A flight of fancy in the Chorister Robin-Chat (*Cossypha dichroa*):

An isotopic standpoint.

Thesis submitted in fulfilment of the requirements for the degree of
MASTER OF SCIENCE at RHODES UNIVERSITY

By

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Abstract

Forested areas have been cited for their highly diverse floral and faunal assemblages, which are currently under threat from anthropogenic activities that restrict their range and deplete the resources produced within these naturally fragmented patches. Historically, up to 67% of avifaunal species associated with well-treed areas have undergone localised extinctions, consequentially affecting biodiversity as a measure of species richness and ecosystem functionality. To date, more than 900 of the bird species affiliated with forests are under threat and despite the theory surrounding functional redundancy, the mass extinction that is currently underway poses considerable limitations on the ecological integrity of these biomes. In South Africa, indigenous forest (one of the rarest biomes), occurs predominantly in small isolated patches along the eastern escarpment. With mountainous terrain emphasised as 'prominent hotspots of extinction', the limited dispersal and habitat sensitivity of montane forest fauna renders these species more prone to localised extinctions. BirdLife International, the IUCN and SABAP2 all indicate reductions in the range and abundance of the Chorister Robin-Chat (*Cossypha dichroa*) - an endemic forest specialist that is reported to move seasonally between high-altitude forest patches where they breed in summer, and lowland coastal forests where they overwinter. Beyond diet, body morphology and vocalisations, much of the information available on the altitudinal movements of *C. dichroa* is based on secondary sources and the assumptions therein. This study aimed to investigate the potential utilisation of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes in determining the dietary niche width and altitudinal movements of *C. dichroa*. Feathers obtained in forested patches of the Limpopo, KwaZulu-Natal and Eastern Cape provinces exhibited a wide trophic niche width and generalised diet. Strong regional separation is apparent in the isotopic signatures suggesting little movement between provinces. A comparison of ^{13}C-isotopes showed minimal variation that point to a uniformity in the carbon-base utilised by *C. dichroa* across their range. The ^{15}N-signatures obtained in Limpopo, however, revealed a distinct trophic segregation between the northern-most Chorister populations and their southern counterparts. No altitudinal movements were detected in the isotopic signatures of recaptured Choristers, but more research is needed to investigate the long-term accuracy of these results and the breeding potential of resident Choristers in lowland coastal forests; especially when considering the reduced range and abundance reported for this endemic species.

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Declaration

This dissertation, submitted for the degree of Master of Science in the Department of Zoology and Entomology, Rhodes University, represents original work by the author and has not been submitted in any form to any other institution. Where mention has been made of the work of others, it has been duly acknowledged in the text.

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Milena Helena Louise Wolmarans

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Foreword

Anthropogenic effects have negatively influenced every biotope known from equatorial zones in the lower latitudes to the peripheral axes of the North- and South- Poles (Hannah *et al.*, 1995; Fahrig, 2003; Hoekstra *et al.*, 2005; Dobson *et al.*, 2006; Cumming, 2007; Fischer & Lindenmayer, 2007; Bongaarts, 2009; Chapman, 2009). In the wake of urban sprawl, as demographic transitions continue to shift the focus of production toward industrial manufacture and the service sector (*id est*, away from the harvesting of raw materials), farmers are compelled to intensify agricultural land-use practices that demand progressively more from the (already) dwindling reserves of globally cultivated land (Conway, 1997; Myers, 1999; Kerr & Deguise, 2004; Luck *et al.*, 2004; Bongaarts, 2009; Pingali, 2012). Irrespective of modern agricultural advancements and the 'green revolution'[1], socio-economic traits persist in determining global food allocations (49 per cent of which is expended on one-quarter of the World's population – AAAS, 2013) resulting in inequalities that only serve to deepen the inter-hemispheric divide between the richer North and (generally) poorer South (Lewis, 1966; Pimentel, 1993; Edwards, 1998; Myers, 1999; Pingali, 2012). Supporting only 17 % of the worlds' population (Haub & Kaneda, 2014), the economic 'prosperity' associated with More Developed Countries (MDCs)[2] contrasts sharply with that of Less Developed Countries (LDCs), where access to education and pharmaceutical supplies[3] are often superfluous against a backdrop of poverty (Lewis, 1966; Edwards, 1998; FAO, 2000, 2003; Shackleton, 2004; AAAS, 2013). Despite extensive swathes of agricultural crops, which are grown and cultivated in LDC's around the World (Conway, 1997; Myers, 1999; Pingali, 2012), annually, more than 790 million malnourished people invade the ecosystems that surround them in order to subsist (Daily, 1997; FAO, 2003; Shackleton, 2004; AAAS, 2013), where native species are harvested, unreservedly, for food, medicine and fuel (Costanza *et al.*, 1997; Mander, 1998; Hassan, 2002; Williams & Shackleton, 2002; Shackleton & Shackleton, 2003). Valued at $33 trillion US dollars more than a decade ago (Costanza *et al.*, 1997) – quadruple that of the Gross World Product (Boumans *et al.*, 2003), ecosystem services and their 'safety net' (Shackleton, 2004; Costanza & Kubiszewski, 2012)

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[1] Instituted in 1961 to enhance the yield and resistance of agricultural crops, 'green packages' - containing modified seeds - were widely distributed (alongside monetary incentives) to promote the growth and cultivation of grain, cereal, and other food crops, raising the calorie intake per person by 38 % per day (Conway, 1997; AAAS, 2013).

[2] where towns and cities dominate the landscape leaving very few 'natural' ecosystems intact (Hannah *et al.*, 1995)

[3] which both promote self-sustainability through subsistence farming and family planning (*exempli gratia*, free contraceptives).

of resources shape the very livelihood of rural communities (Daily, 1997; Kaimowitz, 2003; Bongaarts, 2009) that are caught in the 'trap' of poverty (Lewis, 1966; Edwards, 1998; Myers, 1999).

Since 2005, the environmental cost of supporting 6.5 billion people (United Nations, 1962, 1973, 2007; Bongaarts, 2009) and an additional 11 million species[4] (Chapman, 2009) has escalated exponentially, culminating in human-modified landscapes that are less diverse (Myers, 1999; Sala *et al.,* 2000; Liu *et al.,* 2001; Fahrig, 2003; Foley *et al.,* 2005; Klink & Machado, 2005; Fischer & Lindenmayer, 2007). In the 20 years preceding the turn of the century, soil erosion led to the displacement of more than 500 billion tonnes of top-soil (Pimentel, 1993; Pimentel *et al.,* 1995; Myers, 1999), desertification encroached upon 45 million km^2 of land (Dregne & Chou, 1994), and salinisation combined with water logged soils necessitated the reclamation of 450,000 km^2 of irrigated farmlands (Myers, 1999; Novacek & Cleland, 2001). Additionally, exacerbated by deforestation[5], water deficits have affected 40 % of the Worlds' population in 88 developing countries (Salati & Nobre, 1992; Myers, 1999), many of which were unable to meet the growing demands of a rapidly expanding population (Edwards, 1998; Bongaarts, 2009; AAAS, 2013). Over time, as 130,000 km^2 of native vegetation continues to be cleared each year (BirdLife International, 2013), the unsustainable levels of over-exploitation have displaced millions of species around the world, contributing to their localised extinction (Novacek & Cleland, 2001). Of the 71,576 species[6] assessed by the International Union for the Conservation of Nature (IUCN), 21,286 are currently listed as Threatened ('Vulnerable', 'Endangered', or 'Critically Endangered'); 4,822 as Near-Threatened; 799 as Extinct; and 61 species that no longer occur in the wild[7]. Data deficient records preclude an accurate assessment of the conservation status of an additional 11,881 species, which (all-in-all) amounts to a questionable future for more than half of the species evaluated. As habitat degradation, isolation and loss drive the mass extinction that is currently underway (Bender *et al.,* 1998; McIntyre & Hobbs, 1999; Myers, 1999; Zanette *et al.,* 2000; Fahrig, 2003; Battin, 2004; Hoekstra *et al.,* 2005; Chapman, 2009; Mikkelson, 2009), knock-on effects cascade through ecosystems - both terrestrial (Sala *et al.,* 2000; Hoekstra *et al.,* 2005) and marine (Jackson, 2001; Knowlton, 2001) - in a downward spiral of environmental decline

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[4] Compiled in 2009 by the Australian Government in the 'Department of the Environment, Water, Heritage and the Arts', the World estimates for Chordates enumerate 80,500 species; Invertebrates at 1,359,367; Plants at 390,800; Fungi at 1,500,000; and 'Others' to include Prokaryotes and Viruses at 2,600,500 species.

[5] For example, in the last 50 years the Amazon lost around 17 % of its forest cover (WWF, 2014)

[6] 4.1 % of the 1.75 million *species* described thus far (Hawksworth & Kalin-Arroyo, 1995; Gaston & Spicer, 2004)

[7] IUCN Red List version 2014.2. http://www.iucnredlist.org/about/summary-statistics#Tables_1_2

that increasingly undermines food security (Conway, 1997; Myers, 1999; Novacek & Cleland, 2001; Shackleton, 2004; Fischer & Lindenmayer, 2007). As human populations[8] expand at an annual rate of 1.2 per cent (0.1 % in MDC's; 1.7 % in LDC's [excluding China]; and 2.4 % in the least developed – Haub & Kaneda, 2014), over-population, poverty, landlessness (Myers, 1999), climate change (Bazzaz & Sombroek, 1996; Willis *et al.*, 2009), and war (Salehyan & Hendrix, 2014), all add to the massive demands that are placed on natural resource reserves (Lehman & Tilman, 2000; Loreau *et al.*, 2002; Chase & Leibold, 2003; Ives & Carpenter, 2007).

Documented as a 'biome crisis' in 2005, Hoekstra and his colleagues categorised 305 of the 847 ecoregions (Olsen *et al.*, 2001) as Vulnerable (161), Endangered (80), and Critically Endangered (64). Forested biomes, in particular, are accentuated as 'prominent hotspots for extinction' (Myers *et al.*, 2000; Hoekstra *et al.*, 2005) – especially in mountainous terrain (Aldrich *et al.*, 2001; La Sorte & Jetz, 2010). Prized by rural communities for the commodities they provide (Byron & Arnold, 1999; Koimowitz, 2003), these long-established forms of climax vegetation aid ecosystem functionality by sequestering carbon (Hassan, 2002; WWF, 2014), regulating water yield (and flow – von Maltitz *et al.*, 2003), maintaining pollination services (Shackleton, 2004), and preventing the denudation of top soils - a vital component of the ecosystem that facilitates decomposition, nutrient (re)cycling, and the establishment of primary producers (De Goede & Brussaard, 2002).

Supporting 80 % of the Worlds terrestrial species (WWF, 2014), many of which are yet to be described (Gaston & Spicer, 2004), forests are being rapidly converted into monocultures and plantations (Maclean, 1999; Castelletta *et al.*, 2000; Myers *et al.*, 2000; Daily, 2001; Daily *et al.*, 2001; Olsen *et al.*, 2001; Schmitt *et al.*, 2009; Barker *et al.*, 2013) at an alarming rate of 73–93 million km^2 each year (WWF, 2014). Despite the theory surrounding 'functional redundancy'[9] - with each square kilometre estimated to contain 1,000 different species (WWF, 2014) - mitigation strategies (that ultimately strive to maintain heterogeneity within a diverse array of ecosystems – La Sorte & Jetz, 2010) have become an imperative tool in the fight to conserve global biodiversity (Novacek & Cleland, 2001; Defries *et al.*, 2004; Fischer & Lindenmayer, 2007; Barker *et al.*, 2013).

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[8] which accelerated to unprecedented levels in the second half of the twentieth century from 2.5 billion people in 1950 to 6.5 billion in 2005 (United Nations, 1962, 1973, 2007; Bongaarts,2009).

[9] A form of biological insurance (Naeem & Li, 1997) where the ecological equivalence of one species is fulfilled and substituted by another with minimal detriment (Walker, 1992; Lawton & Brown, 1993; Walker, 1995)

Chapter 1: Patterned mosaics

Based on the size, shape and form of native vegetation patches, ecological connectivity (Taylor *et al.,* 1993; Ward *et al.,* 1999; *i.e.* 'green' corridors – Ueza *et al.,* 2005) and isolation (McKenzie, 1988; Prugh *et al.,* 2008) within a landscape matrix, both affect resilience and the persistence of natural systems (Ricklefs, 1987; Saunders *et al.,* 1993; McIntyre & Hobbs, 1999; Elmqvist *et al.,* 2003; Wethered & Lawes, 2003; Fischer & Lindenmayer, 2007; Pavlacky & Anderson, 2007; Solonen & Jokimaki, 2011; Barker *et al.,* 2013). As human modified landscapes continue to encroach upon these native patches, they become less connected and increasingly isolated from one another often forming distinct spatial islands in a sea of human modified landscapes (MacArthur & Wilson, 1967; MacArthur *et al.,* 1972; Harris, 1984; Pickett & Cadenasso, 1995; Bender *et al.,* 1998; McIntyre & Hobbs, 1999; Haila, 2002; Fahrig, 2003). With unique biotic assemblages that have co-evolved over time, long-established stands of climax vegetation exhibit environmental flexibility that often correlates with highly diverse communities[10] (Rosenfeld, 2002; Tilman *et al.,* 2006; Winfree & Kremen, 2008) where multiple surrogate species function in any available niche ('functional redundancy' – Walker, 1992; Lawton & Brown, 1993; Walker, 1995; Fonesca & Ganade, 2001; Rosenfeld, 2002; Elmqvist *et al.,* 2003).

As floral assemblages change in response to environmental disturbance and climatic conditions (Daily, 2001; Hobbs & Yates, 2003; Barker *et al.,* 2013), 'habitat-sensitive' species (particularly endemics – Maclean, 1999; Coetzee *et al.,* 2009) retreat from transitional zones at the edge (Harris, 1984; Luck & Daily, 2003) – ecotones which are particularly susceptible to climatic fluctuations in woodland (Allen & Breshears, 1998), forest (La Sorte & Jetz, 2010; Barker *et al.,* 2013), and grassland (Tilman *et al.,* 2006) biomes. As smaller patches produce fewer resources that support a smaller number of native species (Bellamy *et al.,* 1996; Bender *et al.,* 1998; Zanette *et al.,* 2000), competition and predation have a tendency to increase, resulting in ecological shifts that disrupt the natural flow and ebb of resources (ecosystem stability) in a system over time (Mayr, 1970; Ives & Cardinale, 2004; Hoekstra *et al.,* 2005; Ives & Carpenter, 2007). When one resource becomes limiting, or changes abruptly, subsequent effects often cascade through an ecosystem and may result in the movement of habitat sensitive

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[10] Maximum richness is achieved when the corresponding land area is large enough to maintain edge species as-well-as those that inhabit the patch interior (Hansen *et al.,* 1988; Ward *et al.,* 1999).

species out of an affected area (Johnson & Maclean, 1994; Norris & Marra, 2007; Brown, 2006; Boyle, 2010). Knock-on effects, which vary within and between guilds (Landres, 1983; Verner, 1984)[11], render pattern-scale approaches to landscape modification too coarse to detect local disparities within biotic assemblages – a hindrance to conservation strategies in highly fragmented systems (Hoekstra *et al.*, 2005; Fischer & Lindenmayer, 2007). By adopting a finer scale, changes in the occurrence, density, dispersal, diet and fecundity of endemic vertebrate species can be used as patch-specific indicators to mitigate habitat-loss and ensure the persistence of small complementary patches in larger area-networks (Villard *et al.*, 1993; Villard *et al.*, 1995; Tilman, 1996; Carignan & Villard, 2002; Kerr & Diguise, 2004).

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[11] where access to fundamental resources like water, shelter, food and space are key contributors to the longevity of territorial animals (Schoener, 1983; Polis & Strong, 1996; Lehman & Tilman, 2000; Loreau *et al.*, 2002; Symes & Woodborne, 2009)

1.1. Avifauna

The highly diverse array of behavioural and ecological traits exhibited by birds parallels their colourfully patterned plumages and varied feeding adaptations, allowing them to proliferate across a wide range of environmental conditions from the dry Atacama Desert to the icy polar caps (Maclean, 1999; Prum, 1999; Hill & M^{c}Graw, 2006; Salewski & Bruderer, 2007; Whelan *et al.,* 2008). These evolutionary characteristics display a tight coupling with the habitat(s) and environmental conditions that promote their development, resulting in the convergent evolution of generalist and specialist species from five primary functional feeding groups (Verner, 1984; Blondel, 2003).

Nectarivores, frugivores, granivores, insectivores and carnivores provide supporting services that maintain floral assemblages through pest control, pollination, dispersal and endozoochory (Stiles, 1985; Kay *et al.,* 1994; Kirk *et al.,* 1996; Howe & Smallwood, 1982; Blondel, 2003; Sekercioglu, 2006; Terborgh *et al.,* 2006; Brown *et al.,* 2007; Whelan *et al.,* 2008; Wenny *et al.,* 2011). Although insects contribute more to the pollination of cultivated plant crops, birds pollinate approximately 5 % of native plants in each of their respective areas (10 % on islands), producing comparatively more fruit and/or larger seed-sets in most instances (Carpenter, 1976; Howe & Smallwood, 1982; Stiles, 1985; Hargreaves *et al.,* 2004; Anderson *et al.,* 2006). As many seeds cannot germinate without being processed, endozoochory facilitates the expansion of flora (*see* Wenny *et al.,* 2011), effectively increasing the propagule pressure of various fruit-bearing plants, which is of particular interest to the recruitment of saplings in fragmented forest patches. The top-down effects of foraging also aid in the regulation of pest species, providing more food of a better quality (reduced pesticides) for human use and consumption (Kay *et al.,* 1994; Schwarz, 1998; Hooks *et al.,* 2003; Philpott *et al.,* 2004; Shackleton, 2004; Kremen & Ostfeld, 2005). As both predator and prey, birds form integral links within the biotic assemblages around them (Ives & Cardinale, 2004), benefitting a variety other taxa in their daily activities (e.g. Woodpeckers as 'ecosystem engineers'). Even in the absence of large carnivores and scavengers, a number of bird species assist in the break-down and removal of animal carcasses, reducing the colonisation potential of pathogenic bacteria and limiting the spread of diseases like canine distemper, rabies, and anthrax (Pain *et al.,* 2003; Whelan *et al.,* 2008).

Regardless of the benefits they provide, birds are often overlooked and undervalued in nature conservation practices (Carignan & Villard, 2002; Sekercioglu *et al.,* 2004; Anderson *et* *al.*, 2006; Sekercioglu, 2006; Whelan *et al.*, 2008; Wenny *et al.*, 2011). By monitoring the movement and density of avian populations, birds can provide unique insight into pattern-scale processes that affect biogeography (MacArthur & Wilson, 1967; Carignan & Villard, 2002; Fischer & Lindenmayer, 2007). Non-destructive sampling, from feathers or blood (M^{c}Donald & Griffith, 2011) allows conservationists to assess abiotic elements like environmental pollutants and nutrient cycling (Morrison, 1986; Underwood, 1994; Jaspers *et al.*, 2007; Bond, 2010), as-well-as species-specific information pertaining to population dynamics, morphometrics, phylogenetics and gene flow (Mayr & Greenway, 1956; Haig *et al.*, 2011). In the absence of visual confirmation, vocalisations that differ within and between species (Ames, 1971; Whelan *et al.*, 2008) are easily identifiable and can often be used to discern a whole suite of birds in any given place at any time (Verner, 1984; Bibby *et al.*, 2000; Buckland *et al.*, 2001; Carignan & Villard, 2002; Thompson, 2002; Solonen & Jokimaki, 2011). Employing the ‘guild-indicator’ approach (Verner, 1984; Block *et al.*, 1987; Landres *et al.*, 1988; Blondel, 2003), these environmental snapshots have been used to decipher trends within and between species to monitor the effects of environmental change on community structure and habitat quality across the globe (Underwood, 1994; Bibby *et al.*, 2000; Stoeckle & Winker, 2009).

1.2. Indigenous forests of South Africa

Forested areas have been cited for their highly diverse floral and faunal assemblages, which are currently under threat from anthropogenic activities that restrict their range and deplete the ‘safety net’ of resources produced (Allan *et al.*, 1997; Conway, 1997; Bender *et al.*, 1998; Maclean, 1999; McIntyre & Hobbs, 1999; Castelletta *et al.*, 2000; Daily, 2001; Daily *et al.*, 2001; Fahrig, 2003; Berliner & Benn, 2004; Shackleton, 2004; Schmitt *et al.*, 2009).

In South Africa, indigenous forest covers 3,500 km^2 (0.1 % - Shackleton, 2004) to 5000 km^2 (0.5% - Mucina & Rutherford, 2006) of the total land surface area (Shackleton, 2004; Thuiller *et al.*, 2006), from the Soutpansberg in the North (22˚57’S), southwards to Tongaland (26˚52’S) and west to the Cape Peninsula (34˚S) - (Hamilton, 1981; Geldenhuys, 1987). As an artefact of climatic conditions during the Pleistocene era (which were compounded by the logging activities of European settlers – Downs & Symes, 2004), they occur as naturally fragmented patches along the Eastern Escarpment and southern coasts (Diamond & Hamilton, 1980; White, 1981; Lawes *et al.*, 2004; Lawes *et al.*, 2007), in areas that annually receive between 500 – 2000 mm of summer and winter rainfall (Geldenhuys, 1987). The majority of fragments (~ 80 %) are less than 1 km^2 (Geldenhuys, 1989), and cumulatively generate millions each year from medicinal products (Mander, 1998; Cocks *et al.*, 2004; Williams, 2004) and tourism (minimum R79 million – Harvey, 2003; Saayman & Saayman, 2003). More often than not situated in unfavourable terrain that precludes urban and structural developments, forest fragments have been left to persist in isolated patches, coinciding with the rural communities that exploit them (Botha, 2001; Hassan, 2002; Williams & Shackleton, 2002; FSA, 2003; Madubansi, 2003; Cunningham & Shackleton, 2004; Shackleton, 2004).

Despite very few large-scale commercial logging activities, a driving need for poverty alleviation and food security (NFAP, 1997; Byron & Arnold, 1999; Neumann & Hirsch, 2000; Cavendish, 2000; Botha, 2001; Lawes *et al.*, 2000; von Maltitz & Grundy, 2000; FSA, 2003; Madubansi, 2003; Cunningham & Shackleton, 2004; Lawes *et al.*, 2004; AAAS, 2013) has resulted in escalated deforestation (e.g. Knysna; Shackleton, 2004; Wethered & Lawes, 2005), as well as an increase in the conversion of forests to agriculture (regardless of the markedly drier and less favourable conditions in the south - Shackleton, 2004). Despite the long-established resilience of South African forests (Geldenhuys, 1989; Lawes *et al.*, 2000; von Maltitz & Grundy, 2000; Berliner & Benn, 2004), severe exploitation over the last few decades (Geldenhuys, 1987; Geldenhuys, 1989; Eeley *et al.*, 1999; Maclean, 1999; Barker *et al.*, 2013) has resulted in localised extinctions in up to 67 % of the original forest-bird assemblages (Castelletta *et al.*, 2000; Daily *et al.*, 2001; Whethered & Lawes, 2005; Brocklehurst, 2009) – a potentially worrying pre-cursor of environmental instability (Sekercioglu *et al.*, 2004; Sekercioglu, 2006; Whelan *et al.*, 2008; Wenny *et al.*, 2011) where forest dwelling species simply disappear from the system (Vernon, 1989; Du Plessis, 1994).

1.2.1. Forest birds of South Africa

Of the 10,000 bird species (Groombridge & Jenkins, 2002; BirdLife International, 2008; Chapman, 2009) that occur on Earth nearly two-thirds depend upon forest patches and the resources they provide (BirdLife International, 2013), and of these, 900 were listed as threatened in 2008 by BirdLife International due to habitat destruction. Despite a predisposition for flight that allow birds to traverse boundaries and environmental conditions that are often insurmountable to other faunal and floral groups, many forest species have a tendency to be localised within the confines of the trees.

Known as a rich endemic repository for plant and bird species (Maclean, 1999), South Africa contains six phylogenetically distinct biomes that each support unique floral and faunal assemblages (Thuiller *et al.*, 2006). Of the 928 bird species that inhabit them (Harrison *et al.*, 1997), 41 are classified as true forest specialists (Skead, 1964; Oatley, 1989; Symes *et al.*, 2000), and only six are endemic to South Africa (and Lesotho - Maclean, 1999): Brown Scrub-Robin (*Cercotrichas signata*), Bush Blackcap (*Lioptilus nigricapillus*), Chorister Robin-Chat (*Cossypha dichroa*), Forest Canary (*Serinus scotops*), Rudd's Apalis (*Apalis ruddi*), and Knysna Turaco (*Tauraco corythaix*). As a biogeographic mirror of their native habitat, the range of endemic forest birds is superficially demarcated by the Drakensberg Mountain range, which extends south along the Eastern Greater Escarpment from higher areas of the Soutpansberg in the north-east of Limpopo to the mist-forests of KwaZulu-Natal (KZN) and the Winterberg in the Eastern Cape (EC) in the south (Cooper, 1985; Midgeley *et al.*, 1997; Oatley & Arnott, 1998; Symes *et al.*, 2000; von Maltitz *et al.*, 2003; Berliner & Benn, 2004; Symes & Woodborne, 2009; Sinclair *et al.*, 2011).

With a preference for closed and contiguous forest canopies, forest-dependent birds are often confined to and restricted by the availability of suitable habitat where the sheltered conditions of the treed interior buffer them from climatic extremes (Skead, 1964; Oatley, 1989).

The majority of forest patches in South Africa are small with pronounced edge effects (Geldenhuys & Knight, 1989; Oatley, 1989; Lawes *et al.,* 2004) that often pose too much of an ecological disturbance for forest specialists to withstand (Vernon, 1989; Du Plessis, 1994; Renjifo *et al.*, 1997; Maclean, 1999). In these fragments, adverse weather conditions (especially at high altitudes during winter) typically reduce the availability and occurrence of resources (like insects - Gullen & Cranston, 2010), affecting prey abundance and constricting natural dietary supplements (Bearhop *et al.,* 2004; Boyle, 2010). As limiting resources tend to be exploited by one or more dominant species (particularly when there is a high degree of overlap – Polis & Strong, 1996; Jiang, 2007), the abundance of specialists consequently declines (Connell, 1983; Schoener, 1983). Already lacking space and the resource capacity to support larger bodied fauna, an increase in the intensity of both inter- and intra- specific competition (Connell, 1983; Bellamy *et al.,* 1996; Lawes *et al.,* 2007; Ritchie & Johnson, 2009; Spanhove *et al.*, 2009) can lead to the loss of not only one or two forest bird species, but potentially the entire suite (Vernon, 1989).

Recent evaluations have determined the global extinction risk of birds to be heightened in areas previously subjected to heavy human encroachment (like South Africa – Maclean, 1999; FSA, 2003; Shackleton, 2004; Bongaarts, 2009), emphasising forested biomes (especially in mountainous terrain – La Sorte & Jetz, 2010), as ‘prominent hotspots of extinction’. In high-altitude forests (*circa* 1400 m – 1800 m a.s.l.) the limited dispersal and habitat sensitivity of montane forest birds like the Cinnamon Dove (*Aplopelia larvata*), Orange Ground-Thrush (*Zoothera gurneyi*), and White-Starred Robin (*Pogonocichla stellata*), renders these species more vulnerable to ecological disturbances and localised change (Vernon, 1989; Maclean, 1999; Symes *et al.,* 2000). By understanding the role of endemic species like the Chorister Robin-Chat (*C. dichroa*), and their sensitivity to environmental change (Oatley 1970a; Jensen, 1989; Maclean, 1999), population fluctuations within and between patches can be used, quite effectively, as an early-warning detection system for habitat degradation (Morrison, 1986; Kremen, 1992; Underwood, 1994; Bibby *et al.,* 2000; Carignan & Villard, 2002, Sekercioglu *et al.,* 2004; Martinez-Morales, 2005). In addition to aiding conservation efforts in fragmented forest patches (Kremen, 1992; Barker *et al.,* 2013), deciphering the life-history traits of forest-dependent species will increase their efficacy as potential indicator species (Landres, 1983; Landres *et al.,* 1988; Carignan & Villard, 2002; Roberge & Angelstam, 2006).

1.2.2. An endemic piece of the forest puzzle

The Chorister Robin-Chat (*Cossypha dichroa*) was first described by J. F. Gmelin in 1789 from a specimen from South Africa, classified as a flycatcher in the family Muscicapidae (*Muscicapa dichroa* – Oatley, 1970a, 1970b; Jensen, 1989; Oatley & Arnott, 1998; Beresford, 2003). Subsequent revision led to their inclusion within the forest robin-chat assemblage (*Cossypha*) based on their ability to mimic sounds as-well-as the orange/black pigmentation of their tails – both ubiquitous traits in the genus *Cossypha* (Oatley, 1970a; Clancey, 1982; Jensen, 1989; Clements, 2007). Although molecular evidence emphasises a closer genetic affiliation to Old World Flycatchers (Sibley & Ahlquist, 1990; Sibley & Monroe, 1990; Beresford, 2003; Clements, 2007), there is strong nodal support for Turdids and Muscicapids as sister taxa (Sibley & Ahlquist, 1990; Beresford, 2003; Ericson & Johansson, 2003). As the largest robin-chat in southern Africa, Choristers forage and behave more like Thrushes than Flycatchers (a family of birds that are typically small, aerial foragers – del Hoyo *et al.*, 2005, 2006), and for many years they were believed to be a part of the Turdidae family in the Saxicolinae subfamily (Beecher, 1953; Dilger, 1956; Beresford, 2003), where some sources still insist on grouping them (see del Hoyo *et al.*, 2005, 2006).

Choristers inhabit high-altitude forest patches and the cool, moist conditions that the interiors provide (Oatley, 1959; Oatley, 1970a; Clancey, 1982; Oatley, 1998; Oatley & Arnott, 1998; Symes *et al.*, 2000). Within these sheltered habitats, they require well established stands of climax vegetation in order to breed, nesting up to 12.5 m high in natural rot-holes (Clancey, 1982; Oatley & Arnott, 1998; Tarboton, 2011). The majority of sources indicate inland, high-altitude breeding during summer months (October – January), followed by altitudinal movements down to coastal forests before the onset of winter (March – April), and a subsequent inland ascension in preparation for the breeding season (Sept – Oct). As food availability and cold weather have both been dismissed as driving mechanisms for altitudinal movements in Choristers (Oatley, 1970a; Clancey, 1982), it remains unclear as to why individuals would risk the increased physiological stresses associated with migrating; especially considering the deleterious effects of these last minute migratory movements on avian fitness (Alerstam & Lindström, 1990; Thompson *et al.*, 2010).

In 1981, Clancey found distinct size discrepancies between Choristers from the north of South Africa and the original specimen from the south (described by Gmelin in 1789), prompting the subdivision of *C. dichroa* into *C. dichroa mimica* (a smaller northern subspecies) and *C. dichroa dichroa* - their larger counterparts (Clancey, 1982; Oatley & Arnott, 1998; Clements, 2007). Although size discrepancies were enough to warrant their taxonomic split, these geographic variations are not always recognised in modern literary texts (e.g. Chittenden *et al.*, 2011), possibly due to the absence of any other notable variance. Nevertheless, this divergence (of one sub-species from the other within the same native range) raises important questions about the dispersal habits of Choristers that were thought to occur seasonally, facilitating gene flow and the intermingling of sub-populations along the Eastern Escarpment of South Africa.

Choristers have also been shown to successfully breed with Red-Capped Robin-Chats - *Cossypha natalensis* (Clancey, 1982) - a close relative (Jensen, 1989; Beresford, 2003), producing hybridised forms of a mixed plumage phenotype (Harrison *et al.*, 1997; Oatley & Arnott, 1998; Davies *et al.*, 2011) originally thought to be *Cossypha haagneri* or an aberrant form of *C. dichroa* (Clancey, 1982; Schmidt, 2007). Although hybridisation is common in the wild across 18.9 % of avian taxa (Aliabadian & Nijman, 2007), more information is needed to assess this specific instance of interbreeding as inter-specific disparities in plumage, body size, breeding behaviour and geographic distribution have limited the co-occurrence of *C. dichroa* and *C. natalensis* over time (Clancey, 1982; Davies *et al.*, 2011). With recent reports having acknowledged an overall decline in the range and abundance of *C. dichroa* (BirdLife International, 2008; IUCN, 2014; SABAP2, 2014), more in-depth studies are needed to determine if this is the case, and ascertain the survival rates and persistence of Choristers within forest patches of South Africa (Vernon, 1989; Oatley & Arnott, 1998; Davies *et al.*, 2011).

1.3. Chorister Robin-Chat (*Cossypha dichroa*)

The Chorister Robin-Chat – hereafter referred to as 'Chorister' – is an endemic species currently placed in the category of "least concern" (BirdLife International, 2008; IUCN, 2014). Beyond the basics of their biology, morphology and vocalisation, very little research has been conducted on this forest-dependent species (Oatley, 1959; Cyrus & Robson, 1980; Brown & Barnes, 1984; Johnson & Maclean, 1994; Oatley, 1998; Oatley & Arnott, 1998; Maclean, 1999). Sparse information from secondary sources exists on their survival rates and longevity (70 % for females and 87 % for males - Collar, 2005), but baseline estimates are difficult to quantify or even predict (Oatley & Arnott, 1998; Symes *et al.*, 2000; Cochran *et al.*, 2004; Coetzee *et al.*, 2009; La Sorte & Jetz, 2010). Due to their vagile nature, migratory movements can often be misleading resulting in over- or under- estimates of Chorister abundances. This is compounded by annual augmentations (to various sub-populations) prior to the onset of the breeding season (altitudinal migration in adults - Johnson & Maclean, 1994; Maclean, 1999), as-well-as shortly after it (first year recruits - Oatley, 1998; Oatley & Arnott, 1998). Nevertheless, despite these constraints, an overall density of 2.22 ± 0.25 Choristers per hectare (ha^{-1}) was reported in the afromontane forest patches of the Drakensberg (Brocklehurst, 2009), which coincides with the known average territory size of each breeding pair (Oatley, 1998; Oatley & Arnott, 1998; Tarboton, 2011). Assuming static conditions (extinction rate = colonisation rate; birth rate = death rate) for a snap-shot in time (in situ), it is theoretically possible to extrapolate this (2.22 ha^{-1} ± 0.25) to the extent of suitable forest habitat (297,212 ha)[12] in order to determine the approximate size potential of meta-populations in South Africa (119,362 minimum; 150,869 maximum).

However, renowned for nesting in natural rot holes (up to 12.5 m high – Oatley & Arnott, 1998; Tarboton, 2011), the breeding success and fecundity of Choristers are both inextricably linked to the abundance of tall, forest trees (Du Plessis, 1994; Oatley, 1998; Tarboton, 2011). In small (increasingly) isolated forest patches, even the localised removal of dead trees and decaying wood (for fuelwood, in particular, by poor rural communities - Madubansi, 2003) can have large ecological implications (Du Plessis, 1994).

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[12] Adapted from the forest types described by von Maltitz *et al.*, (2003), and laid-out in detail by Berliner & Benn, (2004), and Bongaarts (2009), the following forests were all considered suitable for Chorister habitation (Oatley, 1959; Cyrus & Robson, 1980; Brown & Barnes, 1984; Johnson & Maclean, 1994; Oatley, 1998; Oatley & Arnott, 1998; Maclean, 1999): Amatole Mistbelt (64,424 ha); Drakensberg Mistbelt (1,926 ha); Eastern Mistbelt (42,162 ha); KZN Coastal Forest (21,092 ha); Mpumalanga Mistbelt (34,542 ha); Northern KZN Mistbelt (5,323 ha); Northern Mistbelt (19,349 ha); Southern Cape Afromontane (77,535 ha); Transkei Mistbelt (30,859 ha).

Anthropogenic activities aside, Choristers face a multitude of threats within their areas of occurrence, especially in large forest patches where biodiversity and, by association, competition is high. With more species vying for resources, the energetic requirements needed to forage for food, breed, defend a territory and survive, may influence the movement of Choristers between forest fragments. With much of the data on *C. dichroa* stemming from historical accounts, secondary information and out-dated land coverage assessments (Symes *et al.,* 2000; Mace *et al.,* 2008; La Sorte & Jetz, 2010), additional information on their life-history traits need to be assessed in order to refine their predicted rate of extinction as-well-as the potential of this endemic species to accurately reflect habitat degradation (Vernon, 1989; Oatley & Arnott, 1998; Lawes *et al.*, 2007; Lee & Jetz, 2008; Davies *et al.*, 2011).

1.3.1. Range, habitat and feeding ecology

Across their native range, Choristers inhabit southern afro-montane forest fragments, which occur in isolated patches between *c.* 1400 m and 1800 m a.s.l. (Oatley, 1959; Cyrus & Robson, 1980; Brown & Barnes, 1984; Johnson & Maclean, 1994; Oatley, 1998; Oatley & Arnott, 1998; Hockey *et al.,* 2005). The Grootvadersbos Forest in Swellendam (Western Cape - 20˚53’E) appears to be the western limit of their range (Oatley & Arnott, 1998; SABAP2, 2014), and apart from rare sightings in Lesotho and Swaziland, they are effectively endemic to South Africa (Cyrus & Robson, 1980; Brown & Barnes, 1984; Oatley & Arnott, 1998; Maclean, 1999; SABAP2, 2014), (Figure 1).

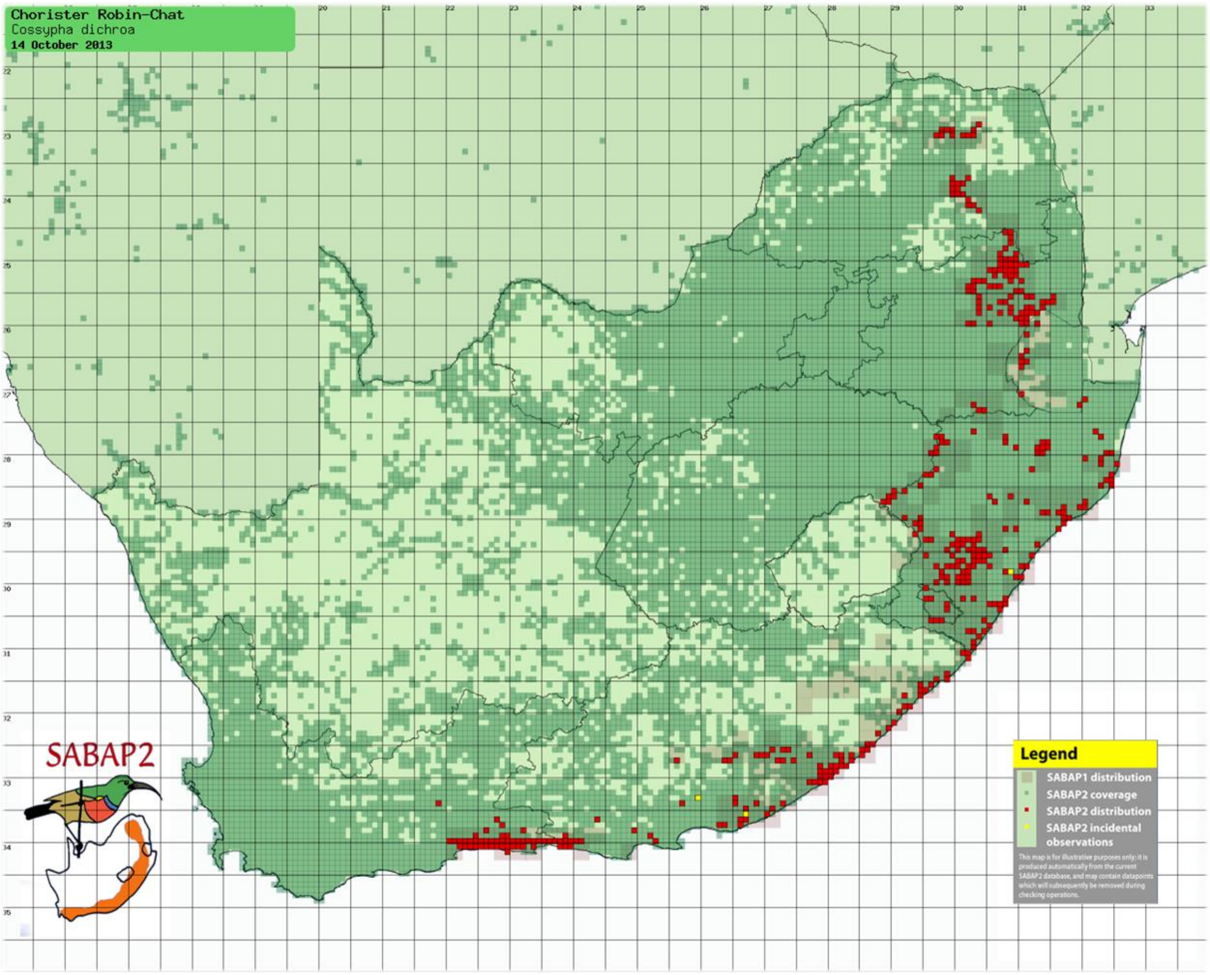

Figure 1: Geographic distribution range of *Cossypha dichroa* across the Eastern Escarpment and coastal forests of South Africa. Excerpt taken from the second South African Bird Atlas Project.

As true forest birds, the range of Choristers extends south across the Greater Escarpment of the Drakensberg from higher areas of the Soutpansberg and Blouberg (in the north-eastern parts of South Africa) to the mist-belt forests of KwaZulu-Natal and the southern coastal forests of Kenton, George and Knysna (23˚ - 34˚ S), (Oatley, 1997; Oatley & Arnott, 1998; Hockey *et al.*, 2005; Sinclair *et al.* 2011). This species occurs at higher densities in areas with a greater moisture content, preferring the cooler shady, low-lit conditions associated with wetter forest patches (Clancey, 1982; Oatley, 1998; Oatley & Arnott, 1998), where reliable sources of food and water are required to survive and reproduce (Oatley, 1970a).

Primarily insectivorous, their diets incorporate a diverse array of arthropod species from arachnids and millipedes to flies and termites (Oatley, 1970a; Oatley & Arnott, 1998; del Hoyo *et al.*, 2005; Chittenden, 2007; Sinclair *et al.*, 2011), all of which are abundant in montane forest patches (Oatley, 1970a, b; Clancey, 1982; Mills *et al.*, 2011). Summer months (October – May) coincide with the breeding season in high-altitude forests, where Choristers spend a large portion of their day opportunistically exploiting local prey abundances in the mid-strata and lower canopy (Oatley, 1970a). The combined dietary analyses of 11 stomachs and 33 fecal samples identified beetles (Coleoptera: 73 %), ants (Hymenoptera: 61 % [2 % wasps]), termites (Isoptera: 7 %), and fruit (57 %) as regular dietary constituents for Choristers in their northern and eastern ranges (Oatley, 1970a; Oatley & Arnott, 1998; Chittenden, 2007); supplemented by smaller contributions of Lepidoptera (34 %), Myriapoda (16 %), Hemiptera (9 %), Diptera (9 %), Orthoptera (9 %), and Arachnida (10 %). Choristers have also been recorded perching on bushbuck (*Tragelaphus scriptus*) and nyala (*Tragelaphus angasii*), gleaning ectoparasites from their coats (Oatley, 1970a; Dean & MacDonald, 1979). Fruit and plant materials from *Asparagus asparagoides, Burchellia bubalina, Celtis africana, Maytenus harveyana, Scolopia mundii, Scutia myrtina, Vepris undulata,* and *Xylamos monospora* were also identified, alongside a number of exotic species like *Hedychium flavum, Rhus succedanea,* and *Rubus* species (Oatley, 1970a). During dry winters, (April – September), Choristers occasionally track ant colonies and mole-rats (*Cryptomys*) when foraging for food (Oatley, 1970a), also entering orchards and garden patches along the forest edge (Clancey, 1982; Oatley & Arnott, 1998; Sinclair *et al.,* 2011). As gardens often act as a reservoir for non-indigenous plants, Choristers may even contribute to the spread of Category 1 invasive species like *Lantana camara, Solanum mauritianum,* and *Psidium pomiferum* – fruits of which have been recorded in their diet (Oatley, 1970a).

Despite their preference for closed and contiguous forest canopies, a subset of Choristers leave the confines of the trees and migrate through thickly vegetated ravines and thicket patches along the escarpment to lowland forests (< 600 m a.s.l.) on the eastern and south-eastern coasts (Johnson & Maclean, 1994; Oatley, 1997; Oatley, 1998; Oatley & Arnott, 1998; Hockey *et al.,* 2005). Without the cover of their forested haunts, one could opine that Choristers would struggle to cope with the necessary metabolic requirements needed to adjust to conditions beyond the forest edge; especially if they cannot regulate their own humidity as Oatley (1970a) suggested. The abrupt presence of direct sunlight, elevated wind and temperature extremes, as well as having to fend off and elude unfamiliar predators or competitors during migratory movements (Alerstam & Lindström, 1990; Gwinner, 1990), may present physiological barriers to habitat sensitive forest flora and fauna. The tendency of Choristers to avoid open dry areas often precludes them from entering valley bushveld, dry deciduous woodlands and sand forest, or the wooded coastal dunes of Mozambique (Oatley &

Arnott, 1998; Hockey *et al.*, 2005; SABAP2, 2014), but it is unknown whether migrating individuals utilise these habitats during their transitional phase, as Johnson & Maclean (1994), and Maclean (1999) suggest. On rare occasions, Choristers have been reported to over-winter in the swamp and dune forests of KZN (Oatley & Arnott, 1998).

1.3.2. Altitudinal migration

In 1959, Oatley reported the altitudinal migration of Choristers in South Africa, from inland forest patches to coastal forest thickets, due to lower winter rainfall and cold temperature extremes (Clancey, 1964; Maclean, 1972; Oatley & Arnott, 1998). When combined, adverse weather conditions decrease the carrying capacity of some forested areas, like the Sandstone belts of the Drakensberg foothills, which become too dry for Choristers to inhabit (Johnson & Maclean, 1994; Oatley & Arnott, 1998). Therefore, depending on the abundance of resources, a full- or partial- migration is undertaken, over relatively short distances to lowland forest thickets (Johnson & Maclean, 1994; Oatley & Arnott, 1998; Hockey *et al.*, 2005). First-year birds, but possibly adults too (Oatley, 1998), are thought to move down and across the Eastern Escarpment to neighbouring coastal thickets (Maclean, 1972; Oatley & Arnott, 1998; Hockey *et al.*, 2005; Davies *et al.*, 2011; Sinclair *et al.*, 2011), where small forest fragments (< 1 ha – Lawes *et al.*, 2007) and other wooded patches provide integral 'stepping-stones' as safe refugia during taxing flights (Fischer & Lindenmayer, 2007) in a landscape matrix of non-indigenous vegetation, exotic plantations, and grassland (FSA, 2003; Wethered & Lawes, 2003; Lawes *et al.*, 2004; Shackleton, 2004). This overland movement may equate to less than 100 km (in most cases - Oatley & Arnott, 1998), but the elevational gradient is substantial enough (> 1800 m in some instances) to warrant the 'altitudinal migration' status (Johnson & Maclean, 1994; Oatley, 1997; Oatley, 1998; Wilkschko & Wiltschko, 2009).

Despite postulations in the literature, the movement that is purported to occur between inland forest patches (*c.* 1400 m – 1800 m a.s.l.) and coastal forest belts (*c.* < 300 m a.s.l.) remains largely undefined (Clancey, 1982; Johnson & Maclean, 1994; M^{c}Donald & Griffith, 2011) - particularly with regards to driving mechanisms (Gwinner, 1990; Symes *et al.*, 2000; Fraser *et al.*, 2008). While the recapture data of colour-ringed individuals at the same sites in Natal (Oatley, 1998) supports the coastal breeding populations that have been reported in KwaZulu-Natal, East London, Tsitsikamma, Knysna, Natures Valley and George (Clancey, 1982; Oatley & Arnott, 1998; FLOCK, 2014 resident reports <*unpublished*>), they could otherwise indicate a return to the same winter haunts over consecutive years. Nevertheless, regardless of a possible link to philopatry (Greenwood, 1980; Gwinner, 1990), environmental cues and geographic landmarks seem to feature more in determining the annual movement patterns of Choristers (Cochran *et al.,* 2004), but genetic predispositions could also be a factor (Schwabl & Silverin, 1990).

1.3.3. Reproduction

During southern hemisphere summers, Choristers breed in mid- to high- altitude afromontane forest patches along the eastern escarpment of South Africa (Oatley, 1997; Oatley & Arnott, 1998; Ferguson *et al.*, 2002; Chittenden, 2007; Tarboton, 2011); but additionally in a few forests (at sea level) along the south-eastern coasts of KwaZulu-Natal and – to a limited extent – the Eastern Cape (Clancey, 1982; Maclean, 1999; Oatley & Arnott, 1998). Pair formation usually occurs in October within a suitable area of the forest, unoccupied by breeding con-specifics (Oatley & Arnott, 1998). Monogamous pairs forage alongside other species for food, water, shelter and nesting material, but each of their core territories (~ 1.2 ha) are actively defended (Oatley, 1970a, b; Clancey, 1982; Oatley & Arnott, 1998; Tarboton, 2011). Suitable rot-holes are lined by the female with vegetable matter (*e.g.* dendrite and root systems of local mosses and epiphytic plants) from the forest interior (Oatley & Arnott, 1998; Tarboton, 2011). Nests are built ± 4.9 m off the ground, (1.5 m minimum, 12.5 m maximum - Oatley & Arnott, 1998; Tarboton, 2011), and contain two or three glossy, oval-shaped eggs by the second week, which vary in colour from olive-blues to rich browns (similar to *C. natalensis* - Oatley & Arnott, 1998; Tarboton, 2011). Clutches are incubated for 15-19 days, and nestlings are brooded for an additional six (Tarboton, 2011). During this time, males defend the territory against bird incursions and provision the nest with food (Oatley & Arnott, 1998). In the final phase of nesting, territorial rivalries are often suspended and both sexes foray out for food (Collar, 2005). Parental care continues for up to six weeks, in some instances, terminating when the fledglings develop their post-juvenile moult (Oatley & Arnott, 1998).

In spite of the difficulties associated with locating and monitoring nests (Davies *et al.*, 2011), the breeding success and fecundity of *C. dichroa* have also briefly been assessed (see del Hoyo *et al.*, 2005). Out of 24 monitored clutches, 69 % of the eggs hatched, and 31 % of 12 nests successfully reared fledglings. At a minimum, seven chicks fledged from 12 nests (out of 24 eggs – two per clutch); at a maximum, 11 (from 36 eggs – three per clutch). Clutches that were initiated in December tended to be late replacements of earlier attempts (Oatley & Arnott, 1998). However, no rates of predation or instances of brood parasitism have been quantified for *C. dichroa*, although some reports have indicated a low and uncommon instance of the latter by the Red-Chested Cuckoo, *Cuculus solitarius* (Kuiper & Cherry, 2002; Chittenden, 2007). Interestingly, eggs laid by *C. solitarius* were found to match those of *C. dichroa* perfectly, as-well-as exhibiting "perfect/good" matching to *C. natalensis* and *Cossypha heuglini* (Kuiper & Cherry, 2002). 'Poor/very poor' matching occurred in their most common host – *Cossypha caffra* (Friedmann, 1948; Jensen & Jensen, 1969; Oatley, 1970b), suggesting a high-degree of host-specificity that hitherto remains undescribed and unaccounted for within the forest robin-chat assemblage (Kuiper & Cherry, 2002).

1.4. Isotopes

Chemical elements exhibit natural variances in the number of neutrons they contain (Peterson & Fry, 1987; Inger & Bearhop, 2008), which often destabilises the isotope resulting in its natural decay over time. The predictable degradation of radio-isotopes like ^{40}K, ^{87}Rb, ^{147}Sm, ^{176}Lu, ^{187}Re, ^{190}Pt, and ^{235}U have been extensively used in the field of geochronology to determine the age of rocks (Begemann *et al.,* 2001). This invaluable tool has not only allowed scientists to age the Earth and its many cataclysmic events, but has also provided them with a geological timeframe that has been used to unravel the evolutionary history of life and subsequent extinction-speciation filtering events (Begemann *et al.,* 2001; Bowie *et al.,* 2006). But, while historical biogeography can be used to predict the outcome potential of species loss in the current biome crisis, detailed studies on present day scenarios are needed to monitor and mitigate possible adverse effects (Bender *et al.,* 1998; Myers *et al.,* 2000; Carignan & Villard, 2002; Fischer & Lindenmayer, 2007).

Unlike the comparatively rapid decay of radiogenic isotopes, stable isotopes (of lighter elements - Inger & Bearhop, 2008) continue to persist and can be accurately measured in natural systems as parts per thousand (‰). A number of stable isotopes have been linked to biologically important elements, like Hydrogen, Carbon, Nitrogen, Oxygen, and Sulphur, which all contribute significantly (in one way or another) to the natural flow and ebb of resources in an ecosystem over time (Peterson & Fry, 1987; Boutton, 1991; Hobson, 1999; Fry, 2006; Craine *et al.,* 2009). Globally, between 14 terrestrial biomes (Olsen *et al.,* 2001; Hoekstra *et al.,* 2005), 810 ecoregions support an astronomical amount of biodiversity that varies spatially and temporally with the fundamental biogeochemical processes that govern them (Peterson & Fry, 1987; Hansen *et al.,* 1988; Hobson, 1999; Craine *et al.,* 2009). In different regions, that may vary spatially and temporally, distinct ‘isoscapes’ (with unique stable isotope signatures for H, C, N, and O) can be created depending on the underlying geology, landscape topography, soil and terrain, local disparities in meteorological events, and biogeochemical pathways, (Peterson & Fry, 1987; Sealy *et al.,* 1987; Hobson, 1999; Dawson *et al.,* 2002; Hobson, 2005; Fry, 2006; Craine *et al.,* 2009; Reichlin *et al.,* 2010).

1.4.1. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes in feathers

In avian biology, dermal condensations stem from feather placodes beneath the epidermis and initiate a proteinaceous growth of beta-keratins that produce the strong, yet light-weight feathers characteristic of the class Aves (Prum, 1999; Hill & McGraw, 2006). Once differentiation of the central shaft has begun, metabolites within the body are sequestered into two vanes of opposing barbs that develop along the rachis at regular intervals. During formation, the deposition of ^{13}C and ^{15}N fluctuates in accordance with dietary constituents and geographic location, remaining fixed and inert in the feather after growth (Hobson *et al.,* 1993; Bearhop *et al.,* 2002; Bearhop *et al.,* 2004; Inger & Bearhop, 2008). As a reflection of the environmental conditions at the time of formation, feathers are often employed as intrinsic spatial and temporal markers for assessing dietary niche-width, landscape utilisation, migratory movements and dispersal (Sealy *et al.,* 1987; Chamberlain *et al.,* 1997; Hobson & Wassenaar, 1997; Marra *et al.,* 1998; Hobson, 1999; Bearhop *et al.,* 2004; Reichlin *et al.,* 2010).

The majority of natural components between marine and terrestrial systems exhibit isotopic ranges from 0 ‰ to -40 ‰ for δ^{13}C (Boutton, 1991; Kelly, 2000), and -20 ‰ to +45 ‰ for δ^{15}N (Peterson & Fry, 1987). Terrestrial plants produce distinct ^{13}C signatures that differ between photosynthetic pathways (C_3, C_4, and Crassulacean Acid Metabolism) and ^{15}N signatures that range quite broadly from -8 to +18 ‰ (Schoeninger & DeNiro, 1984; Sealy *et al.,* 1987). Under the basic premise, 'you are what you eat', the isotopic signatures of consumers and producers can be used to track and monitor the transfer dynamics of energy within and between food webs, providing valuable insights into the foraging ecology of marine and terrestrial species (DeNiro & Epstein, 1978, 1981; Schoeninger & DeNiro, 1984; Ambrose & DeNiro, 1986; Hobson & Clark, 1992; Thompson *et al.,* 1995; Hobson, 1999; Kelly, 2000; Bearhop *et al.,* 2002; Bearhop *et al.,* 2004).

1.4.2. Forest perspectives in South Africa

In the high altitude forests of South Africa, the photosynthetic pathways of primary producers are mostly C_3-based and produce ^{13}C-depleted signatures around -29.5 ± 1.9 ‰ (Symes & Woodborne, 2009) due, primarily, to the enzymatic reactions associated with Ribulose-1,5-biphosphate carboxylase/oxygenase (Peterson & Fry, 1987; Kelly, 2000). Within the landscape matrix, however, these forest fragments are often interspersed with C_4-dominated grasslands and savanna (-12.0 ± 0.6 ‰ ^{13}C – Symes & Woodborne, 2009), producing distinctly unique signatures in the feathers of birds that utilise them (Craine *et al.*, 2009). As carbon isotopes have a tendency to be enriched by 1 ‰ relative to a consumers' diet (Peterson & Fry, 1987; Kelly, 2000; Symes & Woodborne, 2009), these signatures can often be traced back through the food web to the photosynthetic pathways (C_3, C_4, and CAM) in which they were assimilated (DeNiro, 1978; Peterson & Fry, 1987; Kelly, 2000).

Like carbon, nitrogen isotopes enter the system at the base of the food chain through primary producers and their nitrogen-fixing symbionts (DeNiro, 1981; Peterson & Fry, 1987; Ambrose, 1991; Craine *et al.*, 2009). The main sources derive from atmospheric nitrogen (N_2), as-well-as inorganic ammonium (NH_4^+) and nitrates (NO_3^-) in the soil (DeNiro, 1981; Peterson & Fry, 1987; Craine *et al.*, 2009). Various forms are assimilated by plants and passed on to herbivores, frugivores and granivores, before being incorporated into the body tissues of insectivores and carnivores in a step-wise shift that gains 3 - 5 ‰ ^{15}N-enrichment (depending on diet-tissue fractionation) with each trophic level (Schoeninger & DeNiro, 1984; Sealy *et al.*, 1987; Ambrose, 1991; Kelly, 2000; Symes & Woodborne, 2009). As the cool, moist conditions of the forest interior promote the fixation and mineralisation of nitrogen, the high biomass and longevity of forest flora produce comparatively ^{15}N-depleted signatures below 10 ‰ (Ambrose, 1991).

1.5. Aims and objectives

This study aims to investigate the potential utilisation of $\delta^{13}C$ and $\delta^{15}N$ in determining the altitudinal movements of Choristers between inland forest fragments along the eastern escarpment of South Africa and their coastal forest counterparts. As adults undergo a complete post-nuptial moult in February (Oatley, 1959; Craig, 1983), in theory, the isotopic signatures obtained from their feathers could each provide a snap-shot in time for individual birds at the foreclosure of the breeding season. Although these signatures cannot be linked to specific geographic locations, by identifying the ^{13}C and ^{15}N values that deviate significantly from those expected of high-altitude forests, it may be possible to pinpoint individuals that may have remained at the coast during the previous summer.

In accordance with the literature, Choristers signatures from high-altitude forests are expected to reflect carbon isotope signatures consistent with a C_3-based diet (-31.4 ‰ to -27.6 ‰) + 1 ‰ for each trophic enrichment (Symes & Woodborne, 2009), resulting in a range of 3.8 ‰ from -29.4 ‰ to -25.6 ‰ for ^{13}C. Since effluent and fertiliser runoffs never affect N_2-pools[13], Chorister feathers should exhibit a similar depletion to the forest flora that surrounds them (< 10 ‰ – Ambrose, 1991); unless starvation events occurred (Hobson *et al.,* 1993) or a substantial amount of protein was incorporated into their diet during the time of feather formation (DeNiro & Epstein, 1981; Chamberlain *et al.*, 1997; McCutchan *et al.*, 2003; Symes & Woodborne, 2009). As ^{15}N-enrichment increases with each link in the food chain, the isotopic niche-width and dietary preferences of Choristers within and between populations should be decipherable.

Although ^{15}N signatures cannot be directly associated with specific dietary constituents, they can be used as a proxy for delimiting trophic-level feeding (Bearhop *et al.,* 2004). Choristers that ingested a larger percentage of arthropods during February should exhibit higher ^{15}N-enrichment than those that fed primarily on plant matter. In a study conducted by Symes and Woodborne (2009) in the northern high-altitude forests of South Africa, the ^{15}N from 14 insectivorous bird species were pooled together (6.7 ± 1.1 ‰) alongside five frugivores ones (5.3 ± 1.6 ‰). Since the dietary selections of Choristers fluctuate (preferentially – Oatley, 1970a) between fruit and invertebrate prey, ^{15}N can be expected to fall within the range of 3.9 – 7.8 ‰ in the northern forests of South Africa. As northern forests differ geologically from

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[13] The height above sea level ensures minimal contributions from infiltration and surface runoff; even with localised input from cultivated gardens and orchards, the biomass of forests and their nitrogen-depleted soils ensure that any surplus is rapidly sequestered, which dilutes the pool and negates their effects.

those on the Drakensberg escarpment further south (Symes *et al.,* 2000), these values may not be applicable to Choristers feeding in the forests of KwaZulu-Natal and the southern Cape. Nevertheless, bereft of an established isoscape, it would not be misleading to refer to these values as a rudimentary baseline for Choristers in high-altitude forests (especially as their floral and faunal assemblages are very closely affiliated and relatively homogenous - Hahn, 1994; Symes *et al.,* 2000). In the event of a recapture, the isotopic signatures of the initial feather will replace these values as an isotopic baseline for that particular individual. Recaptured Choristers that maintain and defend the same territory throughout the year are expected to incur minor changes, if any, in isotopic signatures between moults or sampling events.

In addition to distinguishing between photosynthetic pathways (^{13}C: C_3 = -35 ‰ to -20 ‰; C_4 = -14 ‰ to -10 ‰ (Boutton, 1991; Ehleringer, 1991)) and trophic-level feeding, ^{13}C and ^{15}N can be combined to assess the trophic niche-width of Choristers between spatially distinct populations (Bearhop *et al.,* 2004).

It is prudent to note at this juncture, that there is hesitancy in referring to the genus *Cossypha* in many instances (despite the common literary referral to this group as the 'Forest Robin-Chat Assemblage') due to the ambiguity surrounding *Cossypha caffra* - the Cape Robin-Chat. The geographic distribution of this species (SABAP2, 2014), their vocalisations (Ferguson *et al.*, 2002) and genetic make-up (Beresford, 2003), while closely comparable to other members of the genus, exhibit discrepancies, which have caused many to question their status as a forest Robin. In addition to this, preliminary isotopic analyses (Appendix A) indicate that *C. caffra* may be feeding in a trophic niche-width (Bearhop *et al.,* 2004) that is not only inconsistent with other robin-chats in the same area, but also distinctly separate from them.

Chapter 2: Methods and materials

Courtesy of Dr Craig T. Symes (CTS) of the University of Witswatersrand in Johannesburg, (South Africa), 34 archived Chorister feathers made up the bulk (87 %) of the feather samples. Twenty of these were collected in KwaZulu-Natal during 2010 by CTS and Gregory Davies (GBPD - of the Ditsong National Museum of Natural History); and 14 were collected by CTS in the Limpopo Province over 2011-2012. These were supplemented by five Chorister feathers obtained from Choristers in the Eastern Cape during 2012/2013. Ethics clearance for this study was granted by the Zoology and Entomology Department of Rhodes University, Grahamstown, South Africa [ZOOL-08-2012].

2.1. Study sites

As CTS collected the feather samples from Limpopo and KwaZulu-Natal, his publications will form the basis of the descriptions for those sites (see Symes *et al.*, 2000; Symes & Woodborne, 2009; Davies *et al.*, 2011). For each area, the geographic coordinates and altitude above sea level (a.s.l.) are outlined in Appendix B, alongside the number of feather samples obtained. The geographic position of each of the five areas are outlined in Figure 2.

Figure 2: Google Earth satellite imagery of southern Africa, indicating the five study sites (from North to South) in the Soutpansberg (Limpopo), Drakensberg (KZN), and Winterberg (EC) mountain ranges of South Africa.

2.1.1. Limpopo

The high-altitude montane forests of the Soutpansberg Mountain range (23˚05’ S - 22˚25’ S, and 29˚17’ E - 31˚20’ E; *c.* 300 – 1,719 m a.s.l.) – a centre of floral endemism (Geldenhuys, 1992; Hahn, 1994); occur in the north of the Limpopo Province on south-facing slopes within a landscape mosaic of grass- and farmlands (Symes *et al.,* 2000; Google Earth, 2014). Despite the distinct underlying geology of these mountains (which affect soil horizons – De Goude & Brussaard, 2002), the floral and faunal assemblages within them are akin to the high-altitude montane forests further south (Hahn, 1994; Barnes, 1998; Symes *et al.,* 2000).

In the northern-most forests of the Soutpansberg, 14 feathers were collected from Choristers across four forest patches that ranged in altitude from *c.* 696 m to 1201 m a.s.l. (Symes <*pers. comm.*>, 2013). During the breeding season (December) in 2011, two Choristers (1 ♂, 1 ♀) were captured by CTS in a forest patch on the southern border of Entabeni State Forest, to the west of Louis Trichardt (Maluma Boerdery, Appendix B). These forest fragments are separated from a land mosaic of farmlands and homesteads (directly south) by the R524. During the same sampling occasion, four feathers (3 ♂, 1 ♀) were additionally obtained from Choristers in Ridgeways, 33 km away (north of the N1, above Louis Trichardt).

The following winter, between June/July 2012, a further four Choristers (1 ♂, 3 ♀) were caught at Ridgeways - one female was a recapture from the same site in December 2011. Incidentally, this rudimentary timeline was used to anchor the isotopic signatures of the second feather to a month (Dec/Jan), year (2011/2012), and geographic location (Ridgeways). During the same sampling event, a female Chorister was recaptured from the same site in Maluma (+ 1 ♂). The remaining two feathers originated from two separate sites - the Schoemansdal Environmental Education Centre (SEEC), 55 km to the east of Maluma and Louis Trichardt (1 ♀); and Vireers Farm (1 ♀), located in a small forest patch within the farmland mosaic, south of Maluma and the R524. The SEEC is located 1.5 km inside the borders of an extensive forest patch, at the base of the south-facing slopes in the Happy-Rest Nature Reserve, which extends up to *c.* 1,666 m a.s.l. (Google Earth, 2014).

The wing and tail measurements of the Choristers captured in Limpopo are listed in Table 4 (page 36).

2.1.2. KwaZulu-Natal

The majority (90 %) of the feather samples collected by CTS and GBPD in KZN originated from Vernon Crookes Nature Reserve (‘VCNR’: 30˚16’ S, 30˚36’ E; *c.* 250 – 480 m a.s.l.; 1,022 mm annual rainfall – Davies *et al.*, 2011), approximately 13 km inland of Scottburgh (bordering Emahlathini to the west) on the eastern coast (north of the R612) – (Google Earth, 2014). This protected area network contains 2,189 ha of sour grasslands (C_3) interspersed with patches of coastal forest (C_4) - (Bourquin & Sowler, 1980 - as cited in Davies *et al.*, 2011). Over 16 days in June and October 2010, 60 – 156 m of mist-net were used to sample the avifauna of seven forest patches within VCNR (Davies *et al.*, 2011). Over this time (106.6 hours in total), 18 Chorister feathers were obtained (June, *n* = 9 (♂), 2 (♀); October, *n* = 4 (♂), 3 unknown (UK)) from five of the forests patches (*c.* 320 m – 420 m a.s.l.; Appendix B). Once in hand, birds were weighed on a Kern and Sohn EM150-IN electronic pocket balance (to closest 0.1 g), ringed according to de Beer *et al.* (2000) and measured (Davies *et al.*, 2011).

During the winter sampling event in June 2010, three males were caught at the VC camp managers’ office and five were caught at the VC campsite, 400 m away. Two feather samples were also obtained from a male and a female Chorister at the VC waterfall, 1 km east; and another female was captured in a forest patch in the eastern valley (1 km north of the waterfall; 1 km west of Emahlathini, just within the borders of VCNR – Google Earth, 2014). At the start of the breeding season in October 2010, a male from the VC camp managers’ office was recaptured, as were an additional two in the VC campsite (+ 1 UK). The remaining three feathers were obtained from a male in the eastern valley, and two *C. dichroa* x *C. natalensis* hybrids from the eastern valley and a forest patch on the northern border (UK).

In June 2010, two male Choristers were also ringed in the Ngele Forest (30°31’ S, 29°42’ E; *c.* 1275 m a.s.l.), 90 km south-east of VCNR close to the N2 (Google Earth, 2014).

2.1.3. Eastern Cape

Unlike the study sites in VCNR and northern Soutpansberg, Fort Fordyce Nature Reserve (FFNR) occurs within a mesic montane-forest corridor that extends north-east through the Winterberg and Stormberg into the Drakensburg Mountain range (Barker *et al.,* 2013). Although agriculture and human habitation are limited by the high-altitude mountainous terrain, fruit orchards and pastoral farms do occur at the base of the forests on the south-facing slopes.

In August 2012, two feather samples were obtained from Choristers (UK) in an afromontane forest patch in Fort Fordyce Nature Reserve (‘FFNR’, 32° 41' S, 26° 29' E; *c.* 700 - 1150 m a.s.l.), 16 km north-east of Fort Beaufort off the R67 (< 10 km directly east of Blinkwater – Google Earth, 2014; at the base of the Winterberg Mountain Range – Barker *et al.,* 2013). On two separate occasions during May and June (non-breeding season) the following year, two additional Choristers (1 ♀, 1 UK) were ringed and released by AJFKC at Fort Fordyce.

During the June 2013 winter, a feather was also collected by Mark Galpin (MG) from a male Chorister in a forest-thicket (Moneysworth Farm, 33˚37’ S, 26˚41’ E; *c.* 10 – 100 m a.s.l.) along the Kariega River, 5 km inland from the coast (5.5 km NNE of Kenton-on-Sea; 4.5 km WNW of Kasouga – Google Earth, 2014). Despite the drier conditions at the coast and lack of tall forest trees, audio and visual observations (MG) confirmed the presence of Choristers at sea-level throughout the year.

2.2. Sampling

The difficulties associated with monitoring avian fauna are largely due to their high mobility (Morrison, 1986; Carignan & Villard, 2002; Whelan *et al.,* 2008; Solonen & Jokimaki, 2011; Wiltschko & Wiltschko, 2009; Wenny *et al.,* 2011). Point counts and line transects provide broad pattern-scale approaches to avian dynamics that are often too coarse for detecting seasonal disparities within and between specific populations (Thompson, 2002; Solonen & Jokimaki, 2011). While the detailed itineraries from radio and satellite tracking yield spectacular daily accounts of individual birds, this method of monitoring is pricey and often reserved for larger species of a higher conservation priority (Hobson, 1999). In lieu of this, to gain the information required, Choristers were captured in mist-nets and a feather sample was obtained from each individual whilst in-hand. As various ornithologists advocate feather sampling as the easiest way of obtaining genetic material with minimal impact on focal individuals (Nur & Geupel, 1993; Bello *et al.* 2001; Smith *et al.* 2003; Harvey *et al.* 2006), this non-destructive method of data collection provided a valuable, cost-effective means of recording detailed measurements across a wide range of forest utilising bird species (Nur & Geupel, 1993; Symes *et al.,* 2000; Bearhop *et al.,* 2002).

2.2.1. Mist-netting and mark-recapture

Depending on accessibility in each of the forest sites, six to eight mist nets (9 x 2.4 m or 12 x 2.4 m, 16 mm mesh, 4 shelf) were assembled on aluminium poles (3 m) along game trails, conjoining one another or spaced at varying distances apart (Figure 3a). Poles were stabilised where necessary with two-pronged guide ropes that were anchored into the ground. To attract birds to the vicinity, feeding party playlists were loaded onto an iPod Nano (3rd generation, 4 GB, 70 mm x 52 mm x 6.6 mm, 49.3 g, Wolfson WM1870 audio processor) and transmitted though portable mini speakers (black ShoX Boom Box, 4 hour battery) situated adjacent to or beneath the nets (Figure 3b). Mealworm-baited clap-traps (Figure 3c) were often interspersed around the site in areas that were clearly visible from overhanging perches. Birds were captured opportunistically throughout the day from 08h00 to 15h00 (depending on the rate of capture), during which time the nets were regularly checked (20 minute intervals) to ensure that any birds caught were not unduly stressed. Under the supervision and tutelage of qualified

SAFRING ringers (Professor Adrian Craig and Professor Pat Hulley of Rhodes University), birds were untangled from the net and placed in a material bag for processing. Uniquely identifiable rings were attached (according to species - de Beer *et al.*, 2000) to the right tarsi using five-holed bird ringing pliers in a procedure that has been shown to have minimal impact on avifaunal species (Nur & Geupel, 1993; Hobson, 1999; de Beer *et al.*, 2000; Symes *et al.*, 2000). In all instances, once the ring was safely secured it was rotated around the tarsus to ensure free movement and unrestricted blood flow. Birds were weighed to the nearest 0.1 g, measured with a stop rule, and assessed for plumage moult on their head, back, body and right wing (Figure 3d). Subsequent to a brood patch inspection, a tail feather was collected and the birds were released on site.

Figure 3: During field work, mist nets (a) and clap traps (c) were deployed along game trails within forest patches, where Choristers were attracted to the nets with portable mini speakers (b), caught, ringed and measured (d).

As isotopic signatures have been shown to vary between feathers of the same individual (Symes & Woodborne, 2011; Bearhop *et al,*. 2012), due to internal diet-tissue fractionation factors and isotopic routing (DeNiro & Epstein, 1978, 1981; Ehleringer, 1991; Hobson & Clark, 1992; Symes *et al.,* 2011), the samples were selected according to the type (inner retrix) collected by CTS in Limpopo and KZN (Symes & Woodborne, 2009; Davies *et al.,* 2011). As the inner most retrices are often moulted early on in the post-nuptial moult, these feathers would be most likely to represent the breeding location of the individual caught (Symes, <*pers. comm.*>, 2015). However, as both of the inner tail feathers form the central melanistic band in the characteristic 'black-orange-black-orange-black' pattern of the *Cossypha* tail, it was deemed ill advised to remove both T6 and T7 (especially during the breeding season when pair formation and territoriality are primary objectives). To ensure minimal disruption to inter- and intra- specific communication (Senar *et al.,* 2003; McGraw, 2005; Hill & McGraw, 2006; Inger & Bearhop, 2008), as-well-as optimal balance in flight (Thompson *et al.,* 2010; McDonald & Griffith, 2011), T5 and T7 were removed from the tail of the Choristers sampled and placed into a dry storage envelope for laboratory analysis (Smith *et al.* 2003; Brown, 2006; Jaspers *et al.*, 2007; Smith *et al.*, 2009; Symes & Woodborne, 2009).

2.2.2. Laboratory work

Feathers were prepared for isotopic analysis in an isolated room with restricted airflow. To prevent cross-contamination, forceps were utilised at all times in the handling of each feather and a methanol spray was used to sterilise implements between samples. Multiple papers advocate the washing of feathers in a 2:1 methanol/chloroform solution (Hobson & Wassenaar 2001; Symes & Woodborne 2009; Symes *et al.,* 2011; Wakelin *et al.* 2011), but without the lipid layer that marine birds naturally produce, a chemical wash may have confounded the isotopic results (Peterson & Fry, 1987). In order to determine the best angle of approach, a simple comparison was undertaken using two retrix feathers from the same bird. The first feather was washed in 2:1 methanol/chloroform solution and allowed to dry at 50^{0}C for 24 hours (Ogden *et al.,* 2004; Szymanski *et al.,* 2006; Symes & Woodborne, 2009; Reichlin *et al.,* 2010; Hill *et al.,* 2012). No visual contaminants were exhibited on the second feather, so preparation was directly from the envelope. The isotopic variance of the two feathers equated to less than what could be expected by the fractionation caused between reactants and products during SIA (*see* Peterson & Fry, 1987). As no obvious differences were exhibited, the methanol/chloroform wash was deemed an unnecessary cost that may have additionally (and unknowingly) influenced the isotopic signatures of terrestrial feathers and each sample was therefore prepared according to the following specifications.

In turn, a feather was placed onto the surface of a sterilised mirror where one side of the vane was cut away from the rachis (at the distal tip), placed into an 8 mm tin capsule (pre-washed in toluene) and weighed out to the nearest decimal place (0.8 – 1.1 mg) on an Ohaus digital micro-balance. These samples were then combusted in an ANCA SL Elemental Analyser (Wakelin *et al.,* 2011; Hill *et al.,* 2012) connected to a SERCON 20-20 isotope ratio mass spectrometer (IRMS) at the IsoEnvironmental Laboratory, Rhodes University (Kaehler <*pers. comm.*>, 2013) to determine the isotopic ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ (Symes & Woodborne, 2009; Wakelin *et al.*, 2011). Stable isotope abundance within each feather was reported in delta (δ) notation as parts-per-thousand (‰) following the equation, δX (‰) = $[(R_{sample}/R_{standard}) - 1] \times 10^3$, where X equates to the element and $R_{sample}/R_{standard}$ to its heavy/light isotope ratios (Peterson & Fry, 1987; Hill *et al.*, 2012). The standard references were relative to Vienna Pee Dee Belemnite (PDB) for $\delta^{13}C$ and atmospheric air for $\delta^{15}N$ (Hobson & Wassenaar 2001, Symes & Woodborne 2009; Hill *et al.,* 2012), calibrated to International Atomic Energy Agency standards (IAEA-N-1), and the analytical precision was 0.08 ‰ and 0.09 ‰ for $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively (Kaehler <*pers. comm.*>, 2013). Feathers were run in two separate batches (n = 36; n = 3) that each contained 96 combustible units of which 29 were in-house standards of beet sugar and ammonium sulphate, and five were certified Casein protein standards (calibrated to IAEA-CH-6 and IAEA-N-1 – Kaehler <*pers. comm.*>, 2013). The remainder of the samples were made up of feathers from marine and terrestrial birds.

2.3. Stable isotope analysis (SIA)

Bivariate plots of $\delta^{13}C$ and $\delta^{15}N$ (± Standard deviation) were initially constructed in Microsoft Excel (2013) to assess the combined isotopic range of *C. dichroa* as a forest-utilising species. These calculations were initially used to infer dietary information for the 39 birds (via trophic niche-widths; Bearhop *et al.*, 2004) and establish an isotopic baseline (mean ± SD ‰) to which sub-sets of the grouped-data could be compared. As feathers were collected over a broad spatial (Limpopo, KwaZulu-Natal and Eastern Cape) and temporal range (four years from 2010 to 2013), these were reflected in the statistical sub-division of the samples across four scales (Appendix C), which vary between the coarse assessments of *Scale 1* (pooled-provincial data), to the finer points of *Scale 4* (per site). Therefore, subsequent to the analysis of the 39 birds as a species, the data were analysed across each scale to investigate whether carbon ($\delta^{13}C$) and/or nitrogen ($\delta^{15}N$) isotopes varied significantly within or between Chorister populations around South Africa.

2.3.1. Assessing significance

Using PAST 3.01 (Hammer & Harper, 2001), a one-way Analysis of Variance (ANOVA) was conducted, separately, on carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values to ascertain whether the isotopic signatures differed significantly between tail feathers from Choristers in each group (as determined by each *Scale* represented in Appendix C). This test assumes that the samples collected from each respective area exhibit equal means, homogenous variance, and a normal distribution curve (Hammer, 2013). In addition to producing an *F*-statistic and *p*-value, this statistical software package subjects the data to further testing to determine whether:

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a) A significant difference in the variance of isotopic signatures exists between Groups.

Two forms of the Levene's test were calculated in this instance. The first indicates homoskedasticity by comparing the means of subsets of data to determine whether variances are equal (an assumption of ANOVA). A significant *p*-value (< 0.05) should illicit the use of the Welch *F*-statistic – a version of ANOVA for unequal variances

(Hammer, 2013). The second version of the test is better suited for use on non-parametric data as it calculates homogeneity of variance from sample medians.

b) Isotopic medians vary significantly between Groups.

Should the data fail the assumptions of an ANOVA, the *F*-statistic and *p*-value reported are no longer viable for assigning significance. In this instance, a Kruskal-Wallis for non-parametric data would be substituted as a reliable surrogate indicator (Hammer & Harper, 2001; Hammer, 2013).

c) Group values for carbon and nitrogen isotopes follow a normal distribution curve.

Should the data fail to meet this assumption (Shapiro-Wilks test, $p < 0.05$), the degree to which it deviates from normality can be determined through the *Normality* tests within the *Univariate* drop-down menu of PAST. In the event of continued failure ($p < 0.05$), parametric tests are substituted for their non-parametric counterparts.

Data should, essentially, satisfy all three of these assumptions ($p > 0.05$) in order to utilise ANOVA as a robust statistical test. However, PAST produces a viable alternative to ANOVA through Kruskal-Wallis, which reliably detects significance in non-parametric data. In the event of either test producing a significant result ($p < 0.05$), the software calculates parametric (Tukey’s Pairwise; Lund & Lund, 1983) and non-parametric (Mann-Whitney Pairwise) *post-hoc* tests to pin-point where the significant difference(s) lie.

To determine the trophic niche-width (Bearhop *et al.*, 2004) of Choristers at each spatial scale (Appendix C), an outer convex hull (CH) and inner standard ellipse (SE) were fitted to the data in R-Studio.

Chapter 3: Isotopic analysis - *Cossypha dichroa*

The isotopic value of Chorister feathers (*n* = 39) ranged from -25.13 ‰ to -20.65 ‰ for $\delta^{13}C$ (mean = -23.60 ± 0.79 ‰ SD), and 6.17 ‰ to 13.52 ‰ for $\delta^{15}N$ (mean = 8.77 ± 1.80 ‰ SD), (Figure 4).

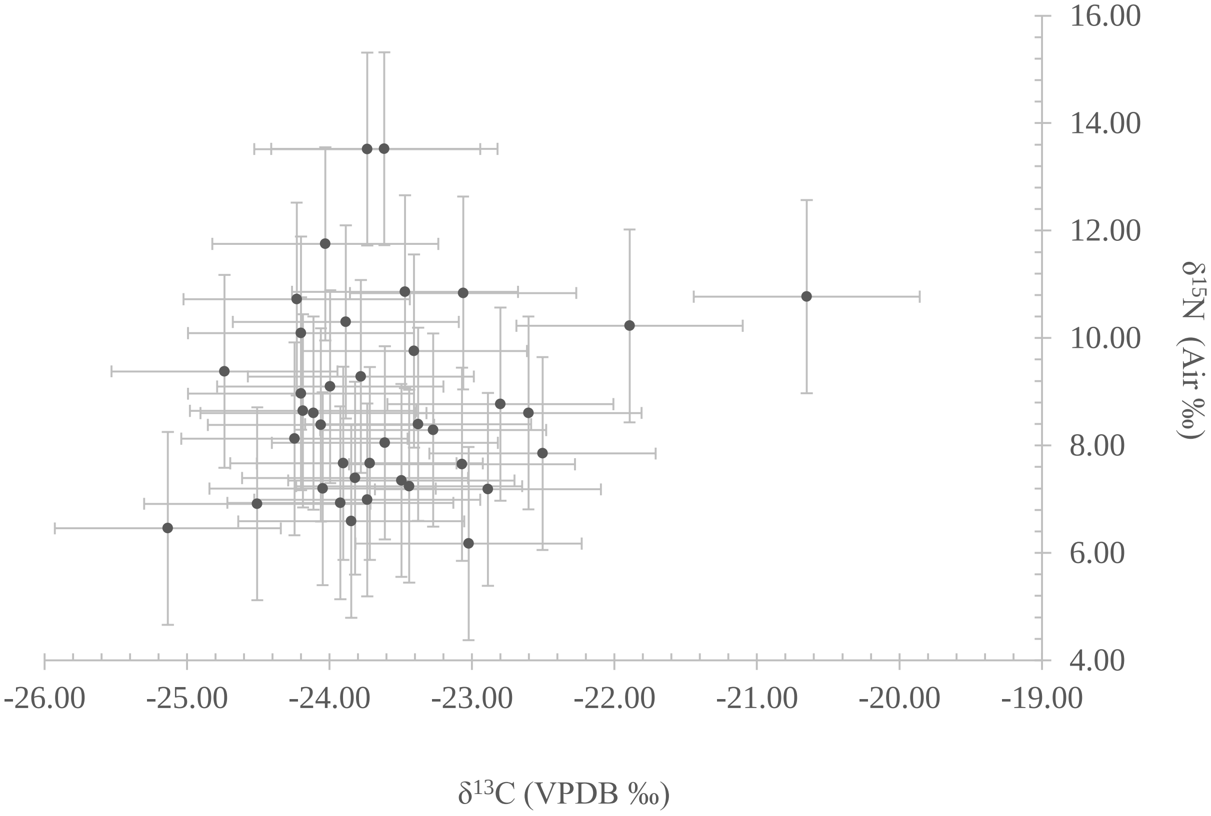

Figure 4: A bivariate plot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signatures from tail feathers of 39 Choristers (*n* = 39; ± SD ‰) sampled across the eastern escarpment and coastal regions of South Africa.

Given the large range of both elements ($\delta^{13}C$ = 4.48 ‰; $\delta^{15}N$ = 7.35 ‰), RStudio was employed as an investigative tool to highlight core areas within the sample where the majority of signatures were clustered. Through R, an outer 'convex hull' (CH) and inner 'standard ellipse' (SE) were fitted to the data (Figure 5), creating a generalised isotopic niche-width for the 39 birds between -22.8 ‰ and -24.3 ‰ for $\delta^{13}C$ [14] (VPDB ‰; range = 1.5 ‰), and 6.9 ‰ to 10.7 ‰ for $\delta^{15}N$ (Air ‰; range = 3.8 ‰).

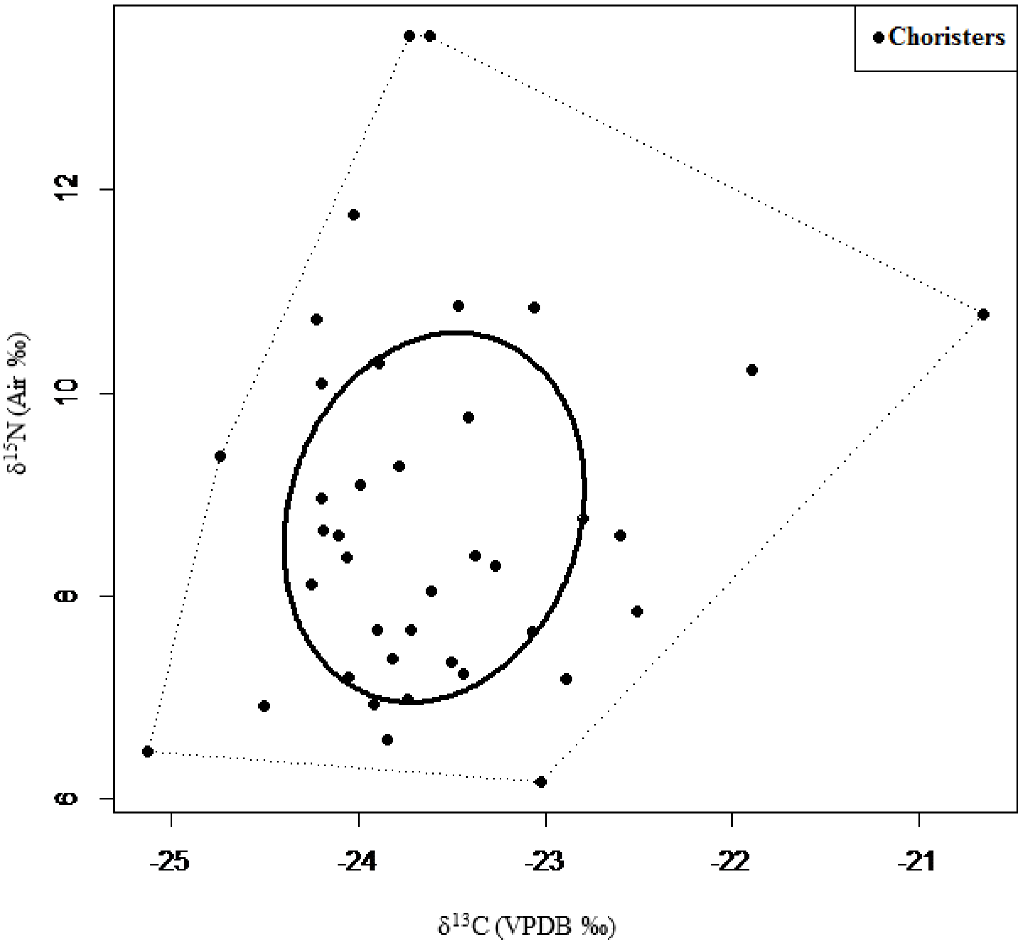

Figure 5: RStudio bivariate plot of the isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of 39 Chorister feathers. An outer Convex Hull (dotted line) and inner Standard Ellipse (solid line) were fitted to the data.

Of the 39 samples collected, 22 (56%) originated from male Choristers (15 from KZN; six from Limpopo; one from the EC), and 11 (28%) from females (two from KZN; eight from L; one from EC). The remaining six samples were taken from unsexed individuals[15] (15%); two of which were *C. haagneri* hybrids from KZN.

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[14] Consistent with a C_3-based diet (Symes & Woodborne, 2009)

[15] Choristers do not exhibit sexually dimorphic traits. Size has often been alluded to as a possible discrepancy between genders (with males attaining a larger body size and weight compared to females – Oatley, 1998), but these parameters remain largely undifferentiated and subject to change between individuals depending on geographic location.

Irrespective of the statistical bias associated with uneven samples (♂ *n* = 22; ♀ *n* = 9) over wide geographic areas (L, KZN, or EC), a graphical representation of the dietary niche-width for male (mean $\delta^{13}C$ = -23.62 ‰; mean $\delta^{15}N$ = 9.07 ‰) and female (mean $\delta^{13}C$ = -23.63 ‰; mean $\delta^{15}N$ = 7.79 ‰) Choristers illustrated a reliance, of both genders, on the same environmental resources (Figure 6).

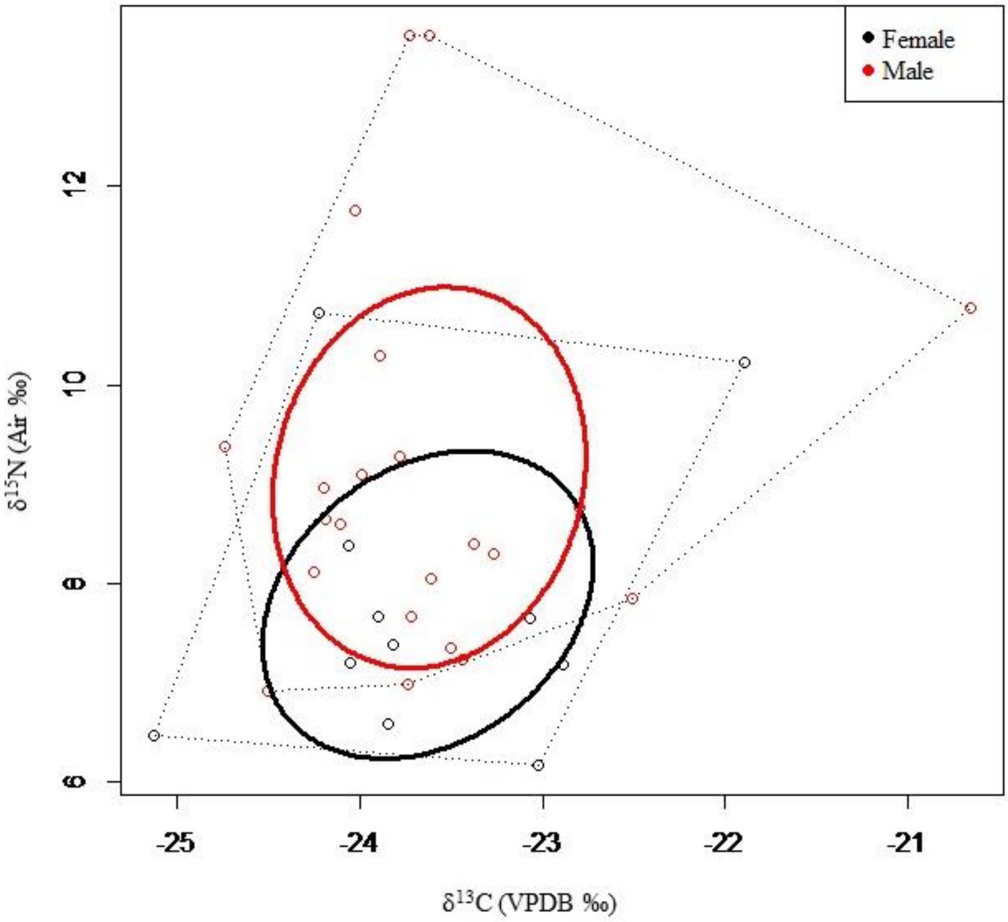

Figure 6: Bivariate plot of carbon and nitrogen isotope signatures illustrating the trophic niche-width of male (*n* = 22) and female (*n* = 9) Choristers around South Africa.

Despite the slight disparity of SE's in Figure 6, the lower trophic level ($\delta^{15}N$) of female birds (in this instance) appears to be an artefact of the area where they originated, as 73 % of the samples were collected in the Limpopo Province (*Scale 1* – Appendix C) where *C. d. mimica* purportedly occurs (*see* Table 4, page 48).

3.1. Scale 1 – Provincial divides

The strong affinity of Choristers to afromontane forest allows for the assumption that this endemic species occurs at high altitudes where climatic conditions have allowed for the proliferation of large tracts of forested areas over time. As some suitably habitable areas may allow individuals of any one generation to flourish while, inadvertently, suppressing the annual recruitment of the next (a default state that induces a population sink – Du Plessis, 1994), the ability to reproduce is a heavily-weighted requirement. Therefore (in accordance with the governmental designation of provincial boundaries), habitable areas containing viable breeding grounds occur predominantly, from North-to-South, within the afromontane forests of the Limpopo (‘L’), KwaZulu-Natal (‘KZN’), and Eastern Cape (‘EC’) Provinces of South Africa (Figure 1, page 15). The latitudinal gradient across which these regions naturally span firmly establishes ‘Province’ - by default - as the largest group component of the four spatial scales (*Scale 1* – Appendix C, *n* = 39).

Statistical analyses are initially reported per province for carbon and nitrogen isotopes as minimum and maximum values. As smaller sample sizes (e.g. *n* = 5 for EC[16]) inevitably increase the risk of a Type I error (which may cause a ‘false’ or premature acceptance of the null hypothesis), additional information is provided pertaining to the size of the samples and their isotopic range. While smaller (isotope) ranges have a tendency to indicate localised movement, if any, of Choristers within populations (or between sub-populations of the same greater-area), this does imply that larger isotope ‘*variances*’ potentially indicate interactions on a larger scale where individuals move between regional or provincial populations – a standpoint that should be approached with due caution when interpreting isotopic data from an uncontrolled open system.

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[16] On statistical odds alone, these five EC samples stand a good chance of overlapping with the 20 samples from KZN, which would be an artefact of sample size rather than a true reflection of the isotopic-picture of Choristers in each province. This “artefact” is of paramount importance when dealing with vagile species, which possess the capacity to move within and between forest patches.

3.1.1. Limpopo

Choristers sampled within the Limpopo province (*n* = 14) ranged from -25.13 ‰ to -21.89 ‰ (Mean = -23.69 ± 0.77 ‰ SD; range = 3.24 ‰) for carbon isotope signatures ($\delta^{13}C$), and 6.17 ‰ to 10.23 ‰ (Mean = 7.43 ± 1.04 ‰ SD; range = 4.06 ‰) for nitrogen isotope signatures ($\delta^{15}N$), (Figure 7).

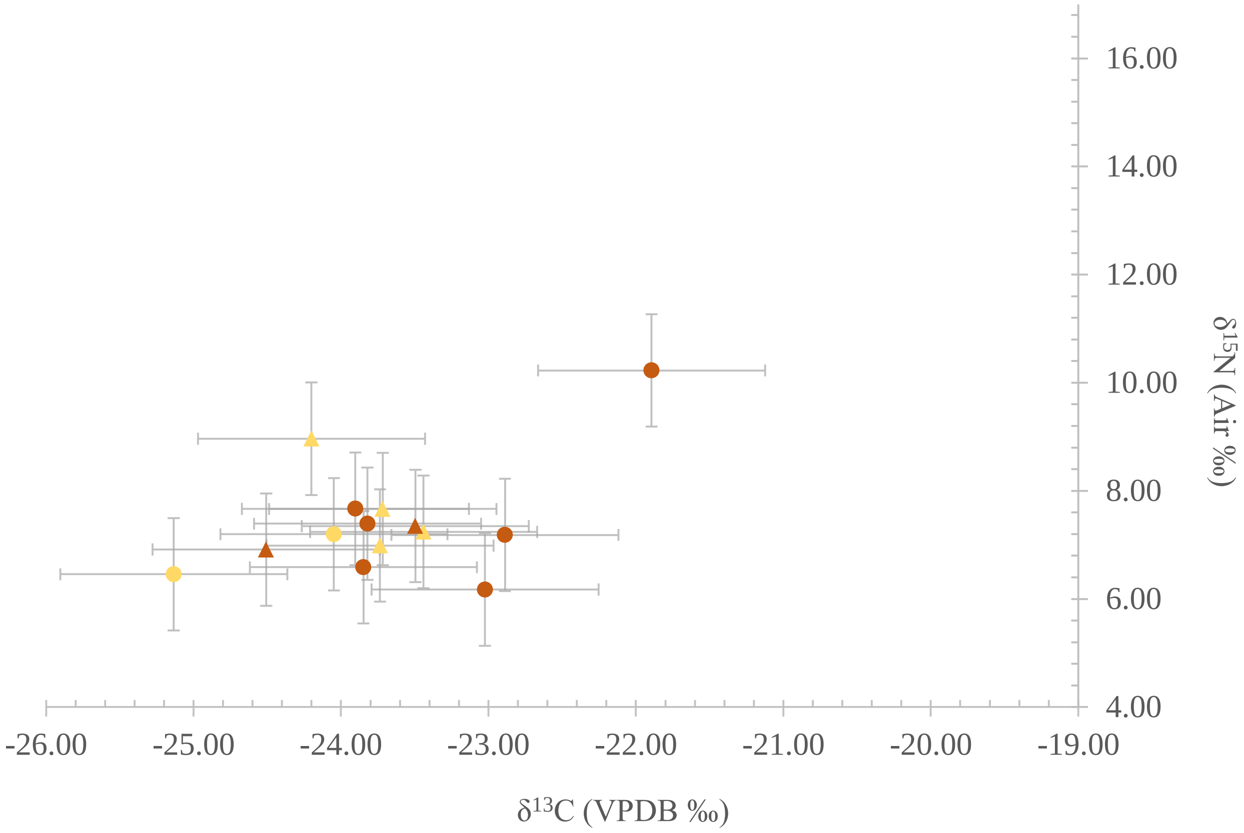

Figure 7: Bivariate plot of isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) from tail feathers of *C. dichroa* collected in the Limpopo Province of South Africa (± SD ‰). Data points denote gender where male and female birds are depicted as triangular and circular data points, respectively. Feathers collected during the breeding (Oct – Jan) and non-breeding (Mar – Aug) seasons are brown and yellow, respectively.

3.1.2. KwaZulu-Natal

Choristers sampled within KZN (*n* = 20) ranged from -24.74 ‰ to -22.51 ‰ (mean = -23.73 ± 0.54 ‰ SD; range = 2.23 ‰) for ^{13}C, and 6.93 ‰ to 13.52 ‰ (mean = 9.57 ± 1.82 ‰ SD; range = 6.59 ‰) for ^{15}N (Figure 8).

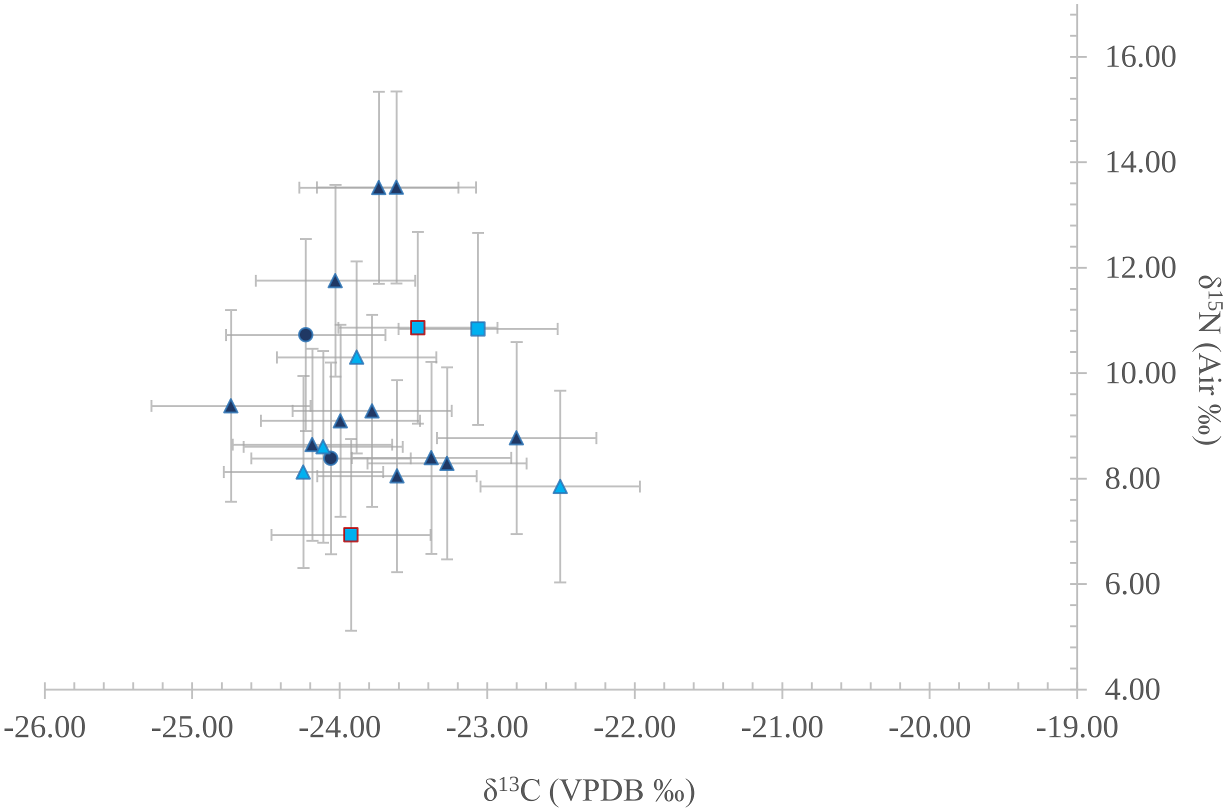

Figure 8: Bivariate plot of δ^{13}C and δ^{15}N from tail feathers of *C. dichroa* collected in the KwaZulu-Natal Province of South Africa (± SD ‰). Data points denote gender where male and female birds are represented by triangular and circular data points, respectively, with squares symbolising 'unknown'. Samples collected during the breeding (Oct – Jan) and non-breeding (Mar – Aug) seasons are dark-blue and light-blue, respectively. Data points outlined in red indicated hybrid birds (*C. dichroa* x *C. natalensis*).

3.1.3. *Eastern Cape*

Isotopes sampled within EC (*n* = 5) ranged from -24.20 ‰ to -20.65 ‰ for ^{13}C (mean = -22.79 ± 1.33 ‰ SD; range = 3.55 ‰), and from 7.65 ‰ to 10.77 ‰ for ^{15}N (mean = 9.37 ± 1.24 ‰ SD; range = 3.12 ‰), (Figure 9).

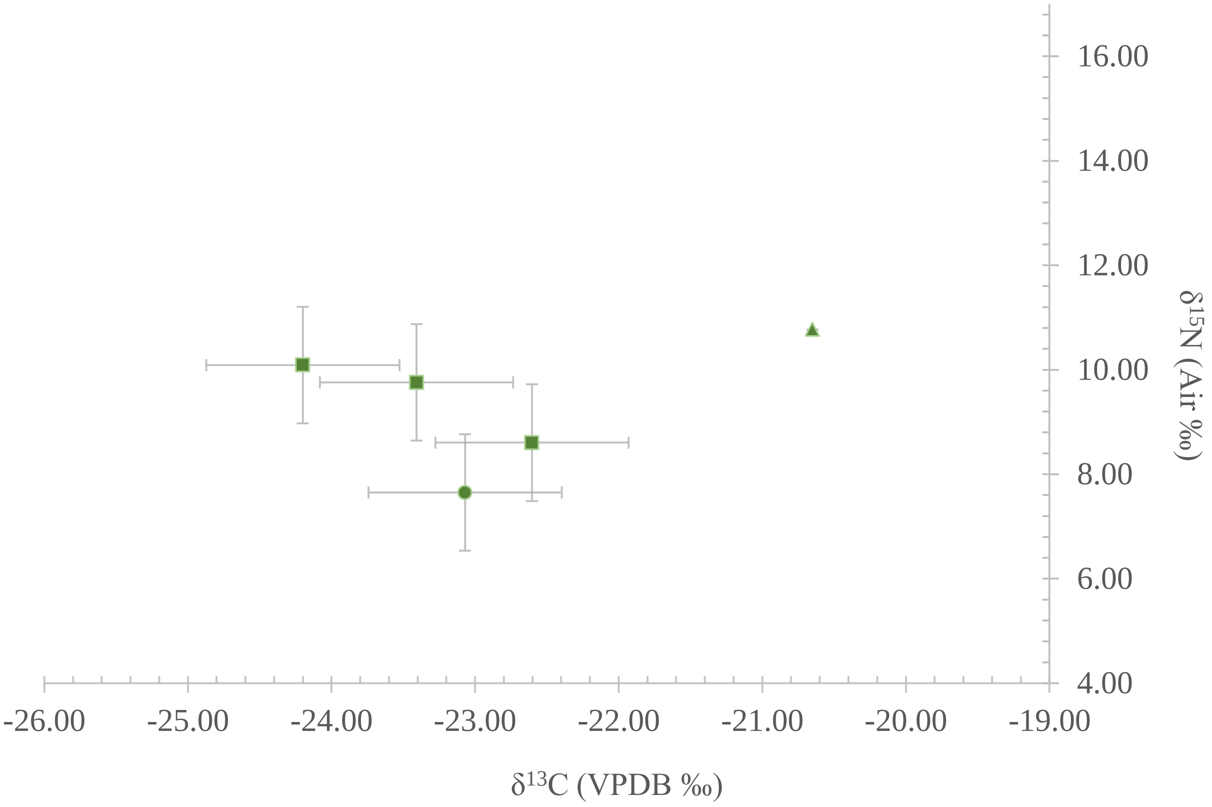

Figure 9: Bivariate plot of isotopic signatures (δ^{13}C and δ^{15}N) from tail feathers of *C. dichroa* collected in the Eastern Cape Province of South Africa (± SD ‰). Data points denote gender where male and female birds are depicted as triangular and circular data points, respectively. Squares symbolise unknown gender 'UK'. All of the samples were collected during the non-breeding season (Mar – Aug).

In 2011, Davies and his colleagues reported a significant difference in the range of wing length (female = 95 – 100 mm [97.6 average]; male = 97 – 105 mm [101.2 average]), and tail measurements (female = 81 – 87 mm [84.7 average]; male = 84 – 92 mm [88.8 average]) of male (*n* = 6) and female (*n* = 7) Choristers in KZN. Based on the wing measurements provided, two of the unsexed Choristers caught in EC are suspected males (103 mm and 105 mm, respectively), but neither bird could be incorporated into the 'male' category until further investigation determines whether the aforementioned dimensions for KZN Choristers can be applied, between sexes, to geo-spatially distinct populations.

3.1.4. Carbon isotope signatures – $\delta^{13}C$

Carbon isotopes were normally distributed in each of the three provinces ($p > 0.05$), with homogenous variance across Provincial means ($p = 0.12$) and medians ($p = 0.23$). Having met the aforementioned assumptions of this test, a one-way ANOVA was used in conjunction with Tukey's *post-hoc* test to determine significance between groups.

Table 1: Stable carbon isotope values (Mean ± SD ‰) of tail feathers collected from *C. dichroa* and the results of a one-way ANOVA for differences in carbon isotope signatures between provinces. *Superscript lettering* denotes the level of significance (Tukey's Pairwise *post-hoc*) where common letters share similar isotopic signatures.

Location	Province	*n*	$\delta^{13}C$ (‰)
South Africa	Limpopo	14	-23.69 ± 0.77^{a}
South Africa	KwaZulu-Natal	20	-23.73 ± 0.54^{a}
South Africa	Eastern Cape	5	-22.79 ± 1.33^{b}
		ANOVA	$F = 3.376$ $p = 0.0467$

A significant difference ($F = 3.367$, $p = 0.0467$) was detected stemming, primarily, from the Eastern Cape Province ($n = 5$) of South Africa (Table 1, page 43), which is of particular interest when considering the sample size (*see* Footnote 16, page 39). Assuming that all Choristers exhibit a similar preference for dietary items (fruit and arthropods), the five carbon signatures (representative of birds in the Eastern Cape) would be expected to overlap, to some degree, with the 34 combined ^{13}C values from birds in KwaZulu-Natal and Limpopo. At this conjuncture, it is important to investigate any possible adverse effects of individual birds within the sample (*n* = 39) exhibiting a carbon signature that differs strikingly from the sample mean(s) and/or median(s) - as small samples, in particular, are highly susceptible to the influence of outliers. To pinpoint anomalies within the dataset, carbon isotopes were plotted against themselves on the *x*-axis and *y*-axis (*n* = 39; Figure 10) to graphically illustrate the range of ^{13}C exhibited by members of *C. dichroa* within South Africa.

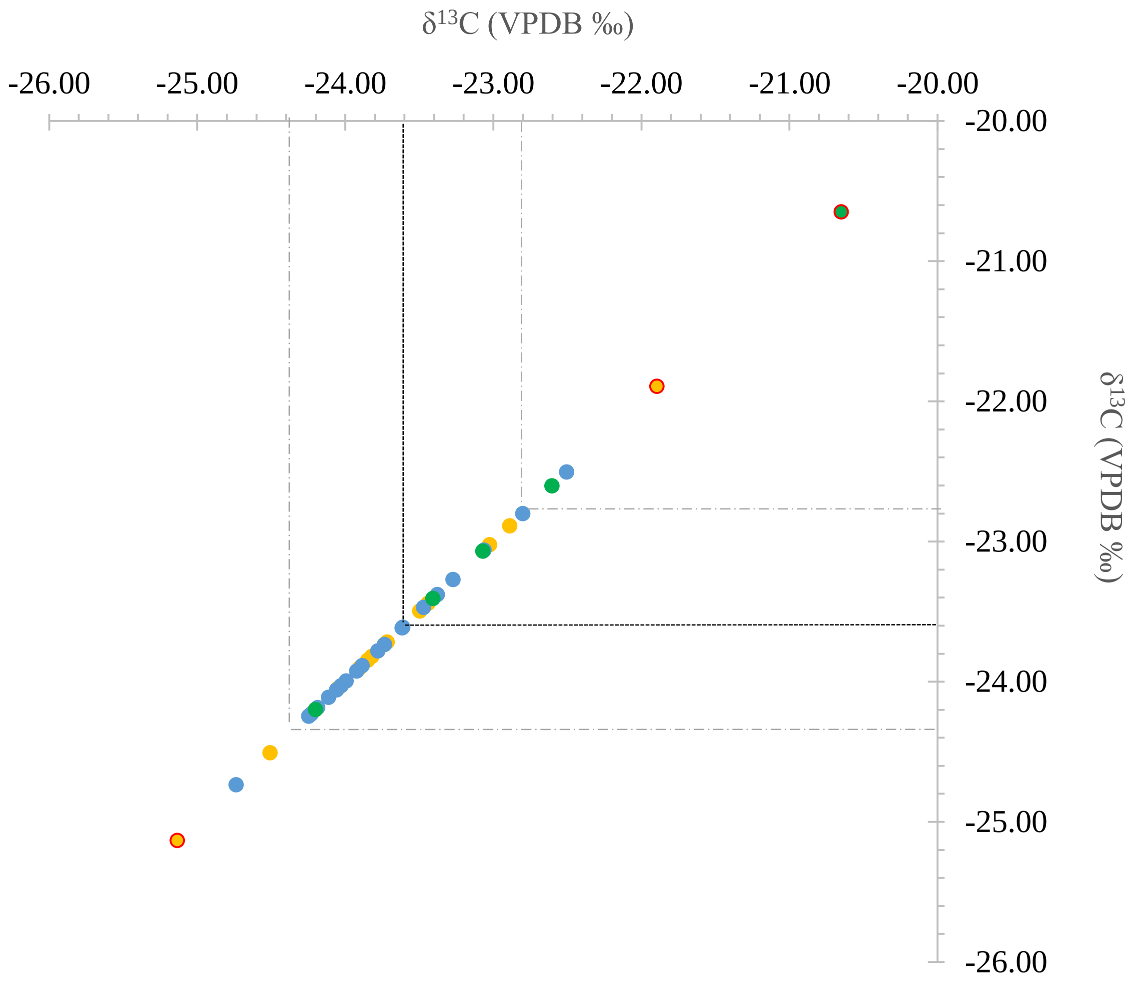

Figure 10: Univariate plot of $\delta^{13}C$ ‰ illustrating a general trend for *C. dichroa* (*n* = 39) around the sample mean (-23.60 ‰; black dashed line) ± SD (0.79 ‰; grey dashed lines). Samples obtained from each province (L, KZN and EC) are yellow, blue and green, respectively. Red-bordered data points indicate potentially confounding outliers.

The provincially-interspersed carbon values suggest that Choristers consume dietary constituents of a similar carbon-base (in a C_3 system), irrespective of population and/or geographic location. However, it must be noted that in the absence of isotopes reflecting a food base, this is speculative. Three individuals (represented by the red-bordered data points in Figure 10) appear to be supplementing, or possibly even replacing, components of their diet with prey or food items well-beyond the δ^{13}C-range of conspecifics (mean = -23.6 ‰ ± 0.79 SD). Particular attention is drawn to the anomalous signature (-20.65 ‰) in the upper right-hand corner, which was obtained from a Chorister in a coastal forest (*c.* 89 m a.s.l.) near Kenton-on-Sea (Figure 2, Appendix B). In this instance, the feather (one of five representing EC) was 1.24 ‰ more ^{13}C-enriched than the next sequential value from Limpopo (-21.89 ‰). Considering the aforementioned effect of an anomalous value within a data set pertaining to very few individuals (especially at the scale represented), the statistics were repeated with the Kenton outlier omitted from the EC data set ($F = 0.61$, $p = 0.51$; Table 2).

Table 2: Carbon isotope signatures (mean ± SD ‰) of *C. dichroa*, excluding the anomalous outlier from Kenton. *Superscript lettering* denotes the level of significance with common letters sharing similar isotopic values.

Location	Province	*n*	δ^{13}C (‰)
South Africa	Limpopo	14	-23.69 ± 0.77^{a}
South Africa	KwaZulu-Natal	20	-23.73 ± 0.54^{a}
South Africa	Eastern Cape	4	-23.32 ± 0.67^{a}
		ANOVA	$F = 0.61$ $p = 0.51$

Excluding the coastal outlier contributed to the absence of any significant difference ($p > 0.05$) between groups, as the elimination decreased the mean of EC (*Scale 1*) from -22.79 ‰ ± 1.33 ‰ ($n = 5$) to -23.32 ± 0.67 ‰. As the only sample available from the Kenton area, this individual was excluded from subsequent analyses of ^{13}C, irrespective of *Scale*. It is prudent to note, however, that the four remaining Chorister samples all originate from the high-altitude forests (*c.* 1117 m a.s.l.) of Fort Fordyce (Appendix B), and should be viewed with caution when making inferences at a provincial scale.

3.1.5. *Nitrogen isotopes – $\delta^{13}N$*

Nitrogen isotope signatures were homogenous in their variance across sample means ($p = 0.06$) and medians ($p = 0.19$), but failed to satisfy the normality assumption (Shapiro-Wilk $W = 0.92$, $p = 0.01$) of ANOVA. A significant difference was detected in the Limpopo Province ($n = 14$) of South Africa (Table 3), where *Bonferroni-corrected p*-values (within the Mann-Whitney *post-hoc*), were used (as a conservative measure) to assign significance.

Table 3: Stable nitrogen isotope values (mean ± SD ‰) of tail feathers collected from *C. dichroa* and the results of a Kruskal-Wallis test for differences in ^{15}N between Provinces. *Superscript lettering* denotes the level of significance ($p < 0.05$, Mann-Whitney *post-hoc*) where common letters share similar signatures.

Location	Province	*n*	$\delta^{15}N$ (‰)
South Africa	Limpopo	14	7.43 ± 1.04 ^{a}
South Africa	KwaZulu-Natal	20	9.56 ± 1.82 ^{b}
South Africa	Eastern Cape	5	9.37 ± 1.24 ^{b}
		KRUSKAL-WALLIS	$H = 15.85$ $p = 0.0004$

Conspecifics from KZN and EC appear to exploit resources at a similar trophic level ($U = 49.5$, $p = 1$) within the forest patches sampled, as the mean for each area deviates around 9.45 ‰ (but this may be an artefact of sample size as $n = 5$ for EC). Unlike the southern provinces, Choristers foraged consistently lower on the trophic scale in the Soutpansberg, deviating around 7.43 ‰ for ^{15}N (Figure 11).

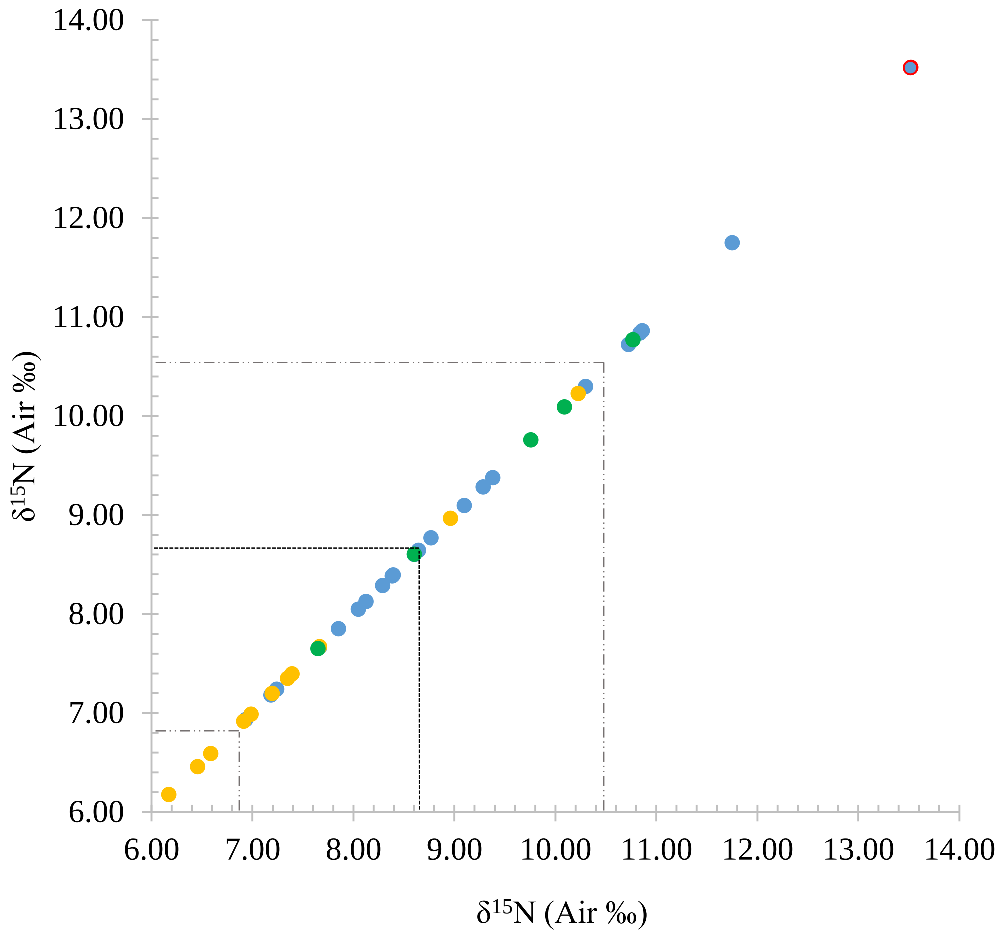

Figure 11: Univariate plot of nitrogen isotope signatures ($\delta^{15}N$ ‰) illustrating a general trend for *C. dichroa* (*n* = 39) around the sample mean (8.77 ‰; black dashed line) ± SD (1.80 ‰; grey dashed lines). Samples obtained for each province (L, KZN and EC) are yellow, blue and green, respectively. Red-bordered data points indicate potentially confounding outliers.

As feathers from the Limpopo differed significantly from those collected further south (EC[17], $U = 8$, $p = 0.04$; KZN, $U = 31$, $p = 0.0004$), it seems plausible that the northern-most populations subsided on a higher proportion of fruit (as described in section 1.3.1.) than their southern counterparts. In lieu of the size discrepancies between the two subspecies (outlined by Clancey, 1982; *see* Table 4), *C. d. dichroa* - in the south - may be able to consume food of a larger diameter than *C. d. mimica* in the north (as reported by Oatley, 1970a), which could potentially contribute to the consistently lower $\delta^{15}N$ signatures from Limpopo compared to their counterparts in KwaZulu-Natal and the Eastern Cape.

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[17] As there were no influential outliers for $\delta^{15}N$ (‰), *n* = 5.

Table 4: The wing and tail measurements (mm) of *C. d. dichroa* and *C. d. mimica* described by Clancey in 1982 compared to the wing and tail measurements obtained for Choristers in the Limpopo and KwaZulu-Natal Provinces of South Africa.

		Wing (mm)				Tail (mm)			
		n	Range	Mean	SD	*n*	Range	Mean	SD
Reported by Clancey in 1982	*Cossypha dichroa*								
	mimica								
	♂	13	95 - 100	98.2	1.38	13	75 - 80	77.5	1.73
	♀	2	91, 95	93	2.83	2	74, 74.5	74.2	0.35
	dichroa								
	♂	15	101 - 107	102.8	1.87	16	82.5 - 89.5	86.2	2.61
	♀	12	95 - 101	98.12	2.07	12	80 - 84	82	1.23
	Cossypha dichroa								
	Limpopo								
	♂	6	98 - 105	101	2.73	6	84 - 89	87	1.83
	♀	8	92 - 99	96	2.07	8	79 - 84	82	2.07
	KwaZulu-Natal								
	♂	15	95 - 110	100	4.18	15	81 - 96	87	4.05
	♀	2	98, 101	100	2.12	2	86, 92	89	4.24

The wing and tail lengths of male Choristers from L and KZN did not differ from one another ($p > 0.05$). Although males from KZN exceeded the upper limit of the size-range for Choristers in Limpopo (by 5 mm on the wing and 7 mm on the tail), none of the birds met with the sizes described by Clancey (1982) for *C. d. mimica* in the north. The same can be said for females; even though these individuals differed significantly from one another in wing ($t = 2.36$, $p = 0.046$) and tail lengths ($t = 3.81$, $p = 0.005$). Therefore, despite the inclination to report this trophic segregation as a physiological consequence of body size, it may be prudent to shy away from such inferences as dietary shifts may be obligatory (in response to natural environmental conditions) rather than facultative. Nevertheless, the potential ramifications of a smaller body size should not be overlooked, as size discrepancies reportedly prompted the initial division of *Cossypha dichroa* into *C. d. mimica* in the north and *C. d. dichroa* in the south of South Africa (Clancey, 1982; Oatley & Arnott, 1998; Clements, 2007).

When ranked (

Appendix **D**), seven of the top ten signatures (which were all above 10 ‰ for $\delta^{15}N$) originated from KZN - four of the top five from Choristers within the campsite itself; the fifth from a hybrid of *C. dichroa* x *C. natalensis*. The top two anomalies (13.52 ‰ in Figure 11, page 47) are 3.95 ‰ more enriched than the upper limit of the group mean + SD (9.57 ‰), which may be due to seasonal fluctuations in tourism (camping in particular), as the more protein and animal tissues consumed, the more enriched the feather becomes (Peterson & Fry, 1987; Kelly, 2000; Bearhop *et al.*, 2004; Symes & Woodborne, 2009). Choristers may therefore be scavenging from the discarded bones and left-overs of campers in and around the campsite - behaviour that is readily observed in *C. caffra <pers. obs.>*, a robin-chat that has also been shown to favour dairy products like cheese, butter and egg yolk (Oatley, 1970a). The comparatively $\delta^{15}N$-enriched values of Choristers could also implicate natural dietary shifts that may or may not be linked to movement on a local or regional scale. As true forest birds, Choristers tend to avoid open dry ecotones and rarely stray far from the forest edge. Nevertheless, depending on the availability of resources (like food, water and shelter - Oatley, 1970a), low rainfall and cold temperature extremes may decrease the carrying capacity of some forested areas, especially in winter, forcing some individuals to either exploit dietary constituents from a different nitrogenous base (within the same vicinity), or seek refuge elsewhere.

The sample from Kenton yielded similarly high values for isotopic nitrogen (10.77 ‰), which is more consistent with open, dry terrestrial habitats (Ambrose, 1991); but as the only potential representative sample for coastal forest thicket, this abnormality can only be noted.

3.1.6. *Isotopic niche width - $\delta^{13}C$ ‰ and $\delta^{15}N$ ‰*

A bivariate plot of $\delta^{13}C$ and $\delta^{15}N$ (Figure 12) illustrates the isotopic values and potential trophic niche-width (Bearhop *et al.*, 2004) of Choristers in each respective province.

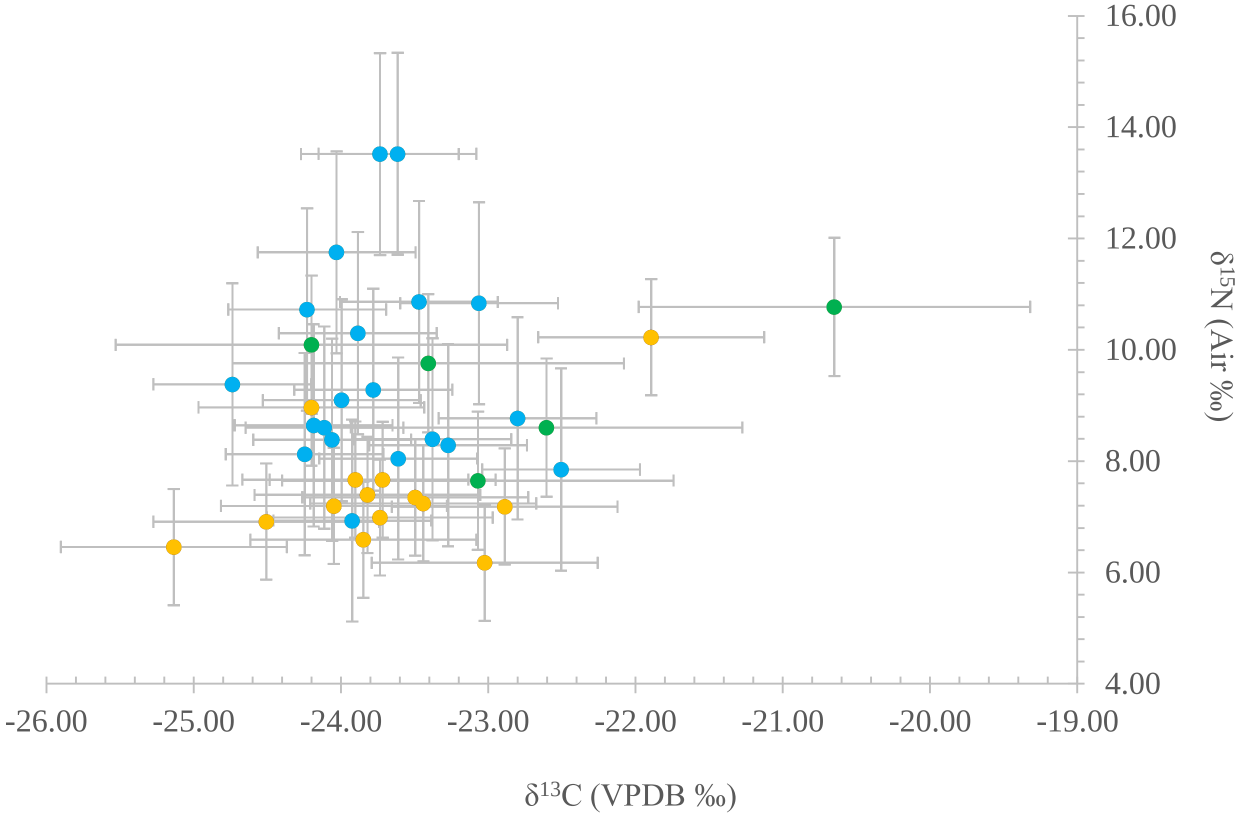

Figure 12: Carbon and nitrogen isotope signatures (± SD ‰) from tail feathers of *C. dichroa*. Colour denotes grouping where yellow, blue and green represent the Limpopo, KwaZulu-Natal and Eastern Cape Provinces, respectively.

To supplement the statistical analyses conducted in PAST and further investigate the degree of isotopic overlap (range of 0 – 1) between groups, the data were entered into RStudio where an outer convex hull (CH) and inner standard ellipse (SE) were calculated for each province (Figure 13). Values closer to 1 indicate a high degree of overlap and very little difference between groups.

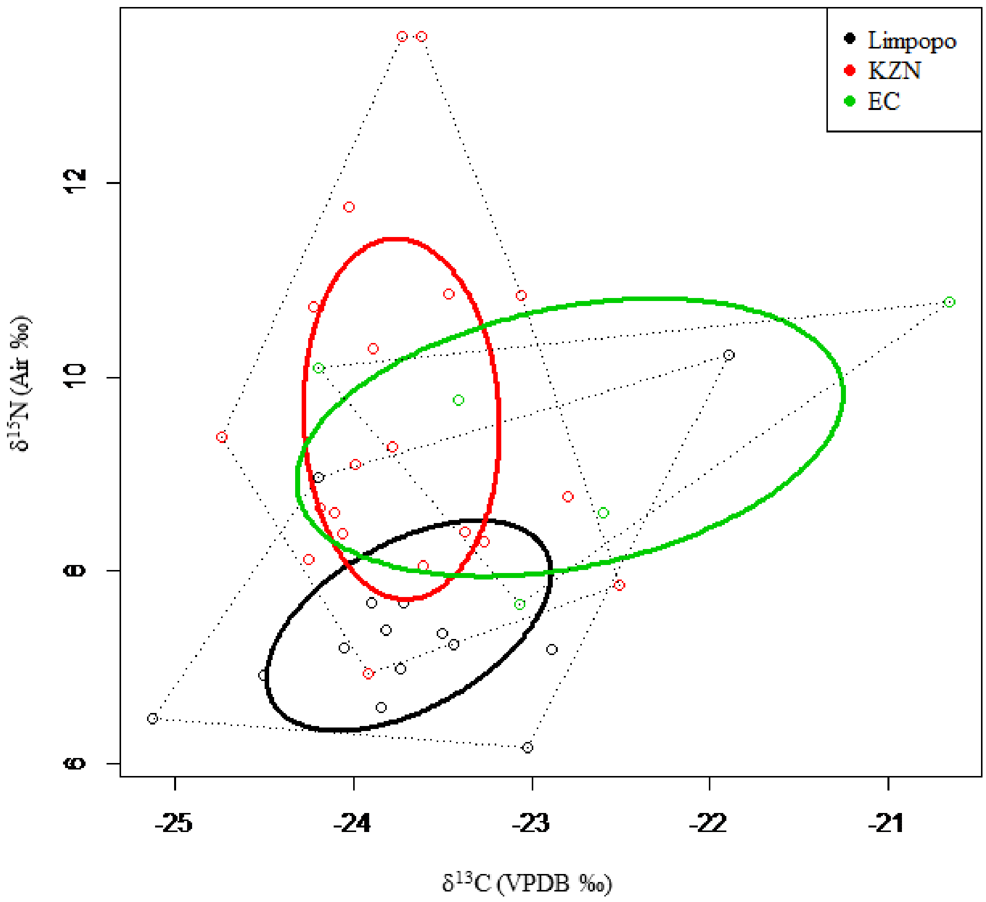

Figure 13: Bivariate plot of δ^{13}C and δ^{15}N signatures representing Choristers in the Limpopo, KwaZulu-Natal and Eastern Cape provinces of South Africa. Outer convex hulls (dotted lines) and inner standard ellipses were added to the data-set for each group.

When graphically incorporated, SE characterises an isotopic niche-width for *C. dichroa* that can be used to denote dietary preferences (carbon source and trophic level) in each province. Given the obvious overlap of provincial ellipses, the sample from Kenton was retained within the EC group. Its omission did, however, result in a noticeable constriction of the isotopic niche-width for Choristers in EC (Appendix E).

3.2 Scale 2 – Within-Province split

The variance observed within and between Provinces provoked the sub-division of *Scale 1* into the ‘Provincial split’ of *Scale 2* (Appendix C). Samples obtained from the Limpopo were divided into two groups, L1 (Ridgeways and SEEC) and L2 (Maluma and Vireers), while the Eastern Cape was divided between EC1 in the north and EC2 in the south. As only one sample represented EC2, it was excluded from the statistical analyses of *Scales 2*, *3* and *4*. Due to the large isotopic range and variation exhibited by Choristers in areas frequented by humans (such as the campsite), KZN was sub-divided into areas that were ‘tamer’ (more human activity - KZN1) and ‘wilder’ (less human activity - KZN2). At this *Scale*, statistical analyses are reported (separately for δ^{13}C and δ^{15}N) for each area, and significance is assigned in PAST and subsidised by a bivariate plot in RStudio.

3.2.1 Carbon isotopes – $\delta^{13}C$

Carbon isotope signatures were normally distributed ($p > 0.05$) in each of the five areas, with homogeneity of variance across sample means ($p = 0.45$) and medians ($p = 0.53$). No significant differences were detected between groups for $\delta^{13}C$ (Table 5).

Table 5: Stable carbon isotope values (Mean ± SD ‰) of tail feathers collected from *C. dichroa* and the results of a one-way ANOVA for differences within provinces, and between groups (Tukey's *post-hoc*). *Superscript lettering* denotes the level of significance where common letters share similar isotopic signatures.

Location	Provincial split	*n*	$\delta^{13}C$ (VPDB ‰)
South Africa	Limpopo 1	9	-23.55 ± 0.86^{a}
South Africa	Limpopo 2	5	-23.94 ± 0.56^{a}
South Africa	KwaZulu-Natal 1	12	-23.61 ± 0.64^{a}
South Africa	KwaZulu-Natal 2	8	-23.92 ± 0.27^{a}
South Africa	Eastern Cape 1	4	-23.32 ± 0.67^{a}
		ANOVA	$F = 0.923$ $p = 0.46$

The similarity within and between provinces is consistent with the findings of *Scale 1* for $\delta^{13}C$, which reiterates the fact that Choristers exploit the same energy source irrespective of geographic location. To prevent unnecessary repetition at a finer scale (from which no inferences can be made), ^{13}C will be excluded from the analytical breakdown of Univariate data in *Scale 3* and *Scale 4* (Appendix C); suffice to say that no significant differences were detected between groups ($p > 0.05$).

3.2.2 Nitrogen isotopes – $\delta^{15}N$

Nitrogen isotope signatures failed to meet the assumption of normality (Shapiro-Wilk $W = 0.93$, $p = 0.02$) for L1 ($p = 0.003$) and the human habituated areas of KZN1 ($p = 0.019$). Homogeneity of variance occurred between sample medians ($p = 0.39$), but not means ($p = 0.07$), failure of which prompted the utilisation of a Kruskal-Wallis test to detect significant differences between groups. As the total number of samples (n) representing each group were more evenly distributed than those of *Scale 1*, uncorrected p-values were used to assign significance (Table 6).

Table 6: Stable nitrogen isotope values (Mean ± SD ‰) and the results of a non-parametric Kruskal-Wallis for differences within provinces and between groups (Mann-Whitney *post-hoc*). *Superscript lettering* denotes the level of significance (uncorrected p-values) where common letters share similar isotopic signatures.

Location	Provincial split	n		$\delta^{15}N$ (Air ‰)
South Africa	Limpopo 1	9		7.46 ± 1.11^{a}
South Africa	Limpopo 2	5		$7.38 \pm 1.04^{a,c}$
South Africa	KwaZulu-Natal 1	12		9.86 ± 2.05^{b}
South Africa	KwaZulu-Natal 2	8		9.12 ± 1.40^{b}
South Africa	Eastern Cape 1	4		$9.03 \pm 1.12^{b,c}$
			KRUSKAL-WALLIS	$H = 15.63$ $p = 0.004$

When ranked (

Appendix **D**), nine of the lowest ten signatures (all < 7.5 ‰ for δ^{15}N) derived from Limpopo (*Scale 1*); the tenth (6.93 ‰) originated from a hybrid in KZN. Choristers from L1 occupied six of the bottom-ten ranks, while birds from L2 occupied the remaining three. The δ^{15}N similarity of Choristers between L1 and L2 (^{a}; $U = 21.5$, $p = 0.95$) implies that individuals obtained their dietary constituents from the same trophic level(s), which would be expected considering the close proximity of the study sites. These signatures were consistently and significantly lower than the trophic level of conspecifics in KZN and EC, which could possibly be due to isotopic discrepancies between years and/or sampling events[18]. Likewise similarity also occurred in KwaZulu-Natal (^{b}, $U = 40$, $p = 0.56$) between KZN1 and KZN2, despite the anomalous enrichment observed in some individuals around the campsite. The four Choristers from Fort Fordyce, in the Eastern Cape, produced δ^{15}N values consistent with all ($p > 0.05$) but one group – L1 ($U = 5$, $p = 0.05$). However, this tenuous result only bordered significant ($p = 0.053$), as did the pair-wise comparison between L2 and KZN1 ($U = 6$, $p = 0.048$), which called into question the robustness of 'uncorrected *p*-values' as a method of discovery. In lieu of this, Bonferroni-corrected *p*-values were employed to strengthen the detection potential of trophic segregation between groups, where only one significant difference ($U = 8$, $p = 0.01$) was found to occur between KZN1 and L1 (Figure 14). The spread of data from these two groups indicates that all but one – an individual from the Limpopo that was caught at the SEEC (Appendix B), adhered to the generalised feeding pattern of each area.

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[18] as feathers obtained from KwaZulu-Natal were collected in June and October 2010; from the Limpopo in December 2011 and June 2012; and in the Eastern Cape in August 2012, May and June 2013

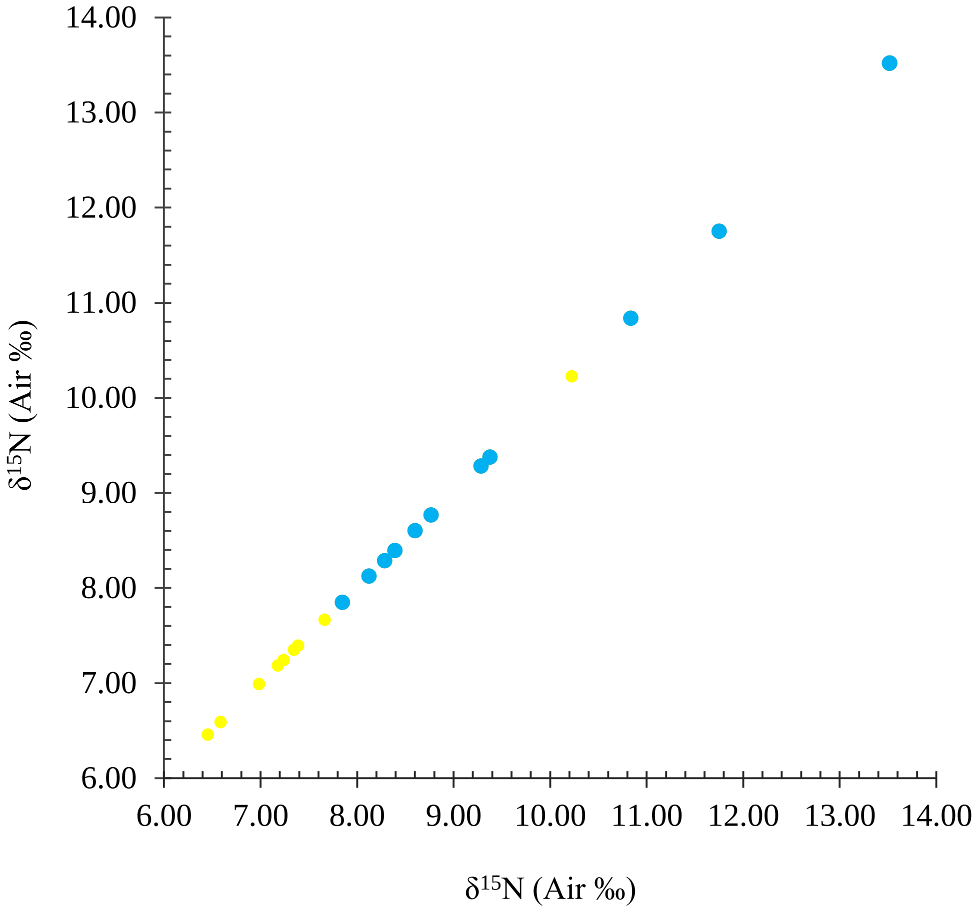

Figure 14: Univariate plot of nitrogen isotope sigatures highlighting the significant trophic difference found between Choristers in the northern sites of Limpopo (L1 – yellow) and human-frequented areas of KwaZulu-Natal (KZN1 – blue).

Within the L1 sub-set, the comparatively enriched value of 10.23 ‰ stemmed from a Chorister ringed near the Schoemansdal Environmental Education Centre (SEEC). Akin to the δ^{15}N-enrichment of Choristers around the VC campsite in KZN, this individual may also be noteworthy in its opportunistic scavenging of human food. However, as the only sample obtained for SEEC ($n = 1$, a statistical *faux-pas* that parallels the Kenton outlier in *Scale 1*), one cannot discount movement as a potential influencing factor. Without further justification, the employment of isotopes (from an open system) to infer migratory movements are limited, rendering at least one of the two aforementioned possibilities obsolete.

3.2.3. *Trophic niche width - δ^{13}C ‰ and δ^{15}N ‰*

Dietary suppositions based upon univariate tests indicate that similarities exist in all but one instance, for ^{15}N between L1 and KZN1. While essential for statistical purposes at *Scale 2*, these separate pairwise comparisons only conveyed one half of the total isotopic picture. To assess the trophic niche-width of Choristers in each respective area, δ^{13}C and δ^{15}N were combined for each sample (Figure 15).

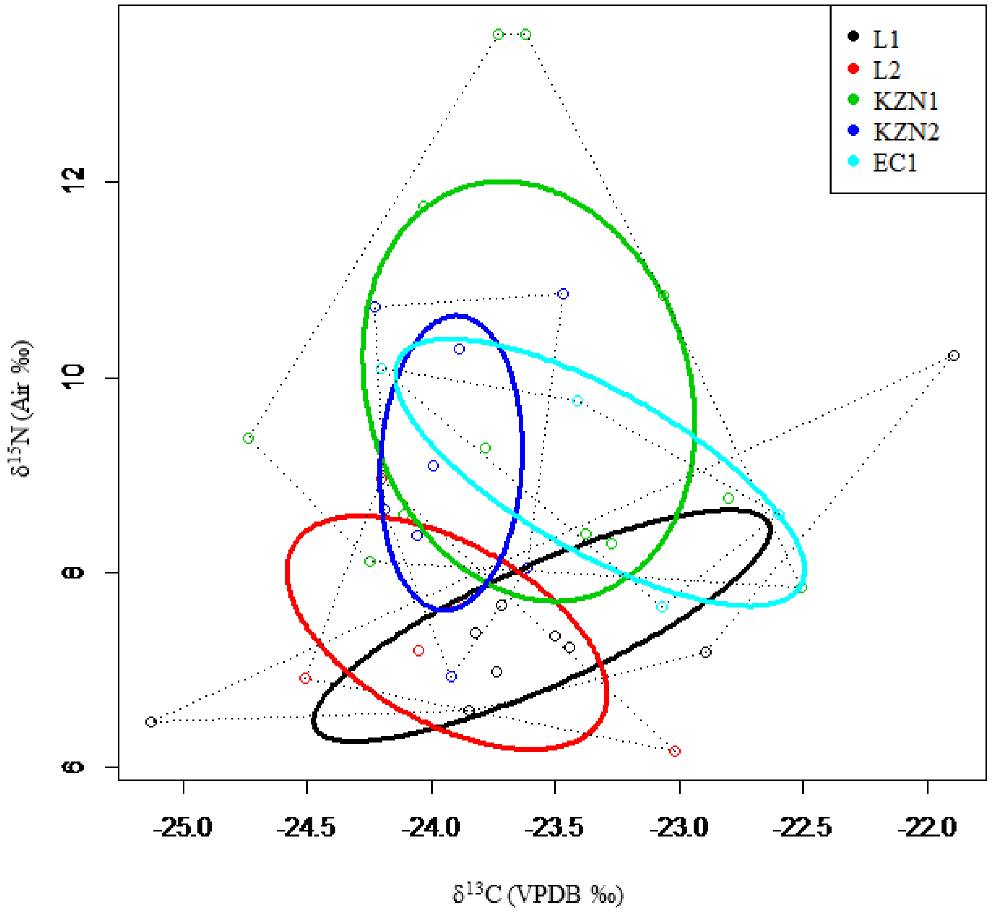

Figure 15: Bivariate plot of stable carbon and nitrogen isotope signatures representing Choristers in five areas of South Africa. Outer convex hulls (dotted lines) and inner standard ellipses have been added to the groups.

As suspected, the large isotopic range of KZN1 (which includes four of the five most enriched δ^{15}N-values;

Appendix **D**) indicates a substantial increase in the percentage of animal tissue consumed by individuals in this region (Symes & Woodborne, 2009). The comparatively smaller (more conservative) ellipses of the other four groups exemplifies the opportunistic nature of *C. dichroa* in KZN1, demonstrating their potential capacity to adapt to higher incidences of anthropogenic activity (as suggested by Maclean, 1999).

In accordance with the trophic segregation of *Scale 1*, Choristers from L1 and L2 appear to forage at a lower trophic scale on a wider range of dietary constituents (from within a C_3-based system) than conspecifics in KZN and EC. Based on the small overlap of Limpopo Choristers (L1 = 0.29; L2 = 0.119) and those of KZN1, one could opine that during the time of feather formation Choristers in Limpopo subsisted on very little, if any, animal tissue ($n = 13$; except for the anomalous signature from SEEC). Furthermore, the propensity for northern populations to exploit food sources from a lower trophic level is also highlighted by the slight overlap (0.0106) of L1 and KZN2.

However, the fact that the L1 and KZN1 ellipses do overlap indicates that the ^{15}N separation of each area ($U = 8$, $p = 0.01$ - as previously determined) is not fully upheld when δ^{13}C is incorporated, cautioning any inferences based singularly upon univariate analyses. To compound this, the complete separation of trophic niche-widths of Choristers in L2 and EC (overlap = 1.3 e^{-17}) – hitherto undetected, implicates a potential dietary shift (obligate or facultative) in northern populations. This, however, requires further investigation as the four birds representing EC all stem from the same source forest (Appendix B), and it may be presumptuous to compare the niche-widths of four individuals from one forest (Fort Fordyce; *Scale 3* & *4*) to four individuals (plus a recapture, $n = 5$) from two (Maluma Boerdery; *Scale 3* & *4;* and Vireers Farm).

As a pre-emptive measure to prevent erroneous conclusions, the anomalous L1 sample (Figure 14, page 56) obtained from SEEC ($n = 1$)[19] was excluded from the finer scales of subsequent analyses (Appendix C), alongside an L2 sample from Vireers Farm ($n = 1$)[20]. The omission of these signatures enabled the refinement of L1 and L2 to ‘Ridgeways’ and ‘Maluma Boerdery’, respectively (*Scale 3*). In addition to these omissions, the two signatures from Ngele forest (Appendix B) were removed from the KZN2 grouping, which narrowed the scope of KZN1 and KZN2 to ‘Vernon Crookes camp’ and ‘Vernon Crookes wild’ (*Scale 3*).

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[19] which reflected an isotopic enrichment of both δ^{13}C (-21.89 ‰) and δ^{15}N (10.23 ‰)

[20] The 7th highest carbon signature (-23.02 ‰) and lowest (39th), most depleted, nitrogen source (6.17 ‰).

3.3 Scale 3 – Nitrogen isotopes ($\delta^{15}N$) and dietary niche-width

A re-analysis of these signatures (in accordance with the new groupings) passed the overall assumption of normality (Shapiro-Wilk $W = 0.94$, $p = 0.82$), but additional testing[21] illustrated an aberration within the 'Vernon Crookes *camp*' (Shapiro-Wilk $W = 0.83$, $p = 0.019$; Anderson-Darling $A = 0.8657$, p(Monte Carlo) = 0.02). A highly significant difference was detected between sample means ($p = 0.002$), but not medians ($p = 0.11$), prompting the employment of the Welch F test (for unequal variance) and non-parametric Kruskal-Wallis to detect significant differences between groups (Table 7); but other than identifying a similarity between VC *wild* and Maluma ($p = 0.17$), these results paralleled the uncorrected p-values (Mann-Whitney *post-hoc*) of *Scale 2* (Table 6, page 54).

Table 7: Stable nitrogen isotope values (mean ± SD ‰) and the results of two non-parametric tests for differences between areas (Mann-Whitney *post-hoc*). *Superscript lettering* denotes the level of significance (uncorrected p-values) where common letters share similar isotopic signatures.

Location	Area	*n*		$\delta^{15}N$ (‰)
South Africa	Ridgeways	8		7.11 ± 0.41^{a}
South Africa	Maluma	4		$7.69 \pm 0.91^{a,c}$
South Africa	Vernon Crookes *camp*	12		9.86 ± 2.05^{b}
South Africa	Vernon Crookes *wild*	6		$9.21 \pm 1.64^{b,c}$
South Africa	Fort Fordyce	4		$9.03 \pm 1.12^{b,c}$
			WELCH F	$F = 7.653$ $p = 0.0052$
			KRUSKAL-WALLIS	$H = 17.06$ $p = 0.0019$

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[21] considering the potential ramifications of investigating isotopes at such finite scales, results are extrapolated from conservative tests wherever possible to ensure accuracy

Bonferroni-corrected *p*-values resulted in only one significant difference, which also mirrored that of *Scale 2*. However, in this instance (without interference from the SEEC outlier; Figure 14, page 56), a more prominent difference was detected between ‘Ridgeways’ and ‘Vernon Crookes *camp*’ ($U = 0$, $p = 0.002$), which was affirmed through a one-way PERMANOVA (Group variables = ‘Area’ caught and ‘Year’; $F = 4.577$, $p = 0.007$). This separation was maintained (overlap = $4.12\ e^{-18}$) subsequent to the incorporation of $\delta^{13}C$ (Figure 16).

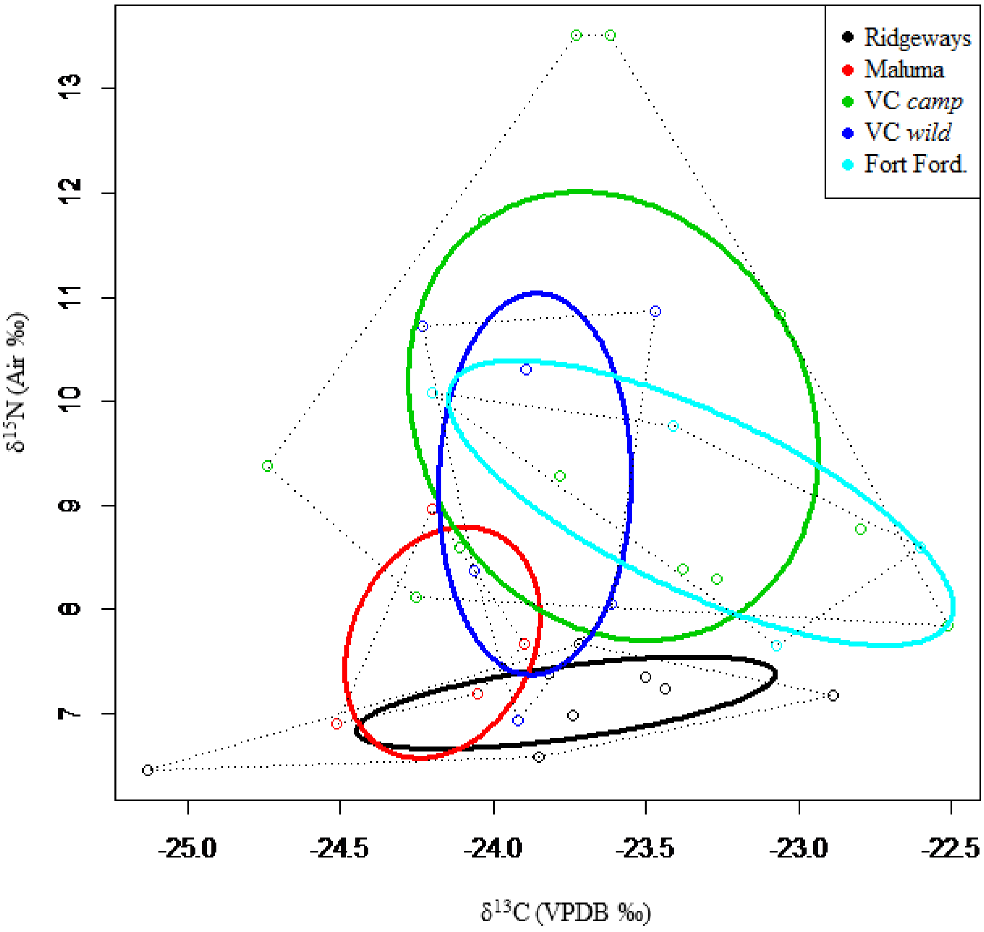

Figure 16: Isotopic niche widths of Choristers ($n = 34$) in five distinct regions of South Africa (*Scale 3*). Outer convex hulls (dotted lines) and inner standard ellipses – denoting isotopic niche widths – were added to the data through RStudio.

Additional variances in trophic niche-width occurred between Ridgeways and Fort Fordyce (overlap = $1.39\ e^{-17}$); Maluma and Fort Fordyce (overlap = $1.52\ e^{-18}$); and, to a much lesser extent, between Ridgeways and VC *wild* (overlap = 0.00395); as-well-as Maluma and VC *camp* (overlap = 0.0879). However, the latter groups – representing Choristers in VCNR – were comparatively ill defined (as they were represented at a coarser geographic scale than other groupings at *Scale 3*). To facilitate the break-down of 'VC *wild*' and 'VC *camp*' (and assess isotopic signatures at the finest scale possible), the data were sub-divided into *Scale 4* (Appendix C).

3.4 Scale 4 – Individual Sites

The final break-down of isotopic signatures are in accordance with their site of capture. Despite exhibiting normal distributions ($W = 0.97$, $p = 0.53$), both instances of the Levene's test were failed (for homogeneity of variance across sample means ($p = 0.0004$) and medians ($p = 0.014$)). A Welch F test and supplementary Kruskal-Wallis were therefore used to denote significance (Table 8).

Table 8: Nitrogen isotope values (Mean ± SD ‰) and the results of two non-parametric tests for differences between Sites (Mann-Whitney *post-hoc*). *Superscript lettering* denotes the level of significance (uncorrected *p*-values) where common letters share similar isotopic signatures.

Location	Site	*n*		δ^{15}N (‰)
South Africa	Ridgeways	8		$7.11 \pm 0.41\ ^{a}$
South Africa	Maluma Boedery	4		$7.69 \pm 0.91\ ^{a,c}$
South Africa	V.C. campsite	8		$10.52 \pm 2.24\ ^{b}$
South Africa	V.C. camp manager	4		$8.55 \pm 0.57\ ^{b,c}$
South Africa	V.C. eastern valley	3		$9.32 \pm 2.08\ ^{a,b}$
South Africa	Fort Fordyce	4		$9.03 \pm 1.12\ ^{b,c}$
			WELCH F	$F = 6.707$ $p = 0.0097$
			KRUSKAL-WALLIS	$H = 17.06$ $p = 0.0044$

Despite the constriction of 'VC *camp*' (from *Scale 3*), samples originating from Choristers within the VC campsite exhibited significantly different ^{15}N signatures than conspecifics in Ridgeways ($U = 0$, $p = 0.0009$) and Maluma Boerdery ($U = 3$, $p = 0.03$). Additionally, differences were also detected between Ridgeways and the VC camp managers' office ($U = 0$, $p = 0.0085$), as-well-as Ridgeways and Fort Fordyce ($U = 1$, $p = 0.014$). However, at this finite scale, four of the six sites are represented by less than five samples eliciting the use of Bonferroni-corrected *p*-values, which indicated only one significant difference ($U = 0$, $p = 0.014$) between Ridgeways ($n = 8$) and VC campsite ($n = 8$).

Subsequently, an all-inclusive one-way PERMANOVA was conducted to allow for the statistical inclusion of smaller samples ($n \leq 2$) from SEEC, Vireers' Farm, a waterfall in Vernon Crookes,a forest patch on the northern border of Vernon Crookes, Ngele Forest and Moneysworth Farm (Appendix B). The incorporation of these study sites highlighted significant differences between Choristers in Ridgeways and conspecifics sampled at the waterfall in VC ($F = 12.7$, $p = 0.02$); Ridgeways and the eastern valley in VC ($F = 9.76$, $p = 0.04$) – hitherto undetected; and Ridgeways and Ngele Forest ($F = 30.91$, $p = 0.02$). A graphical representation of the mean (± SD) for each site clearly illustrates the dietary enrichment of Choristers in human-habituated areas (VC campsite, SEEC and Moneysworth Farm), compared to conspecifics from other regions of South Africa (Appendix F). In fact, although '*wild*', the close proximity (1 - 5 km east) of Emahlathini to the VC northern forest patch may have cause the slight enrichment detected in this particular feather ($n = 1$; Appendix F); but this is merely pause for thought at this juncture and nothing conclusive can be established.

3.5. Recaptures

From the 39 samples obtained, 32 originated from different individuals (*C. dichroa*), five from recaptures, and two from *C. dichroa* X *C. natalensis* hybrids. Of the five Choristers recaptured, the isotopic signatures generated from feathers taken in the first instance were supplemented (five-to-six months later) with the same retrices that had regrown during the interim. This facilitated the direct appraisal of $\delta^{13}C$ and $\delta^{15}N$ for each respective bird, as isotopes from the initial capture were employed as baseline data to which the latter could be compared (a crude inter-seasonal depiction of the recaptured birds' respective diets subsequent to the post-nuptial moult during feather formation in February (Oatley, 1959; Craig, 1983). However, the ten feathers that were acquired (from five recaptures) stemmed from Ridgeways (*n* = 2; N = 1) and Maluma (*n* = 2; N = 1) in Limpopo, as-well-as the managers' office (*n* = 2, N = 1) and campsite (*n* = 4, N = 2) in Vernon Crookes Nature Reserve (KZN). Due to this, and based on the size of the sample, any significance found to exist would be fraught with ambiguity, rendering them relatively useless in terms of quantitative data. Although statistical analyses were precluded in this instance, a visual representation of the paired isotopic values was utilised in Figure 17 ($\delta^{13}C$) and Figure 18 ($\delta^{15}N$) to evaluate the 'movement potential' (depicted by the measure of '*variance*' between each signature) of each bird. Differences exceeding 1‰ for $\delta^{13}C$ and 2‰ for $\delta^{15}N$ indicate a substantial shift in either isotope (Peterson & Fry, 1987) – a factor that has been linked, quite successfully, to movement patterns in terrestrial animals.

3.5.1 *Carbon isotopes – $\delta^{13}C$*

The two notable variances (> 1 ‰) in δ^{13}C originated from a female bird captured in Ridgeways (*variance* = 2.25 ‰; Figure 17: [1]), and a male from the Vernon Crookes campsite (*variance* = 1.52 ‰; Figure 17: [3]).

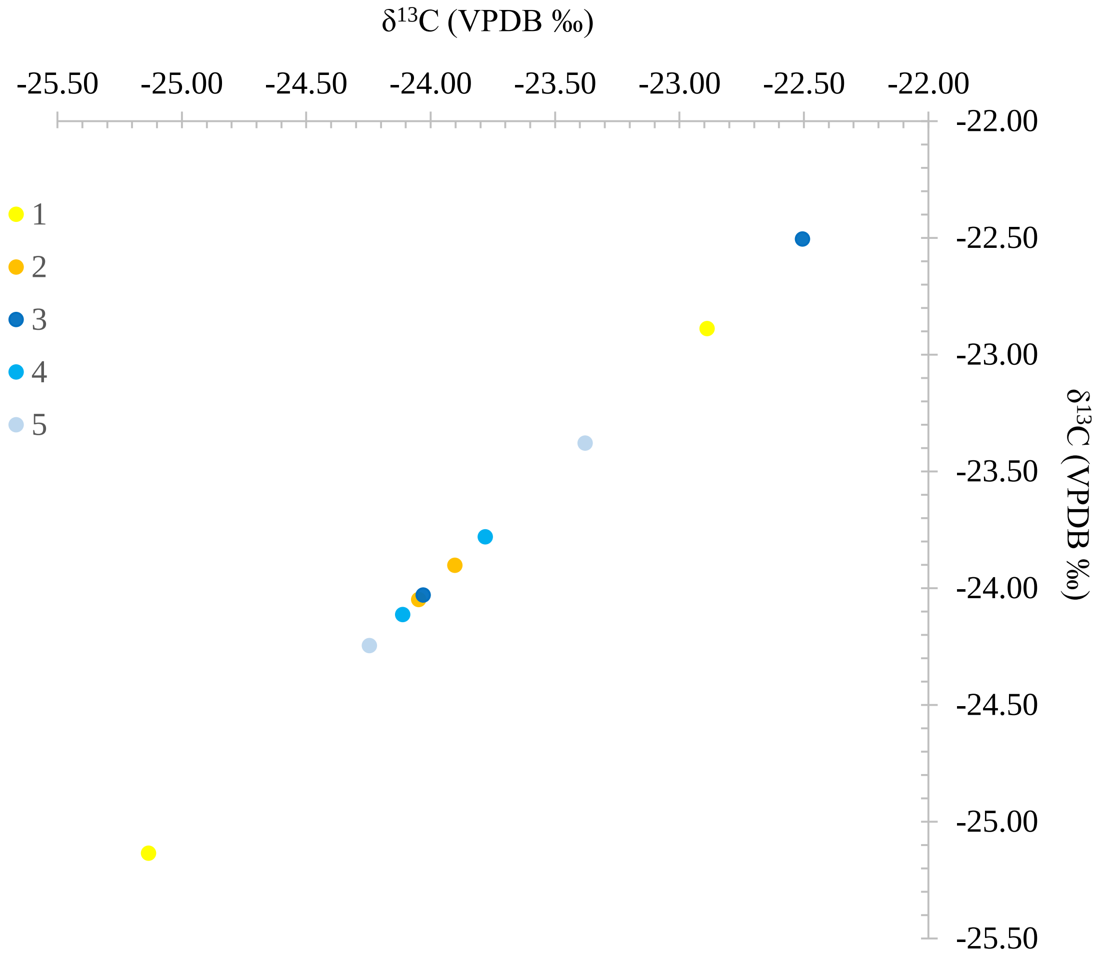

Figure 17: Univariate plot of carbon isotope sigatures collected from tail feathers of recaptured Choristers in Ridgeways [1] and Maluma [2] – Limpopo Province; the Campsite in VC [3, 4], and the Camp managers' office in VC [5] – KwaZulu-Natal. The two recaptured birds from Limpopo were female while the remaining recaptures from KwaZulu-Natal were male.

Both instances indicate a substantial shift in the energy resources (^{13}C) exploited by each bird between the time-frames represented, respectively, by feathers 1 and 2, which may be a potential outcome of their seasonal movement between environmental gradients. However, the distance covered by each individual remains a point of contention as *variance* may accrue in the presence of extraneous factors. For instance, in the immediate vicinity (within a home range, for example), food availability and the abundance of dietary constituents fluctuate in response to environmental conditions and seasonal changes (which are known to be less pronounced in equatorial zones due to the high angle of incidence). In South Africa, cyclical variations in precipitation, temperature and day-length initiate physiological responses in plants (e.g. growth or reproduction), which may have beneficial and/or detrimental effects on local avifauna, depending on the time of year (Peterson & Fry, 1987; Thuiller *et al.*, 2006; Barker *et al.*, 2013). At high altitudes, between May and July, temperatures tend to plummet well below 0˚C, inhibiting the activities of epigaeic arthropod species (Gullen & Cranston, 2010), many of which enter into a state of diapause. The carrying capacity of an area during this time may not meet the resource demands of its summer population forcing many Choristers (notably first year birds that have no established territory) to either forage in adjacent ecotones or move further afield (Vernon, 1989).

3.5.2 Nitrogen isotopes – $\delta^{15}N$

The isotopic signatures from four of the five recaptures were unremarkably similar for ^{15}N (< 1 ‰) – an indication of the propensity of Choristers to remain in their respective territories throughout the year. Only one significant change (> 2 ‰) was found for ^{15}N between Feathers 1 and 2. The surprisingly large trophic shift (*variance* = 3.90 ‰) exhibited by the third recapture (Figure 17) originated from a male Chorister in the VC campsite. In this instance, the shift in parts per thousand of ^{13}C and ^{15}N may be regarded as a prime exemplar of the ways in which naturally occurring stable isotopes can be employed to determine the movement potential of an individual, regardless of the origin of capture. It should however be noted that while *variance* may be substituted as a quantitative proxy for movement, it is a tentatively robust affirmation of the occurrence of a 'movement event' (between sequential samples from the same individual) rather than a 'statistical bridge' linking any one animal to a specific geographic location. To tie an isotopic signature to its place of origin, an extensive *isoscape* matrix (e.g. δ^2D, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$) would be required for floral and faunal assemblages in each of the habitats that fall within the target species' distribution range.

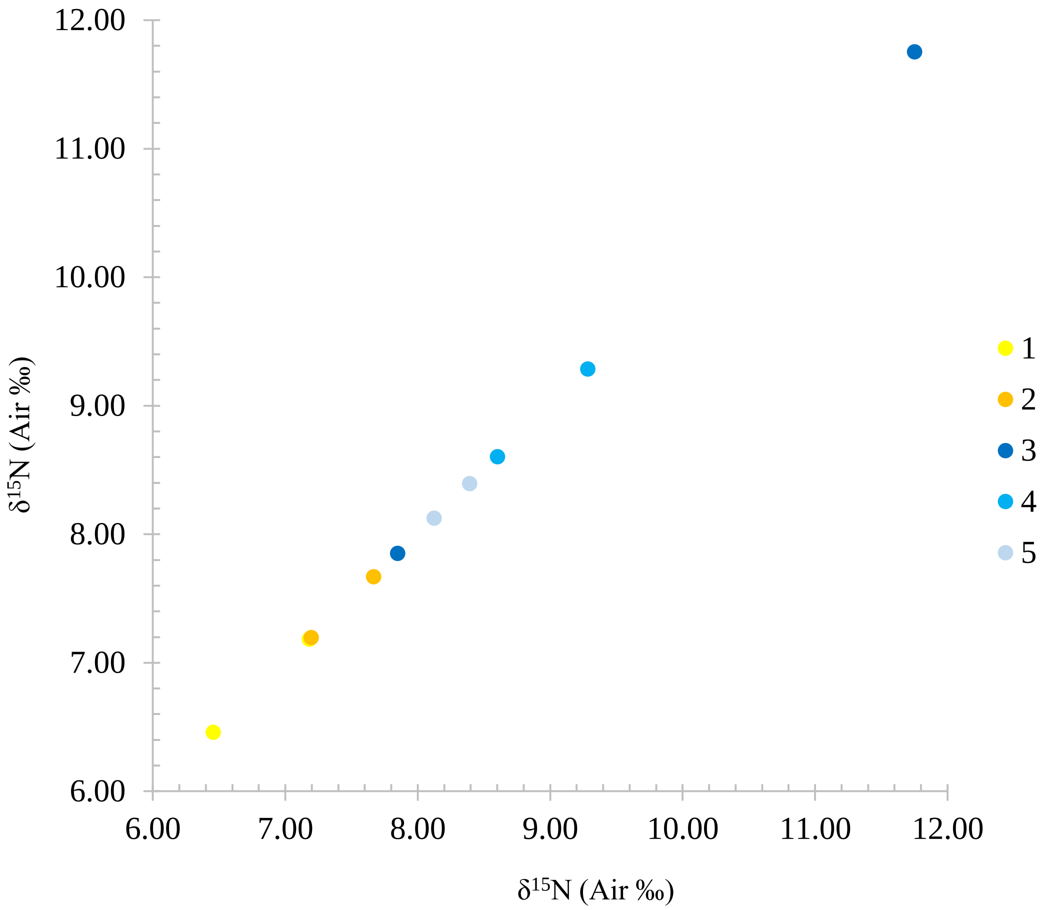

Figure 18: Univariate plot of nitrogen isotope signatures collected from tail feathers of recaptured Choristers in Ridgeways [1] and Maluma [2] – Limpopo Province; the Campsite in VC [3, 4], and the Camp managers' office in VC [5] – KwaZulu-Natal.

Despite the close association of this particular recapture with anthropogenic activities in and around the campsite, coupled with its recapture at the same location six months later, indicates that the *variance* exhibited may not be due to seasonal movements but rather an artefact of the generalised diet and opportunistic nature of *C. dichroa* (Figure 4, page 36).

Chapter 4: General Discussion

In the absence of an isoscape, many studies advocate sampling local floral assemblages to link the isotopic signatures of animals to a particular geographic region (Ambrose, 1991; Hobson, 1999; Symes & Woodborne, 2009). In forest patches where the botanical diversity is notoriously high (Hahn, 1994; Symes *et al.,* 2000), fulfilling this requirement necessitates intensive and costly sampling across the Greater Escarpment of South Africa. As ^{13}C and ^{15}N have both been shown to vary inter- and intra-specifically, as-well-as between tissues of the same plant (Craine *et al.,* 2009), multiple replicates of each species would need to be sampled to obtain representative signatures. Since Choristers occasionally foray into residential gardens, orchards and montane grasslands to forage, there is no guarantee that the arthropods (most of which are highly vagile) and fruit consumed would reflect the signatures of the plants sampled in each forest patch; or that the feather was even formed within one of the patches sampled. To compound this, Choristers have the capacity to move between forest patches that are geologically distinct from one another (*i.e.* the Soutpansberg and Drakensberg mountain ranges - Symes *et al.,* 2000), which exponentially increases the amount of sampling needed to create a floral isoscape to which their signatures can accurately be compared. As the natural abundance of ^{13}C and ^{15}N fluctuate inter-annually and between precipitation events (Craine *et al.,* 2009), the additional recommended sampling was deemed biologically uninformative and beyond the scope of this project (to assess the utilisation of carbon and nitrogen isotopes in determining the altitudinal migration of Choristers). However, despite limited progress on a South African isoscape, the paper published by Symes and Woodborne in 2009 provides an informative framework of ^{13}C and ^{15}N signatures for forest plants (n = 38) and birds (n = 27 species) in Woodbush, approximately 120 kilometres south of the Soutpansberg Mountains. When combined with the reported moulting strategy (Oatley, 1959; Craig, 1983), dietary analyses (Oatley, 1970a), habitat preferences and breeding behaviour (Clancey, 1982) reported for *C. dichroa*, a strong regional separation is apparent in the isotopic signatures that suggests very little movement between populations in the forest patches sampled.

4.1. Altitudinal migration

Historically, migration has been described as a seasonal journey that is annually undertaken between breeding and non-breeding grounds before the onset of adverse weather conditions that limit resource availability (Alerstam & Lindström, 1990; Oatley, 1998; Hobson, 1999; Burgess & Mlingwa, 2000; Royle & Rubenstein, 2004; del Hoyo *et al.,* 2005; Norris & Marra, 2007; Brown, 2006; Boyle, 2010). Altitudinal migration is well-established in temperate and tropical latitudes (Gwinner, 1990), where migrant species undertake annual movements between highland breeding grounds and the lowlands that they overwinter in (Boyle, 2010). Depending on the distance covered and the altitude at which a population breeds, this form of migration can be divided into one of four categories, which often overlap (Cyrus & Robson, 1980; Johnson & Maclean, 1994). Birds that remain at altitude throughout the year, voluntarily moving between montane (*c.* > 2400 m a.s.l.) and low-altitudes (*c.* < 600 m a.s.l.) during severe weather conditions are described as 'Category A' migrants; while those in 'Category B' all relocate to sub-montane and mid-altitudes (*c.* 1500 m – 900 m a.s.l.) each winter. Avian species undertaking long distance migrations from high to low altitudes (*c.* < 900 m a.s.l.) or mid- to low-altitudes are placed in Categories C and D, respectively, but neither applies to *C. dichroa*. Initially, the short, overland movements of Choristers were considered a mixture of categories A and B, depending on the severity of the winter conditions within high altitude forests. However, regardless of the clear-cut groupings described above, the driving mechanisms associated with altitudinal migrations are poorly understood (Gwinner, 1990; Schwabl & Silverin, 1990; Hobson, 1999; Brown, 2006).

Considering the key role that food availability and climatic conditions play in triggering long-distance migration (Clancey, 1964; Maclean, 1972; Cyrus & Robson, 1980; Brown & Barnes, 1984; Alerstam & Lindström, 1990; Gwinner, 1990; Johnson & Maclean, 1994; Oatley & Arnott, 1998; del Hoyo *et al.*, 2005), both factors have been implicated as the likeliest drivers of altitudinal movements in *C. dichroa* (Hobson, 1999). During adverse weather conditions when high-altitude resources may be constricted, ecological competitors that vie with Choristers directly for food, water, shelter and space are assumed to parallel those of the closely related robin-chat, *C. natalensis* (Roberts, 1922; Oatley, 1970a, b; Clancey, 1982; Davies *et al.*, 2011), where medium-sized insectivorous birds (30 – 200 g), like Thrushes (genus: *Turdus*) and Shrikes, occupy analogous niche widths within forested habitats (sympatry – Bearhop *et al.*, 2004; Jiang, 2007). As the majority of forest patches harbour a disproportionately high number of insectivorous bird species (Symes *et al.,* 2000), competition could foreseeably affect food availability as a direct or indirect consequence of inter- and/or intra- specific interactions. However, the trophic niche-width exhibited by *C. dichroa* (*n* = 39; Figure 5, page 37) indicates a broad generalised diet rather than a specialist one (Bearhop *et al.*, 2004), which would allow individuals to opportunistically switch between seasonally abundant resources should one or more become limiting or change abruptly. Furthermore, the wide range of $\delta^{13}C$ and $\delta^{15}N$, combined with the large body size of *C. dichroa*, their solitary nature and aggressive territorial behaviour (Oatley, 1970a; Clancey, 1982) suggests that this forest endemic should feasibly be able to out-compete other forest-dependent birds. As Choristers are routinely recorded and/or captured during cold winter months in high altitude forest patches, the early reports of resident populations maintaining their breeding territories throughout the year are consistent with the findings of this study; especially the work conducted by Oatley (1970a), which revealed ample insect prey groups in the stomach content analyses of Choristers in high-altitude forests throughout the year.

Altogether, the snippets of quantitative data accrued thus far suggest that Choristers exert a certain degree of 'control' over their migratory movements (*see* Schwabel & Silverin, 1990), allowing individuals to move independently of the population, or not at all (Clancey, 1982). The mechanistic theories on 'competition', 'food limitation' and 'adverse weather conditions' that have so far been proposed as driving forces of altitudinal migration seem weak in light of the aforementioned data; but one cannot ignore the combined effect that all three could have on any number of species during extreme weather events[22]. Based on the isotopic signatures exhibited and the presence/absence data gained, it does not seem likely that Choristers are undertaking any form of seasonal migration (partial or otherwise). However, with so many sources having acknowledged these altitudinal movements over the years, it seems prudent to investigate this phenomenon more thoroughly over a longer time scale than represented herein. If indeed altitudinal movements are occurring, they may be doing so on a smaller geographic scale, rather than an inter-regional one (e.g. the same mountain range, which $\delta^{13}C$ and $\delta^{15}N$ would not detect in the absence of a detailed isoscape). This movement may also be occurring on a regular basis as daily or weekly excursions, which would allow pairs to maintain their territories throughout the year, providing the added advantage of an established territory before the onset of the breeding season as well as the chance to lay an early clutch (and

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[22] However, since this would not follow an annual pattern, it would not be considered as migration, (merely movement).

possibly even a second later on in the breeding season should the first attempt fail). Regardless of these assumptions, should migration be occurring, the driving mechanisms that initiate it are clearly not based upon a strong genetic predisposition or governed by rigid internal controls (Schwabel & Silverin, 1990). Based on the preferences that Choristers exhibit for mesic conditions (Oatley, 1970; Clancey, 1982; Oatley, 1998; Oatley & Arnott, 1998; Symes *et al.,* 2000), and considering their daily water requirements (Oatley, 1970), moisture gradients, precipitation and humidity may feature more prominently in the range, occurrence and distribution of Choristers around South Africa (especially if they struggle to regulate their own humidity – Oatley, 1970).

4.1.1. Coastal populations

Across the whole sample (*n* = 39), the ^{13}C signatures of Choristers were consistent with a C_3-based diet, although the range was below the expected values for frugivores and insectivores in forest patches of South Africa (-31.4 ‰ to -27.6 ‰ + 1 ‰ for each trophic enrichment, *see* section 1.5., page 23). The two comparatively ^{13}C-enriched signatures from Schoemansdal Environmental Education Centre (-21.89 ‰) and Moneysworth Farm (-20.65 ‰) may be due to the incorporation of a higher proportion of C_4-based food, but this cannot be conclusively stated based on the limited sample size. The large range of both ^{13}C (4.48 ‰; *n* = 39) and ^{15}N (7.35 ‰) does, however, suggest that this forest endemic can survive and may even be able to adapt to conditions beyond the forest edge (as indicated by Maclean in 1999), lending credence to local reports of Choristers maintaining breeding populations (and singing) throughout the year at sea level in the coastal forests of Natures Valley, Knysna, George, and Kenton (FLOCK, 2014 resident reports <*unpublished*>). In addition, the three recaptures from KZN indicated year-long occupation of coastal forests (Clancey, 1982), which is consistent with reports of a territorial male remaining in the Kilgobbin Forest for 15 consecutive breeding seasons (Oatley & Arnott, 1998).

Choristers that are reported to reside at lower altitudes remain sedentary throughout the year (Oatley, 1970a, b; Clancey, 1982; Oatley & Arnott, 1998), and a few resident populations have been recorded breeding in selected forest fragments along the KwaZulu-Natal coast (Clancey, 1982). While first year birds are purported to migrate to coastal forests during winter (*see* section 1.3.2, page 17), 12 of the 13 Choristers captured in Vernon Crookes Nature Reserve and Ngele during the winter June/July 2010 sampling event were adults; and only two of the 17 Choristers that were caught in KZN during 2010 were female[23]. Although these statistics may be an artefact of sampling, in the event that they do (to some degree, at least) reflect local population demographics, the highly skewed age and sex ratios could potentially be inducing a negative feedback loop whereby a high male-to-female ratio (15:2 in this case) results in a low juvenile-to-adult ratio (1:16) that continues to depress the male-to-female ratio and the subsequent number of juveniles that are successfully reared, fledged and recruited into the population each year. In light of the longevity of Choristers and their monogamous nature, a lack of non-breeding (single) females within a population would preclude a large proportion of mature males from annually reproducing (intra-sexual competition – Schwabl & Silverin, 1990); which is quite a concern if little or no regional movement is occurring as the δ^{13}C and δ^{15}N signatures suggest. As strong regional separation was apparent between the three provinces, and no evidence of inter- or regional movements were exhibited by the recaptured Choristers, a lack of responsive females may plausibly explain the interbreeding that occasionally occurs between *C. dichroa* and *C. natalensis*; both of which are closely related, lack the characteristic white supercilium of other *Cossypha* species, and mimic one another in their repertoire of calls throughout the breeding season (Oatley, 1997; Oatley, 1998; Ferguson *et al.,* 2002; Beresford, 2003; Sinclair *et al.,* 2011). However, these assumptions are tentative and based on a small representative sample of each population over the course of one year. Further research is necessary to ascertain the demographic and genetic make-up of *C. dichroa* in coastal forests throughout their range (Cracraft, 1987; Houde, 1987; Haig & Allendorf, 2006; Harvey *et al.,* 2006).

Aside from demographic ratios, breeding conditions can also affect fecundity (Gwinner, 1990; Schwabl & Silverin, 1990). Traditionally, Choristers were thought to require the high altitude mistbelt forests in the interior of South Africa to breed, utilising natural rot holes within well-established 1 ha territories. While the intolerance of Choristers for drier conditions prevent them from residing within woodlands for extended periods of time (Clancey, 1982; Oatley & Arnott, 1998; Davies *et al.,* 2011), resident populations have been established in lowland forests with a higher moisture content. While these areas provide ample food, water and shelter for the survival of *C. dichroa* throughout the year, many of these forests lack suitable nesting sites for resident populations to breed, inducing a population sink of non-breeding birds (Clancey 1982;

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[23] The two *C. haagneri* hybrids (one sub-adult and one adult) along with one other ‘unknown’ Chorister were excluded from this tally.

Gwinner, 1990; Battin, 2004). Although Choristers have been observed nesting in bamboo and utilising old Brown-hooded Kingfisher (*Halcyon albiventris*) excavations in earthen banks (Oatley & Arnott, 1998), this behavioural shift and its effect on reproductive output remains unclear. Obligate cavity nesters (especially those that rely on natural rot holes in long-established trees) are reported to be the first to disappear from a system that is heavily exploited for its wood (Du Plessis, 1994), and while large-scale logging occurs predominantly in the afforested plantations of South Africa (Allan *et al.,* 1997; Shackleton, 2004; DAFF, 2010), the removal of dead and dying trees from coastal forests (even when based on a pre-emptive death system) restricts the amount breeding resources available to natural cavity nesters (Du Plessis, 1994; Allan *et al.*, 1997). Limited by the availability of suitable nesting sites, local Chorister populations may dwindle over time as birth rates are suppressed and death rates continue to rise due to habitat degradation, increased competition and the over-exploitation of forest patches (Alerstam & Lindström, 1990; Schwabl & Silverin, 1990). Since the ability to reproduce (or replicate) is inextricably linked to the continued persistence of any living species, deleterious effects on achieved fecundity (especially a lack thereof) in a long-lived bird species that does not appear to be moving could cause local populations to crash and may even plausibly explain the decrease in the abundance of Choristers reported by BirdLife International (2008), the IUCN (2014), and SABAP2 (2014).

4.2. Population threats

In addition to the aforementioned limitations, the population dynamics of Choristers are furthermore affected by predation and competition (MacArthur *et al.*, 1972; Connell, 1983; Schoener, 1983; Jiang, 2007). The majority of forest patches in South Africa are < 1 km^2 (*see* section 1.2) and many fragments are unable to support larger bodied carnivores. Without the top-down control exerted by apex predators, smaller generalist omnivore populations have a tendency to increase (meso-predator release hypothesis – Elmhagen & Rushton, 2007; Ritchie & Johnson, 2009). Snakes, mammals and larger birds of prey do feed upon birds, but any attributable impact on Chorister populations would likely be nest predation (Lahti, 2009) by Vervet monkeys (*Chlolocebus pygerythrus*), Chacma baboons (*Papio ursinus ursinus*) and/or egg-eating reptiles. Brood parasitism by the Red-Chested Cuckoo (*Cuculus solitarius*) can also influence the annual turn-over rate of Chorister populations, resulting in the loss of a whole clutch (Oatley & Arnott, 1998; Kuiper & Cherry, 2002; Chittenden, 2007). As a summer breeding migrant to forests, woodlands and gardens of the Greater Escarpment (Kuiper & Cherry, 2002; SABAP2, 2014), the range of the Red-Chested Cuckoo overlaps extensively with Choristers, and over two field excursions to the high-altitude forests of Hogsback during November and December 2012, the repetitive 'piet-my-vrou' call of *Cuculus solitarius* was heard non-stop throughout the forest, day and night (*pers obs*). Since the incidence of brood parasitism is reportedly uncommon in Choristers, no noticeable impact on their achieved fecundity should occur. However, the distribution range of Cape Robin-Chats (the preferred hosts of the Red-Chested Cuckoo) appear to be expanding westwards into the drier, more open areas of South Africa (SABAP2, 2014)[24], beyond the natural range of the brood parasite, which may explain the poor egg-matching that was found to occur between the two (Kuiper & Cherry, 2002). Unlike the observed colour disparities that were found between the eggs of *Cuculus solitarius* and *Cossypha caffra*, perfect matches were recorded between the cuckoo and *Cossypha dichroa*. As a higher, more common incidence of brood parasitism may negatively affect the breeding success of Choristers, the ease with which a host-shift could naturally occur needs to be considered and assessed (where possible), as it may already be affecting local populations across their range.

Aside from natural enemies, over-exploitation and the removal of dead and dying trees by local rural communities - for fuelwood in particular (Du Plessis, 1994; *see* section 1.2, page 8)

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[24] which may explain the disparities observed in the preliminary isotopic analyses conducted on the genus *Cossypha* in South Africa (Appendix A)

pose the largest threat to Choristers. During 1997, two-to-three million households benefitted significantly from forested areas of South Africa (NFAP, 1997) where up to 27-million people utilised plant products (primarily from forested areas - Dold & Cocks, 2002) for their medicinal properties (Mander, 1998); and nine-to-twelve million people (mainly from rural communities; Byron & Arnold, 1999; Neumann & Hirsch, 2000; Cavendish, 2000) exploited well-treed areas for fuelwood, tools and perishable goods (Byron & Arnold, 1999; Botha, 2001; Williams & Shackleton, 2002; Cocks *et al.,* 2004; Shackleton, 2004; Williams, 2004). While the exploitation of forest resources (generally to meet the demands of rural subsistence living; NFAP, 1997; Madubansi, 2003; Lawes *et al.,* 2004) fulfil a vital role in the alleviation of poverty within South Africa (Byron & Arnold, 1999; Neumann & Hirsch, 2000; Cavendish, 2000; Shackleton, 2004), over-harvesting directly affects ecosystem functionality and the persistence of forest patches; especially considering the high proportion (44 % - Statistics SA, 2000) of the country's total population (0.4 billion in 2002 – WHO, 2012) residing in informal settlements (approximately 176 million inhabitants). The direct removal of trees (living, dead or dying) and plants in the under-canopy, combined with the indirect effects of clearing and deforestation, all decrease the size and extent of indigenous forest patches and detract from the number of suitable breeding sites and habitable areas that were once available to Chorister populations.

While predation, parasitism and over-exploitation each have noticeable (and often measurable) qualities, unseen threats also play a veritable role in the conservation and preservation of flora and fauna in South Africa. Global warming, in particular, has the capacity to detract from indigenous forest patches, rendering the demarcation of nature reserves and important bird areas less effective under climate change (Allen & Breshears, 1998; Eeley *et al.,* 1999; Millar *et al.,* 2007; Coetzee *et al.,* 2009; Willis *et al.,* 2009; La Sorte & Jetz, 2010). Although the gradual shifting of montane forests pose considerable limitations on habitat specialists that selectively live and feed within a specific niche, the isotopic signatures and generalised niche-width exhibited by Choristers during this study suggests a certain degree of environmental flexibility that may facilitate adjustments over time. A few signatures (from Schoemansdal Environmental Education Centre and the picnic site in Vernon Crookes, *see* page 54) even alluded to the inclination of some individuals to incorporate a higher degree of meat into their diet in areas frequented by humans, which bodes well for this endemic species in the current biome crisis, despite the population expansion predicted.

Another vital component that plays an integral role in the conservation of Choristers, as well as a plethora of other species, is centered on modern-day forms of information sharing. Regulatory conservation authorities like BirdLife International and the International Union for the Conservation of Nature are often cited by the scientific community as well as governmental and non-governmental organisations (NGOs) that utilise these popular websites as a way to gain fast and easy access to information on a vast number of extant species around the world. However, while these sources contain accurate information on species that are popular to science as well as those that are in the 'public eye', a few of the 'lesser knowns' have a tendency to be overlooked. Although each authority lists *C. dichroa* as a species of Least Concern and acknowledges an overall decline in their numbers, neither website provides a baseline estimate for Choristers; which is understandable given the difficulties associated with monitoring avian populations (Oatley & Arnott, 1998; Symes *et al.,* 2000; Cochran *et al.,* 2004; Coetzee *et al.,* 2009). However, BirdLife International (2008, 2013, 2015) and the IUCN (2012, 2014) have both obtained information on *C. dichroa* from secondary sources (del Hoyo *et al.,* 2005) rather than primary literature, which has led them to erroneously report the occurrence of Choristers in Angola, Ethiopia and western Kenya. In addition to this oversight, not only does BirdLife International (2015) fail to recognise Choristers as an endemic forest robin, it also reports a distribution range for this species that is approximately 2,000,000 ha more than the range of 297,212 ha calculated in Chapter 1 (page 13 - the extent of habitable forest in South Africa as outlined by FSA, 2003; von Maltitz *et al.,* 2003; Benn & Berliner, 2004). Based on the distribution range (2,540,000 ha) defined by BirdLife International (2015), population estimates for *C. dichroa* range between 5,003,800 – 6,273,800 individuals, which differs staggeringly from the 119,362 – 150,869 estimate extrapolated in Section 1.3 (page 13). While Choristers fail to meet any of the criteria set out by the IUCN, these wildly inflated statistics lead to gross overestimates of population abundance that belies the status of this endemic species, which could have serious implications for the management of *C. dichroa* in the future. This not only reinforces the importance of using primary literature (i.e. journal articles) when compiling information on individual species, but also the need for collaborative efforts between primary researchers, the greater scientific community, governmental organisations and various conservation bodies. Accurate information sharing would ultimately aid management practices and increase the efficiency of conservation strategies that are being put into place.

4.2.1. The conservation of Choristers

Over the last two decades, a shift in the biological field has moved the focus of research on ‘stability’ (spatial and temporal consistency; MacArthur, 1955) away from individual populations and on to the structural and functional role that communities play within an ecosystem (MacArthur, 1955; McCann, 1977; Tilman *et al.,* 2006; Mikkelson, 2009), emphasising the importance of biogeography in determining the distribution and abundance of floral and faunal assemblages (Gaston & Spicer, 2004). By independently investigating the life-history and behavioural traits of forest-dependant bird species, accurate and detailed information collated from fecal, feather and blood samples can provide important insights into local resource availability, pollution, and habitat degradation as-well-as the biotic and abiotic factors that govern forest fragments (Midgeley *et al.,* 1997; Symes *et al.,* 2000; Haig *et al.,* 2011; Mills *et al.,* 2011; Solonen & Jokimaki, 2011). To aid conservation efforts directed towards preserving the integrity of South African forests (Kremen, 1992), indicator species should be identified, monitored and employed as ‘early-warning systems’, in a cost-effective, multi-faceted means of tracking biotic changes over time (Landres *et al.*, 1988; Kremen, 1992; Bibby *et al.,* 2000; Carignan & Villard, 2002; Roberge & Angelstam, 2006).

In South Africa, where over-exploitation and the conversion of natural habitat continues to threaten forest fragments and the species within them (Shackleton, 2004; Thuiller *et al.,* 2006), it was originally thought that the narrow distribution range reported for Choristers, combined with their status as an endemic forest specialist, would promote their use as indicators of environmental change. However, despite exhibiting a distribution range sympatric with other sensitive forest species, the wide range of $\delta^{13}C$ (-25.13 to -20.65 ‰) and $\delta^{15}N$ (6.17 to 13.52 ‰) obtained during this study fails to meet the requirements of an endemic forest specialist (*see* Maclean, 1999). As sensitivity to environmental change is purported to increase the efficacy of indicator species (Landres *et al.,* 1988; Carignan & Villard, 2002), Choristers would be ill-suited to this role. Their isotopic signatures indicate a generalist rather than specialist diet that allows Choristers to forage on fruit, invertebrates and possibly even meat, opportunistically, within and beyond the forest interior. Although purported to undertake altitudinal migrations, no evidence was found to support these seasonal movements, suggesting that individuals often maintain their territories throughout the year. A wide diet and lack of seasonal movement implies that Choristers would respond slower to environmental change than other habitat specialists, and could not be used as an early warning detection system for habitat degradation.

Although base line data on *C. dichroa* remains outstanding, del Hoyo *et al.*, (2005), the IUCN (2013) and BirdLife International (2015) all describe a decrease in the number and occurrence of Choristers. In light of the known discrepancies reported by these sources, the accuracy of these reports remain unclear. The most recent account of the distribution of *C. dichroa* in and around South Africa is provided by the South African Bird Atlas Project, which compiles species-specific distribution maps based on reported sightings. To prevent ambiguity, SABAP requires detailed information on the time, date and coordinates of each account; including a photograph of the bird should the sighting occur beyond its range. According to the distribution of Choristers mapped out in SABAP2 (Figure 1, page 15), a distinct decrease has occurred in the range of *C. dichroa* over the last five to six years (Figure 1; SABAP1), lending credence to the population trends reported by BirdLife International and the IUCN. Fortunately, as an unforeseeable advantage of their seemingly sessile nature, a lack of movement between forest patches does limit the number of Choristers that could potentially be re-counted (in different forest patches), rendering over-estimates of populations unlikely. At a best guess, the total population of *C. dichroa* ranges from 119,362 to 150,869 individuals; but it should be noted that these estimates are based on a combination of outdated land cover assessments (2003/2004) and a density of Choristers (2.22 ± 0.25 ha^{-1}) reported for KZN in unpublished work (Brocklehurst, 2009).

Future work on *C. dichroa* would benefit from utilising SABAP2 as a baseline geographic distribution for this endemic species, which could be supplemented with ringing data from SAFRING to obtain size-, age- and sex- ratios of Chorister populations around South Africa. As the isotopic signatures indicate little movement between the populations sampled, DNA analyses are needed to determine the extent of genetic migration that is occurring across the range of *C. dichroa*. Given the skewed age- and sex- ratios exhibited by populations in KZN, a lack of seasonal movements may inadvertently cause genetic bottlenecks in some forest fragments (and may even contribute to the hybridisation of Choristers with Red-Capped Robin-Chats). More research into the life-history traits and population dynamics of this endemic forest robin are needed to ascertain their resistance to environmental change. Extensive sampling is required across the eastern escarpment of South Africa; especially in the isolated Chorister populations that reside within the coastal forests of Knysna and the Tsitsikamma (SABAP2; Figure 1).

4.3. Conclusion

No evidence of movement (inter- or regional) was detected in the ^{13}C and ^{15}N signatures obtained for Choristers in South Africa, which suggests that these birds remained within an established territory throughout the year. As *C. dichroa* reportedly live up to 26 years, maintaining life-long monogamous pair-bonds (*see* Collar, 2005 in del Hoyo *et al.*, 2005; but also Oatley, 1997, 1998; Oatley & Arnott, 1998), forest management strategies need to be instituted to curb the rate of trees removed from high and low-altitude forests each year (Keith *et al.* 1992; Du Plessis, 1994; Oatley & Arnott, 1998). To make informed decisions regarding the conservation management of forest fragments in South Africa, effective wildlife management practices should aim to incorporate as many species specific life-history traits as possible - particularly when making informed decisions regarding the demarcation and utilisation of Nature Reserves and Important Bird Areas (IBAs) in Protected Area Networks around South Africa.

Although various papers have advocated feather sampling as the easiest way of obtaining isotopic and genetic material with minimal impact on focal individuals (Bello *et al.* 2001; Smith *et al.* 2003; Harvey *et al.* 2006), feathers are by no means the most robust form of obtaining quantitative data (Harvey *et al.* 2006; M^{c}Donald & Griffith, 2011). Many studies have subsequently incorporated blood and/or tissue analyses into their research, promoting the former as an unrivalled source of information that can also be easily stored and archived for future use to gain a temporal understanding of population dynamics and migrational movements of a target species (Groth & Barrowclough, 1999; Ericson & Johansson, 2003; Smith *et al.* 2003; Harvey *et al.* 2006; M^{c}Donald & Griffith, 2011). The use of blood work (with its rapid turnover rates) would supplement the isotopic signatures and dietary information obtained from feathers of *C. dichroa*, providing short-term snapshots of their feeding ecology in the areas sampled. This addition would also facilitate a more in-depth and robust means of detecting migrational movements, dietary shifts and lifestyle changes within populations of *C. dichroa* over time, and may even contribute to information on the extent of inbreeding with *C. natalensis* (Smith *et al.* 2003).

Appendix A

Preliminary analyses of stable carbon and nitrogen isotope signatures (mean ± SD ‰) in tail feathers of five robin-chat (genus *Cossypha*) species within South Africa. A one-way ANOVA was used to detect differences among isotopic signatures for each species. Within each column *superscript lettering* indicates the level of significance (Tukey HSD post-hoc test for multiple comparisons, $p < 0.005$), where values that differ significantly do not share a common letter.

Cossypha species	Location	n		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
C. caffra	South Africa	45		-21.73 ± 1.30^{a}	10.42 ± 2.10^{a}
C. dichroa	South Africa	39		-23.60 ± 0.79^{b}	$8.77 \pm 1.80^{a,b}$
C. heuglini	South Africa	11		-23.23 ± 0.95^{b}	8.32 ± 1.29^{b}
C. humeralis	South Africa	4		-21.91 ± 0.14^{a}	8.30 ± 0.50^{b}
C. natalensis	South Africa	61		-23.41 ± 0.73^{b}	8.17 ± 0.50^{b}
			ANOVA	$F = 28.2$ $p < 0.0001$	$F = 11.26$ $p < 0.0001$

Appendix B

Geographic information pertaining to sites within the study where Choristers were captured, measured, and released (*n* = sample size).

Site	Latitude (S)	Longitude (E)	Altitude (meters above sea level)	Province	*n*
Ridgeways, Makhado	22˚59'59.409"	29˚56'43.551"	1201	L	8
Schoemansdal Environmental Education Centre, Schoemansdal	23˚01'04.299"	29˚43'31.598"	969	L	1
Maluma Boerdery, Levubu	23˚02'49.200"	30˚15'52.801"	696	L	4
Vireers Farm, Levubu	23˚04'23.041"	30˚13'57.889"	730	L	1
Vernon Crookes Nature Reserve, forest patch on northern border	30˚15'59.900"	30˚35'54.200"	474	KZN	1
Vernon Crookes Nature Reserve, eastern valley site	30˚16'00.299"	30˚37'10.700"	354	KZN	4
Vernon Crookes Nature Reserve, bush near camp managers site	30˚16'17.000"	30˚36'30.301"	339	KZN	3
Vernon Crookes Nature Reserve, campsite	30˚16'27.901"	30˚36'36.202"	414	KZN	8
Vernon Crookes Nature Reserve, waterfall	30˚16'28.402"	30˚37'00.199"	324	KZN	2
Ngele Forest, Weza	30˚31'36.548"	29˚40'10.261"	1275	KZN	2
Fort Fordyce Nature Reserve	32˚41'02.421"	26˚29'41.690"	1117	EC	4
Moneysworth Farm, Kenton-on-Sea	33˚37'48.280"	26˚41'23.640"	89	EC	1

Appendix C

		Scale 1	*Scale 2*	*Scale 3*	*Scale 4*
Ring number	Ringing location	Provincial	Provincial Split	Area	Site
CC82275	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82276	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82277	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82278	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82280	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC80122	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82280	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82277	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. campsite
CC82295	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. managers office
CC82296	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. managers office
CC82299	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. managers office
CC82295	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 1	V.C. *camp*	V.C. managers office
CC82288	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 2	V.C. *wild*	V.C. eastern valley
BE37939	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 2	V.C. *wild*	V.C. eastern valley
CC80119	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 2	V.C. *wild*	V.C. eastern valley
CC82292	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 2	V.C. *wild*	-
CC82293	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 2	V.C. *wild*	-
BE37965	Vernon Crookes	KwaZulu-Natal	KwaZulu-Natal 2	V.C. *wild*	-
CC80101	Ngele Forest	KwaZulu-Natal	KwaZulu-Natal 2	-	-
CC80103	Ngele Forest	KwaZulu-Natal	KwaZulu-Natal 2	-	-
CC80165	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80167	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80168	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80166	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80211	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80166	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80212	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80213	Soutpansberg	Limpopo	Limpopo 1	Ridgeways	Ridgeways
CC80226	Soutpansberg	Limpopo	Limpopo 1	-	-
CC80177	Soutpansberg	Limpopo	Limpopo 2	Maluma Boerdery	Maluma Boerdery
CC80180	Soutpansberg	Limpopo	Limpopo 2	Maluma Boerdery	Maluma Boerdery
CC80245	Soutpansberg	Limpopo	Limpopo 2	Maluma Boerdery	Maluma Boerdery
CC80180	Soutpansberg	Limpopo	Limpopo 2	Maluma Boerdery	Maluma Boerdery
CC80249	Soutpansberg	Limpopo	Limpopo 2	-	-
BD39194	Fort Fordyce	Eastern Cape	Eastern Cape 1	Fort Fordyce	Fort Fordyce
BD98532	Fort Fordyce	Eastern Cape	Eastern Cape 1	Fort Fordyce	Fort Fordyce
BD98552	Fort Fordyce	Eastern Cape	Eastern Cape 1	Fort Fordyce	Fort Fordyce
BD98554	Fort Fordyce	Eastern Cape	Eastern Cape 1	Fort Fordyce	Fort Fordyce
BE47515	Kenton-on-Sea	Eastern Cape	-	-	-

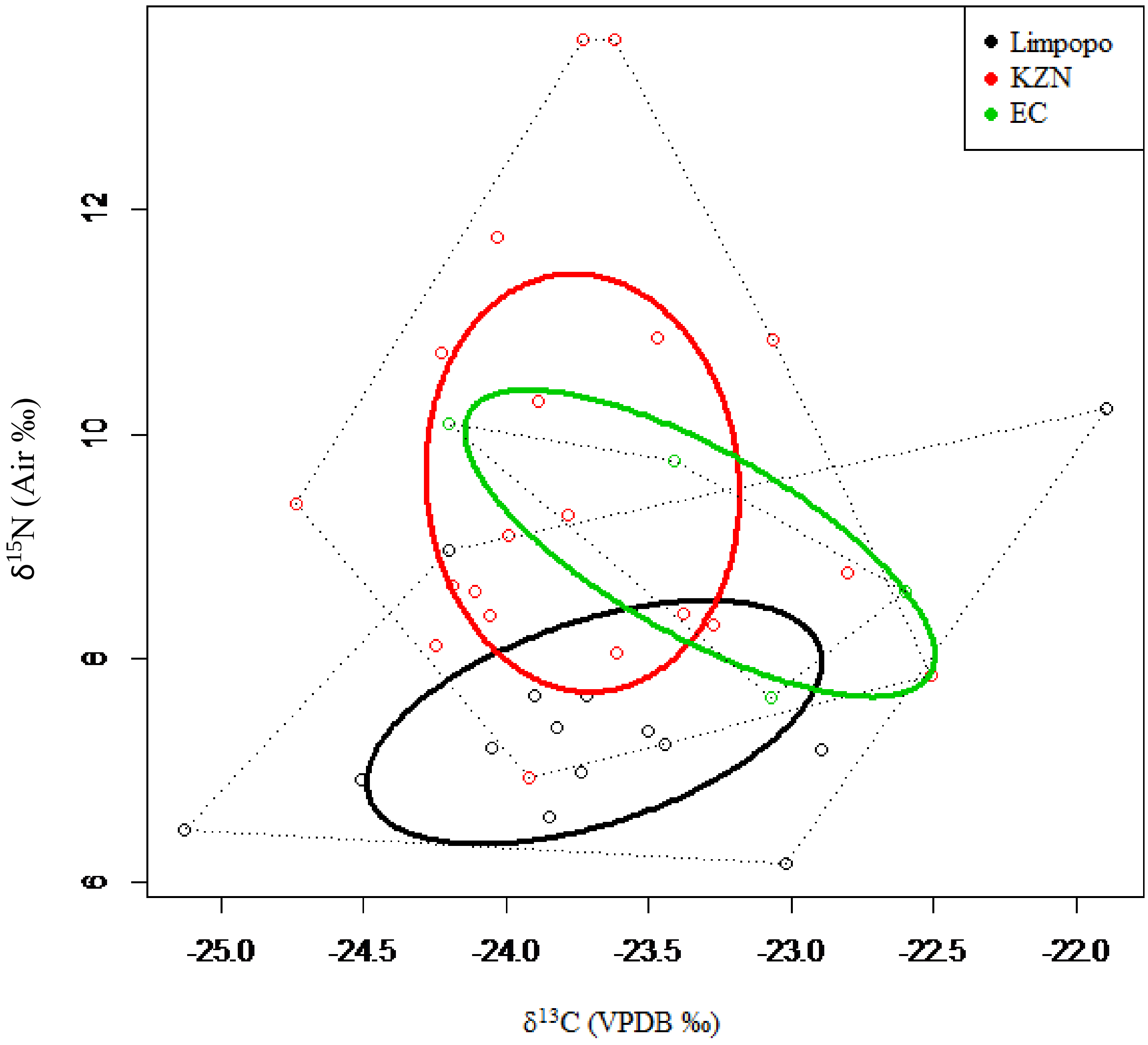
Appendix D

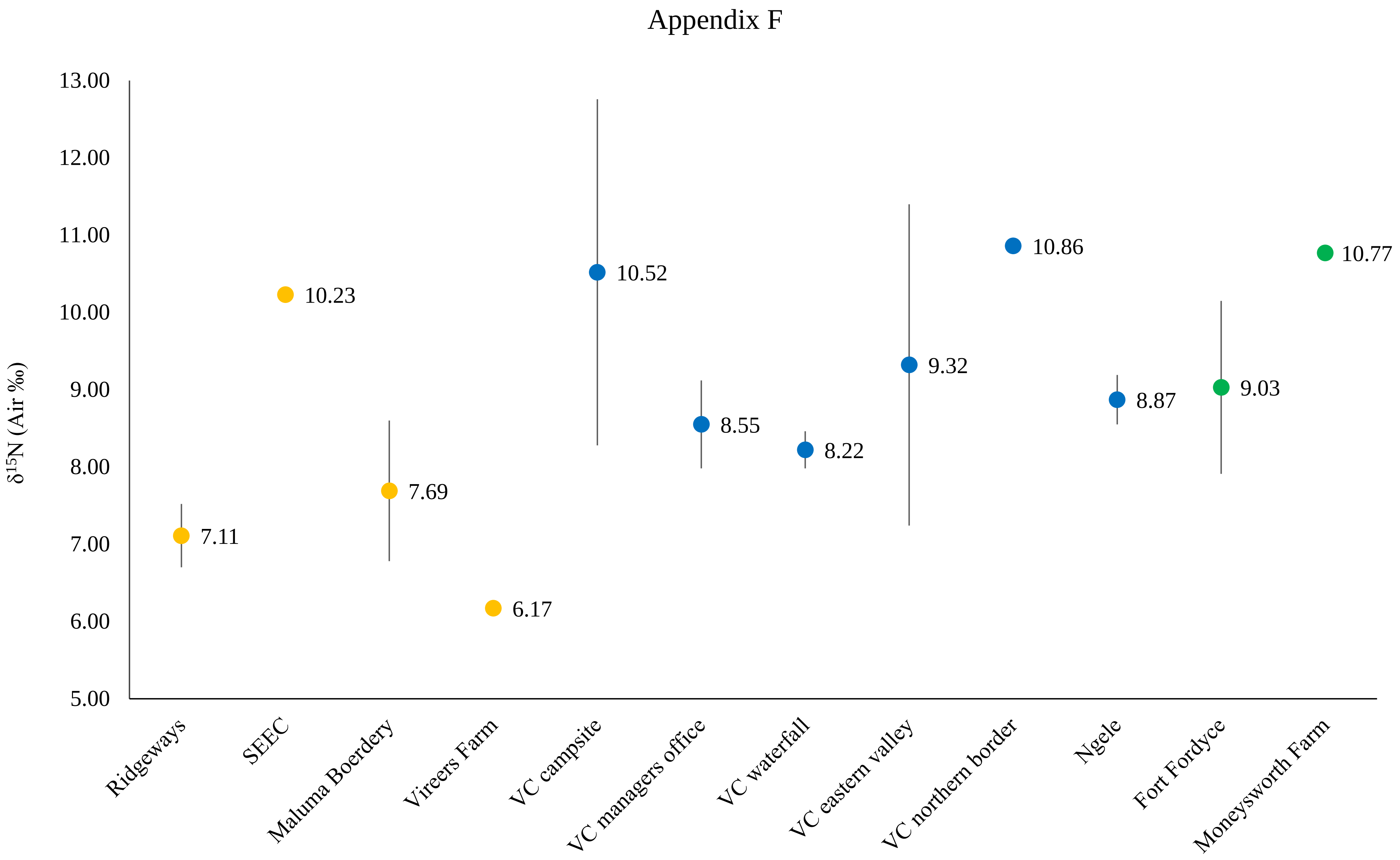
A rank of carbon and nitrogen stable isotope signatures obtained from tail feathers of Choristers in South Africa. Red text represents information pertaining to hybridised birds while colour-paired asterisks (*) illustrate recaptures.

Scale 4	*Scale 3*	*Scale 2*	*Scale 1*	δ^{13}C (VPDB ‰)	**Rank**	δ^{15}N (Air ‰)	*Scale 1*	*Scale 2*	*Scale 3*	*Scale 4*
-	-	-	EC	-20.65	**1**	13.52	KZN	KZN 1	VC camp	VC campsite
-	-	L 1	L	-21.89	**2**	13.52	KZN	KZN 1	VC camp	VC campsite
VC campsite	VC camp	KZN 1	KZN	-22.51 *	**3**	11.75 *	KZN	KZN 1	VC camp	VC campsite
Fort Fordyce	Fort Fordyce	EC 1	EC	-22.60	**4**	10.86	KZN	KZN 2	VC wild	-
VC campsite	VC camp	KZN 1	KZN	-22.80	**5**	10.84	KZN	KZN 1	VC camp	VC campsite
Ridgeways	Ridgeways	L 1	L	-22.89 *	**6**	10.77	EC	-	-	-
-	-	L 2	L	-23.02	**7**	10.72	KZN	KZN 2	VC wild	VC east valley
VC campsite	VC camp	KZN 1	KZN	-23.06	**8**	10.30	KZN	KZN 2	VC wild	VC east valley
Fort Fordyce	Fort Fordyce	EC 1	EC	-23.07	**9**	10.23	L	L 1	-	-
VC office	VC camp	KZN 1	KZN	-23.27	**10**	10.09	EC	EC 1	Fort Fordyce	Fort Fordyce
VC office	VC camp	KZN 1	KZN	-23.38 *	**11**	9.76	EC	EC 1	Fort Fordyce	Fort Fordyce
Fort Fordyce	Fort Fordyce	EC 1	EC	-23.41	**12**	9.38	KZN	KZN 1	VC camp	VC office
Ridgeways	Ridgeways	L 1	L	-23.44	**13**	9.28 *	KZN	KZN 1	VC camp	VC campsite
-	VC wild	KZN 2	KZN	-23.47	**14**	9.10	KZN	KZN 2	-	-
Ridgeways	Ridgeways	L 1	L	-23.50	**15**	8.96	L	L 2	Maluma	Maluma
-	VC wild	KZN 2	KZN	-23.61	**16**	8.77	KZN	KZN 1	VC camp	VC campsite
VC campsite	VC camp	KZN 1	KZN	-23.62	**17**	8.64	KZN	KZN 2	-	-
Ridgeways	Ridgeways	L 1	L	-23.72	**18**	8.60	EC	EC 1	Fort Fordyce	Fort Fordyce
VC campsite	VC camp	KZN 1	KZN	-23.73	**19**	8.60 *	KZN	KZN 1	VC camp	VC campsite
Ridgeways	Ridgeways	L 1	L	-23.74	**20**	8.39 *	KZN	KZN 1	VC camp	VC office
VC campsite	VC camp	KZN 1	KZN	-23.78 *	**21**	8.38	KZN	KZN 2	VC wild	-
Ridgeways	Ridgeways	L 1	L	-23.82	**22**	8.29	KZN	KZN 1	VC camp	VC office
Ridgeways	Ridgeways	L 1	L	-23.85	**23**	8.12 *	KZN	KZN 1	VC camp	VC office
VC east valley	VC wild	KZN 2	KZN	-23.89	**24**	8.05	KZN	KZN 2	VC wild	-
Maluma	Maluma	L 2	L	-23.90 *	**25**	7.85 *	KZN	KZN 1	VC camp	VC campsite
VC east valley	VC wild	KZN 2	KZN	-23.92	**26**	7.67 *	L	L 2	Maluma	Maluma
-	-	KZN 2	KZN	-23.99	**27**	7.67	L	L 1	Ridgeways	Ridgeways
VC campsite	VC camp	KZN 1	KZN	-24.03 *	**28**	7.65	EC	EC 1	Fort Fordyce	Fort Fordyce
Maluma	Maluma	L 2	L	-24.05 *	**29**	7.39	L	L 1	Ridgeways	Ridgeways
-	VC wild	KZN 2	KZN	-24.06	**30**	7.35	L	L 1	Ridgeways	Ridgeways
VC campsite	VC camp	KZN 1	KZN	-24.11 *	**31**	7.24	L	L 1	Ridgeways	Ridgeways
-	-	KZN 2	KZN	-24.19	**32**	7.20 *	L	L 2	Maluma	Maluma
Fort Fordyce	Fort Fordyce	EC 1	EC	-24.20	**33**	7.18 *	L	L 1	Ridgeways	Ridgeways
Maluma	Maluma	L 2	L	-24.20	**34**	6.99	L	L 1	Ridgeways	Ridgeways
VC east valley	VC wild	KZN 2	KZN	-24.23	**35**	6.93	KZN	KZN 2	VC wild	VC east valley
VC office	VC camp	KZN 1	KZN	-24.25 *	**36**	6.91	L	L 2	Maluma	Maluma
Maluma	Maluma	L 2	L	-24.51	**37**	6.59	L	L 1	Ridgeways	Ridgeways
VC office	VC camp	KZN 1	KZN	-24.74	**38**	6.46 *	L	L 1	Ridgeways	Ridgeways
Ridgeways	Ridgeways	L 1	L	-25.13 *	**39**	6.17	L	L 2	-	-

Appendix E

A graphical representation of the isotopic niche width - as illustrated by inner standard ellipses (SE) - of Choristers within the Limpopo (*n* = 14), KwaZulu-Natal (*n* = 20) and Eastern Cape (*n* = 4) provinces of South Africa. The carbon and nitrogen signature from Kenton (*n* = 1) was omitted from this analyses to illustrate the effect of this ‘coastal’ outlier on the original EC group (*n* = 5, Figure 13, page 51).




Appendix F
δ15N (Air ‰)
13.00
12.00
11.00
10.00
9.00
8.00
7.00
6.00
5.00
7.11
10.23
7.69
6.17
10.52
8.55
8.22
9.32
10.86
8.87
9.03
10.77
Ridgeways
SEEC
Maluma Boerdery
Vireers Farm
VC campsite
VC managers office
VC waterfall
VC eastern valley
VC northern border
Ngele
Fort Fordyce
Moneysworth Farm

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