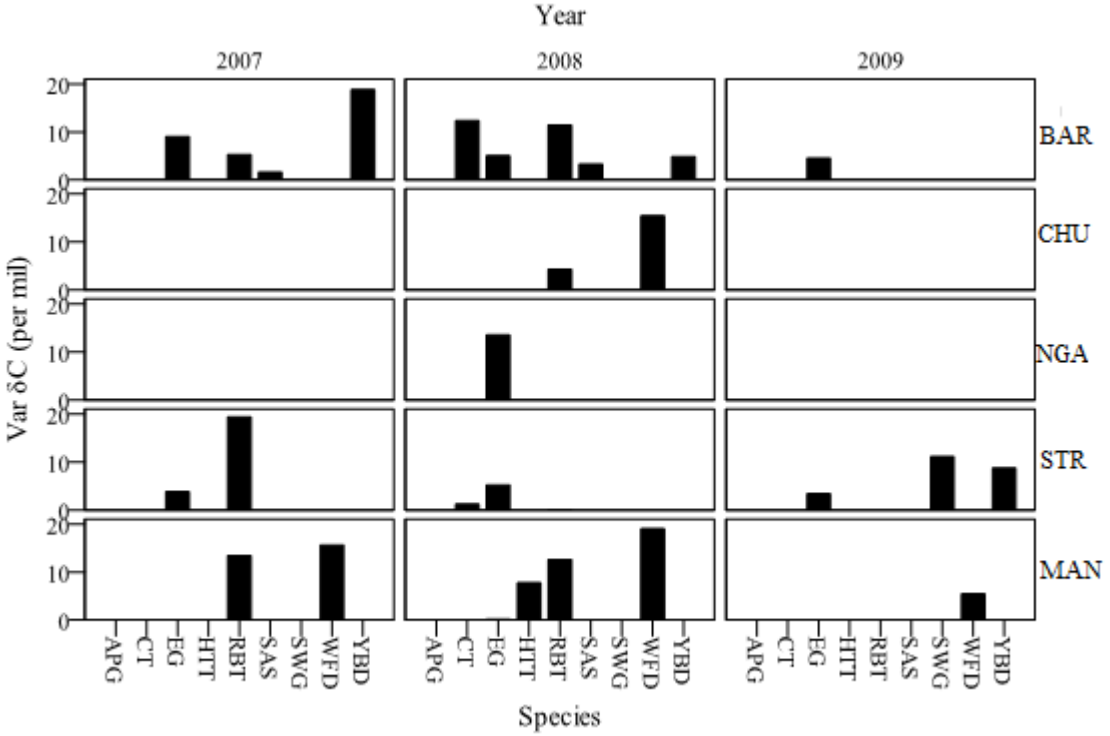
(b)


Year
2007
2008
2009
Var δN (per mil)
0
20
40
BAR
CHU
NGA
STR
MAN
APG
CT
EG
HTT
RBT
SAS
SWG
WFD
YBD
Species

(c)


Season
Summer
Winter
BAR
CHU
NGA
STR
MAN
Var δC (per mil)
20
10
0
APG
CT
EG
HTT
RBT
SAS
SWG
WFD
YBD
Species

(d)


Year
2007
2008
2009
BAR
CHU
NGA
STR
MAN
Var δC (per mil)
0
10
20
APG
CT
EG
HTT
RBT
SAS
SWG
WFD
YBD
Species