The identity, origin and impact of a 'new' buzzard species breeding in South Africa

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November 2014

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Thesis submitted in fulfilment of the degree of Master of Science

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Abstract

South Africa is traditionally known to play host to two taxa of small *Buteo*, the endemic and uncommon Forest Buzzard *B. trizonatus,* and Steppe Buzzard *B. b. vulpinus,* an abundant Palearctic migrant. Since the late 1970s and early 1980s, a number of buzzards appearing unlike *B. trizonatus* have been found breeding in the south-west Cape, particularly on the Cape Peninsula and in and around the Elgin Valley, ca.60km east of Cape Town. Some of these buzzards resemble *B. b. vulpinus,* whilst others appear atypical of both *B. trizonatus* and *B. b. vulpinus*.

This study conducted genetic and morphological analyses on a number of buzzards sampled in the south-west Cape, and compared them with three candidate taxa considered most likely to, in full or in part, explain the identity of these ‘mystery’ buzzards. The candidate taxa were: Steppe Buzzard *B. b. vulpinus*, Ménétries’s Buzzard *B. b. menetriesi* and Forest Buzzard *B. trizonatus.* Morphology data and genetic samples were collected from 23 buzzards through capture with a Bal-Chatri trap, from chicks in nests, from captive birds brought to rehabilitation centres or from birds found dead.

The comparative morphology of the buzzards sampled in the Cape was determined by constructing a Discriminant Component Analysis using 9 morphometric characters which had previously been established as being important in the separation of Old World *Buteo* taxa (Kruckenhauser *et al.,* 2004). Blood samples were then analysed using 18 polymorphic microsatellite loci designed for *Buteo swainsoni* (Hull *et al.,* 2007), using the program STRUCTURE 2.3 to analyse the population assignment of the sampled buzzards. The majority of buzzards were found to most closely match *B. trizonatus* or *B. b. vulpinus* in their morphology (52%), and their genetic signature (65%).

Additionally, two unidentified genetic signatures were evident. One of these signatures remains unresolved, because buzzards with this genetic signature lacked morphological data. The second signature, however, was displayed by buzzards with larger morphology than is known from both *B. b. vulpinus* and *B. trizonatus*. Based on previous research these larger buzzards lay most closely within the morphospace of *B. b. menetriesi*, being far removed from the morphospace of both *B. b. vulpinus* and *B. trizonatus*. Thus, it is conceivable that some of the birds belong to this taxon.

An observation of the foraging and breeding ecology of the buzzards in the study areas was also conducted but did not prove useful in clarifying the identity of the buzzards. The buzzards were observed to feed on a wide variety of prey, with the majority of their diet being made up by small mammals (59.4%) and invertebrates (24.3%), primarily caught through perch-hunting. Almost all nest records to date have been in trees, predominantly *Pinus* sp., although one instance of cliff nesting has been recorded. Interestingly, widespread apparent hybridisation has been observed occurring between *B. trizonatus* and birds appearing typical of *B. b. vulpinus*. As would be expected in such a taxonomically-young and widely hybridising group of raptors, there appear to be no pre- or post-zygotic barriers to hybridisation.

It appears clear that *B. b. vulpinus* is breeding in South Africa, and indeed hybridising with *B. trizonatus.* There also appears to be some argument that birds typical of *B. b. menetriesi* morphology might also be part of the breeding pool. An unresolved puzzle from this study was the presence of buzzards that possess plumage most like that of the uniform morphs of *B. b. vulpinus*, or perhaps *B. b. menetriesi*, but display the genetic signature of *B. trizonatus*. This would appear to suggest that there may be a previously undescribed uniform rufous morph of *B. trizonatus*. However, these birds were also larger in their morphology than typical *B. trizonatus*, being most similar to *B. b. menetriesi.*

Clearly the taxon-dynamics of buzzards in the Cape is complex and further study is required before any definitive conclusions can be drawn, particularly with regard to the presence of *B. b. menetriesi* and the identity of the apparent rufous morph *B. trizonatus*.

Acknowledgements

Firstly, my sincerest thanks must go to the late Professor Phil Hockey, for always being available to chat and discuss theories and issues, and for supporting and encouraging me even in difficult times. Your guidance and willingness to field my imaginative theories will always be appreciated. My sincerest gratitude must also go to Dr. Arjun Amar, for providing guidance and consistently helpful and constructive comments on my work from start to finish. Also, for committing more of his time and efforts to me after Phil had passed.

I must also thank Prof. Rauri Bowie and Beth Wommack for their expertise in the genetic component of this study. I can't thank them enough for guiding me through this stage and for their comments on my work.

Of course, I would like to convey my eternal gratitude to my parents, Bruce and Claire. To my mother, for grinning and bearing my constant need for (mis)adventure and being unwaveringly supportive. To my Dad, for his boundless support, assistance, patience, friendship and companionship both in and out of the field; my thanks to both, for invariably encouraging and nurturing my passion and obsession, and for always supporting my ambitions.

I would also like to thank my tremendous other half, Emma, for constantly providing support, assistance and an ear to listen, and for playing field assistant whenever I needed her. I can't thank her enough, and can't underplay her importance in keeping me on track and on the right side of a mental break down at times.

My greatest thanks to Dr. Anita Gamauf for her comments, support, and for providing the most bewilderingly comprehensive Buteo morphometric data I could ever have hoped for.

I must also thank Margaret Koopman for her incredible support in the Library and for providing a roof and family for me on arrival in South Africa, and indeed throughout my time in the Cape. My thanks together with Patrick Morant for their support, advice, wisdom, care and endless humour; your kindness and generosity will forever be remembered, and one day repaid.

My deepest and sincerest thanks must go to my field team. To Ann Koeslag for her tireless and fantastic efforts and support in the field; also for providing a much needed ear to listen, and many cups of tea while staring at a cage full of rodents. Also, to Johan Koeslag for his

good humour and support in sampling from nests, and to Mark for climbing trees I would have deemed impossible, with great style. To Hank Chalmers and the whole team at Eagle Encounters for their overwhelming enthusiasm and drive, and for the many blood samples and carcasses, advice and practical help in the field. Also to Dennis at Radical Raptors, Plettenberg Bay, for his excellent advice and assistance. To Chris Heward, for his never-waning enthusiasm and for providing a birding companion when the buzzards weren't behaving; to Jessie Berndt for diverting an imminent catastrophe by providing field assistance, and to Sam Jones for helping to inadvertently add a little adventure to proceedings.

My gratitude to SANParks, CapeNature and MTO for access to their land, and to CapeNature for the *B. rufofuscus* specimens held at the Museum of Vertebrate Ecology, University of California, Berkeley. My thanks to Alastair Kilpin, Carin Malan, Andre Du Toit, Jessie Walton, Rob Martin and many of the farmers in Elgin and on the Cape Peninsula for access to their land, assistance and/or companionship in the field, and for data and insights from past seasons.

Last, but far from least, I would like to thank everyone at the Fitz for their help and support in one way or another. Hilary Buchanan, Chris Tobler, Tania Jansen and Anthea Links for being finance, logistics and administrative superstars, and for putting a smile on my face each and every time I visited; Dr. Rob Simmons for his valuable advice and willingness to share his experience; Dr. Rob Little for his down-to-Earth support and encouragement; and to Dr. Graeme Oatley for his assistance and guidance in preparing and shipping genetic material. I would particularly like to thank Owen Davies; from help with trap building and data analysis, to inducting me into the South African way of life, your guidance and friendship is truly valued and appreciated.

Chapter 1: General introduction, hypotheses and aims of the study

Taxonomy, the science of defining groups of organisms for the purpose of identification, nomenclature and classification, recognises and quantifies the geographic variation among species (Judd *et al.*, 2007). The term 'species', being a unit of biological classification and taxonomic rank, defines groups of living organisms consisting of similar individuals, capable of interbreeding or exchanging genes (Soanes and Stevenson, 2010). This system of classification is paramount to how we, as humans, understand and explore the natural world.

The species problem, which addresses the criteria by which species are defined in terms of their traits (Robson, 1928), has been much debated, however under the biological species concept Mayr (1942) proposed that there are three variables to consider when assessing the validity of classifying a taxon as a species: (1) Genetic and (2) phenotypic variation, and (3) an isolated breeding core. However, it is now clear that these three variables are somewhat over simplistic. For example, such variation is more apparent in some species than others, as is the case of the Lesser Whitethroat *Sylvia curruca* complex, which shows vast plumage variation over its geographic range (Shirihai *et al.,* 2001), whereas the Orphean Warblers (Western *Sylvia hortensis* and Eastern *Sylvia crassirostris*) differ little in their phenotypic characters but proves genetically highly divergent. Similarly, some species complexes such as the Band Rumped Storm-Petrel *Oceanodroma castro* feature subspecies and apparently viable species within a single population that breed in the same geographic location, albeit in different seasons (Friesen, 2007; Bolton *et al.,* 2008; Howell *et al*., 2010). In these cases, it is the timing of the breeding that creates the isolation rather than the geography.

Others have defined 'a species' as the largest group of organisms capable of interbreeding and producing fertile offspring (Soanes and Stevenson, 2010), however this definition has proven insufficient or flawed, since there are many species complexes where hybridisation is rife. Thus, the issue of hybridisation is a prominent component in the field of taxonomy. Such hybridisation can in some cases lead to the dissolution of the geographic isolation that once afforded species the ability to evolve and survive separately. In some cases, this can result in extinction through genetic dilution (Rhymer & Simberloff, 1996). One key example is the Black Stilt *Himantopus novaezelandiae*, a critically endangered wader found in the Mackenzie Basin of New Zealand (Wallis, 1999; Robertson & Heather, 2005). The decline of the Black Stilt has been exacerbated by the natural colonisation of the White-headed Stilt *Himantopus leucocephalus,* giving rise to widespread hybridisation and apparent genetic dilution (Pierce, 1996). Similarly, the dire situation faced by the White-headed Duck *Oxyura leucocephala* in Europe is in part a result of widespread hybridisation with introduced Ruddy Duck *Oxyura jamaicensis* (Muñoz-Fuentes *et al.*, 2006) from North America. Following a severe population bottleneck in White-headed Duck, the rapid establishment of introduced Ruddy Duck from just 7 individuals has resulted in prolific hybridization across the White-headed Duck's range, and it appears clear that without effective control and intervention, genetic introgression will compromise the survival of the White-headed Duck as a genetically distinct species (Muñoz-Fuentes *et al.*, 2006).

Given that species can be formed through geographic isolation of populations over long periods of time, the process of colonisation is important in understanding this (Mayr, 1940; Newton, 2007). Though colonisation can occur when small populations are established through vagrancy, for example the Cattle Egret *Bubulcus ibis* in the New World (Crosby, 1972; Maddock & Geering, 1994), it often appears to be pioneered by species that begin as migrants to an area and subsequently abandon their migratory instincts and begin to breed (Newton, 2007). Breeding in isolation, over time, these pioneer populations have the potential to form new species (Darwin, 1859; Bildstein & Zalles, 2005). The *Buteo* buzzards are a perfect example of this process, being known to colonise new areas through 'migration dosing', whereby individuals misdirect their migration and become stranded in areas from which they are unable to return to their traditional breeding grounds (Bildstein & Zalles, 2005). Indeed this is the system by which Steppe Buzzard *B. b. vulpinus* is thought to have colonised southern Africa, and subsequently given rise to Forest Buzzard *B. trizonatus* (Clark, 2007).

The colonisation of South Africa by breeding populations of Palearctic migrant species is not a novel phenomenon, with several species having established populations in the past. European Bee-eaters *Merops apiaster* first bred in South Africa in *ca* 1855 (Hockey *et al.,* 2005) and have continued to expand their population (Brooke & Herroelen, 1988), whilst White Storks *Ciconia ciconia* bred at least as early as the 1930s (Allan, 1997) but the breeding population, which persists today, has never exceeded ten pairs (Brooke, 1984). Common House Martin *Delichon urbicum* has also attempted to breed on several occasions, though there is no evidence that attempts have progressed beyond the nest-building stage in recent times (Hockey *et al.*, 2005). Leach's Storm Petrel *Oceanodroma leucorhoa* was another initial colonisation success story, with breeding first confirmed in 1996 but attempted breeding suspected since the 1970s (Whittington *et al,* 1999; Underhill *et al*, 2002). The initial extent of breeding was 20 - 25 pairs, although it has decreased to just five pairs in recent years (Kemper *et al*., 2006).

Another Palearctic-breeding colonist whose arrival process may have initially gone unnoticed is the Booted Eagle *Hieraaetus pennatus*. The first confirmed breeding of the species in South Africa was in 1973 (Martin & Martin, 1974), but by 2001 the resident breeding population in the Western and Eastern Cape Provinces was estimated at around some 700 pairs, suggesting that colonisation may have started considerably earlier than the 1970s (Pepler *et al.,* 2001). Biometric and mitochondrial DNA analysis of European and South African specimens of Booted Eagle subsequently found marginal differences between the two populations (Yosef *et al.,* 2000), suggesting some genetic isolation and confirming that colonisation took place much earlier than previously suspected, perhaps as early as the 1800s (Brooke *et al.,* 1980).

There is thus precedent for the colonisation of Southern Africa by Palearctic-breeding species. However, to date, the only recorded incidence of hybridisation with an indigenous species is between Cape Gannet *Morus capensis* and Australian Gannet *Morus serrator* in the south-west Cape (McCarthy, 2006; Hockey *et al*., 2005).

Taxonomy and speciation of Old World *Buteo* buzzards

The taxonomy of the Old World *Buteos* is unclear and heavily debated, with their extremely close relatedness being well established (Kruckenhauser et. al., 2004). The genetic component of the seminal Kruckenhauser *et al.* (2004) investigation found almost no sequence divergence amongst the entire *buteo-vulpinus* complex, with this lack of genetic variation extending to Long-legged Buzzard *Buteo rufinus* and Mountain Buzzard *Buteo oreophilus*. This would suggest either widespread gene flow, or an extremely young group of raptors. In support of this, hybridisation is widely encountered in many contact zones (McCarthy, 2006), for example between Long-legged Buzzard *B. r. rufinus* and Common Buzzard *B. b. buteo* (Kotymán *et al*., 2008), and *B. b. buteo* and Rough-legged Buzzard *B. lagopus* (Gjershaug *et al*., 2006), with hybrid birds being frequently encountered throughout the Palearctic.

The Kruckenhauser *et al.* (2004) investigation did however show that morphology can prove useful in discriminating taxa, in some instances. It was found that each of the Old World *Buteo*s could be placed in one of three morphological clades, relating directly to their preferred habitat type. *Buteo b. buteo, B. b. hispaniae, B. b. insularum, B. b. harteri, B. hemilasius, B. r. rufinus* and *B. r. cirtensis* are allied morphologically, and are found in mixed or dry, open habitats. The morphologically similar *Buteo b. arrigonii, B. b. menetriesi, B. b. vulpinus, B. trizonatus, B. japonicus, B. refectus, B. b. toyoshimai,* and *B. oreophilus* occur in forested habitats. The third morphological grouping contains *Buteo b. rothschildi, B. b. socotraensis, B. b. bannermani* and *B. brachypterus*. With the exception of *B. brachypterus*, which is found in densely forested habitats, these are all species of dry, open habitats on islands (Kruckenhauser *et. al.,* 2004).

Colour and plumage pattern can also sometimes provide limited information about phylogenetic relationships, and plumage variability in Old World *Buteo*s appears to be correlated with extent of a taxon's range (Kruckenhauser *et. al.*, 2004). Plumage variation is higher in taxa with large distributions (e.g. *B. b. buteo* & *B. b. vulpinus*) and comparatively lower in taxa with smaller ranges (e.g. *B. b. menetriesi* & *B. trizonatus)* (Kruckenhauser *et. al.,* 2004).

Within this present study, I have chosen to refer to the candidate buzzards as taxa rather than species. This is for the sake of consistency, clarity and accuracy, given the presence of both subspecies and apparently viable species under consideration as candidates in this study.

The *Buteo* buzzards of South Africa

South Africa was previously understood to play host to only two breeding species of *Buteo* buzzard, the Forest Buzzard *Buteo trizonatus,* endemic to South Africa, and the Jackal Buzzard *B. rufofuscus,* endemic to Southern Africa (Boshoff, 1997a; Medelsohn, 1997; Harrison *et al.,* 1997; Hockey *et al.*, 2005). *B. trizonatus* is a relatively recent colonist of the Western Cape, first arriving in the late 1970s or early 1980s (Martin *et al.,* 1979; Martin *et al.,* 1981; Boshoff *et al.*, 1983) from the Eastern Cape, where it was recorded as early as 1939 (Courtenay-Latimer, 1941), though presumably it had been present for a great deal longer than this first record for the Eastern Cape suggests. Throughout the Western Cape it is patchily distributed and uncommon (Boshoff, 1997a).

In addition to these two endemic residents, the Western Cape is host to two Palearctic-breeding 'buzzards' as summer migrants; Steppe Buzzard *Buteo buteo vulpinus* and European Honey Buzzard *Pernis apivorus*, though *P. apivorus* is in fact part of the kite family (Gamauf & Haring, 2004). *B. b. vulpinus* is the most numerous raptor in the Western Cape lowlands during the austral summer (Broekhuysen & Siegfried, 1970). *P. apivorus* was previously only a rare visitor to the north east of South Africa; it is now, however, recorded with increasing frequency in the extreme south-west of the Western Cape (Hockey *et al*., 1989; Pepler & Martin, 1995; Pepler & Martin, 1997), where displaying birds have been observed (P.Whittington, pers. obs.).

History of the atypical buzzards in the south-western Cape

There have been numerous reports of uniform rufous and uniform brown buzzards from across the Western Cape since the 1960s, when Peter Steyn first found 'unusual' buzzards breeding on the Cape Peninsula (P. Steyn, pers. Comm.; Broekhuysen, 1963). At the time, however, these were dismissed as *B. trizonatus* without further investigation. A uniform brown breeding buzzard was observed east of Swellendam in the mid-1980s (R. Martin, pers. comm.), and uniform and 'unusual' buzzards breeding in the Grabouw region were recorded from the mid to late 1980s (J. Walton, pers. comm.).

In 2002, an atypically plumaged pair of buzzards bred on the Constantiaberg on the Cape Peninsula, one of which was uniformly rufous, while the other had extensively dark brown underparts (Curtis & Koeslag, 2007). The plumage of this pair of Buzzards was very different from either of the endemic breeding *Buteo* species (Curtis & Koeslag, 2007), and spawned the term 'mystery buzzard'. This term has now developed to include all breeding buzzards, as well as buzzards occurring in the austral winter, that do not appear typical of *B. trizonatus* or *B. rufofuscus*. It is important to note that *B. b. vulpinus* is known to regularly overwinter in South Africa (Hockey *et al.,* 2005), and this would likely explain the occurrence of individuals appearing most like *B. b. vulpinus* during the austral winter however they have yet to be documented as breeding in South Africa.

Subsequent to the 2002 discovery, many atypical individuals and indeed breeding pairs have been discovered throughout the Western Cape at sites ranging from Kirstenbosch National Botanical Gardens and Tokai Forest Plantation on the Cape Peninsula, to Stellenbosch and a now stronghold in the Elgin Valley area east of False Bay (Clark, 2009; Martin & Walton, 2011). More recently (since 2011), birds have also been observed along the west coast in winter as far north as Veldriff, and have been recorded breeding as far east as George (per. obs.) (Figure 1.1). There has also been a single report of a 'rufous' Buzzard in winter as far east as Port Elizabeth, which is in the core of the Forest Buzzard's breeding range (Clark, 2009), alongside several observations of uniform buzzards in Knysna and reports of uniform brown buzzards from the forests of Limpopo (L. Rodrigues, pers. obs.), also in the Austral winter.

The plumage of these now widespread resident and breeding buzzards ranges from entirely rufous and entirely 'chocolate-brown' to varying degrees of brown or rufous with heavy abdominal streaking and a pale breast band, phenotypes most common among Steppe Buzzard *B. b. vulpinus* and apparently also Ménétries's Buzzard *B. b. menetriesi*, which ranges from Russia west of the Caspian Sea to Iran and Iraq (Perrins & Snow, 1998).

With regards to nest location of these breeding 'mystery buzzards', all but one of the nests found to date have been in alien trees (Koeslag, 2010a, unpubl. data; Martin & Walton, 2011, unpubl. Data), which is the primary site choice of *B. b. vulpinus, B. trizonatus* and *B. b. menetriesi* (Dementiev & Gladkov, 1966; Perrins & Snow, 1998; Hockey *et al.,* 2005). The one exception was a nest on a cliff face on the Cape Peninsula in 2002. Cliff nesting is utilised habitually by *B. b. buteo, B. r. rufinus* and *B. r. cirtensis* (Perrins & Snow, 1998) whilst, pertinent to this study, it has also been recorded rarely in *B. b. vulpinus* and *B. b. menetriesi* (Gavrin *et al.*, 1962; Dementiev & Gladkov, 1966; V. Amanian pers. comms.). It appears cliff nesting has never been recorded in *B. trizonatus*, further confusing the likely identity of these birds.

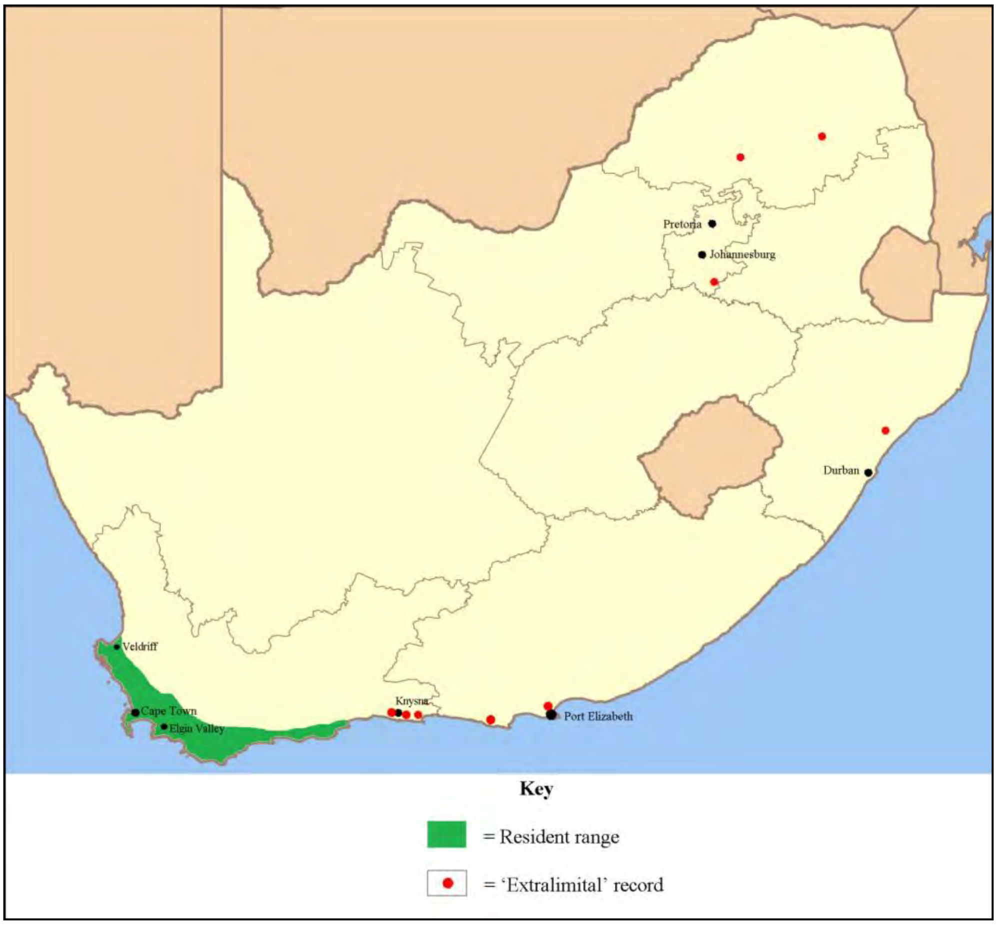

Figure 1.1 Map of South Africa displaying current known resident range of 'mystery buzzards' and records of uniform brown or rufous buzzards outside of this resident range during the Austral winter, based on information gathered from a public appeal for sightings, reports and information, and previous nesting records.

Hypotheses

There are several hypotheses that may singularly, or in combination, explain the identity of the 'mystery' buzzards:

Hypothesis 1: The 'mystery' buzzards are *B. trizonatus*

This hypothesis is considered very unlikely. Forest Buzzard *B. trizonatus* is considered monomorphic, making it very unlikely that such variation could occur in the taxon (Rudebeck, 1957; Siegfried & Frost, 1973; Clark, 2007). The phenotype of *B. trizonatus* remains defined by key features within a single but variable trait, notably 'teardrop' streaking rather than barring on the chest and abdomen, and more importantly, the absence of uniformly coloured morphs (Siegfried, 1971; Hockey *et al*, 2005; Perrins & Snow, 1998).

Clark (2007) endeavoured to shed light on the origins of the geographically isolated *Buteo trizonatus* by hypothesising that it could have originally evolved from overwintering *B. b. vulpinus* that subsequently bred in the austral summer. Over time, this eventually gave rise to the morphologically and genetically distinct *B. trizonatus*, which has evolved short, broad wings for manoeuvrability in the forest habitat that it favours, alongside being on average slightly smaller than *B. b. vulpinus.*

Siegfried (1969) gives a convincing argument for the speciation of *B. trizonatus* to have occurred during the Pleistocene when a continuous belt of forest stretched from the Cape to Ethiopia. These conditions may have persisted up until around 15,000 years ago and it may be reasonable to consider *B. trizonatus* an isolated relic of Mountain Buzzard *B. oreophilus*. Assuming its ecological requirements were similar to present, *B. oreophilus* would appear to have occupied this entire range from the Cape to Ethiopia, but is now confined to the Afromontane forests of East Africa (Sinclair & Ryan, 2010).

Hypothesis 2: The 'mystery' buzzards are *B. b. vulpinus*, some of which have hybridised with *B. trizonatus*

This hypothesis appears the most parsimonious of the four possibilities. The difficulties of field identification of *B. b. vulpinus* and *B. trizonatus* are recognised (Snow, 1978; Hockey *et al*, 1995; Boshoff, 1997a; Clark, 1999), with habitat seemingly being a key consideration in the puzzle. *B. b. vulpinus* is a species of open landscapes, especially outside of the breeding season (Boshoff, 1997b), which in South Africa largely separates *B. b. vulpinus* from the hill-dwelling *B. rufofuscus* and the forest-dependent *B. trizonatus* (Newton, 1979). If *B. b. vulpinus* are opting to stay and breed in South Africa it is, however, possible that when the breeding season approaches, *B. trizonatus* and *B. b. vulpinus* come into contact and likely conflict over territory as *B. b. vulpinus* become more attracted to forest-edge, ecotonal areas for nest sites, which are favoured by *B. trizonatus* on a more permanent basis (Boshoff, 1997a; Boshoff, 1997b). In the Palearctic breeding grounds, *B. b. vulpinus* nests in coniferous and broadleaf trees close to open areas, and has been recorded nesting on a crag (Gavrin *et al.*, 1962; Dementiev & Gladkov, 1966). Furthermore, *B. trizonatus* are uncommon at the western edge of their range (Hockey *et al*, 2005) and may encounter difficulties finding a conspecific mate (i.e. the 'Allee Effect' - Short, 1969; Helbig *et al*, 2005). This is especially true given that *B. b. vulpinus* are regularly observed remaining in

South Africa during the Austral winter (per obs.; Hockey *et al.,* 2005), providing ample stock for potential hybridisation.

In the case of this potential hybridisation, there appear to be no pre-zygotic barriers because both *B. trizonatus* and *B. b. vulpinus* display similar preference for forest nest sites, and appear to have similar social and behavioural traits when breeding (Ferguson-Lees & Christie, 2001; Newton, 1979; Boshoff, 1997a; Boshoff, 1997b; Steyn, 1982; Kruckenhauser *et al*., 2004). Likewise, it is improbable that there are post-zygotic barriers preventing successful hybridisation, due to their close genetic relatedness (Kruckenhauser *et al*., 2004).

Given the likely reproductive viability of a *vulpinus x trizonatus* buzzard hybrid, and the precedent set among the genus *Buteo* in the form of hybridisation between the *B. buteo* and *B. rufinus* group (Kotyman *et al*, 2008), *vulpinus-trizonatus* hybridisation seems plausible, even likely.

Hypothesis 3: The 'mystery' buzzards are Ménétries's Buzzard *B. b. menetriesi,* some of which have hybridised with *B. trizonatus*

This taxon, found throughout the Caucusus' from Russia west of the Caspian Sea to Iraq and Iran in the south, was widely believed to be at most a short distance migrant (Dementiev & Gladkov, 1966; Perrins & Snow, 1998) with some individuals dispersing into the Middle East (Vasil Amanian & Richard Porter, per comms.). However, the occurrence of this race as a migrant to Africa has been reported by McLachlan & Liversidge (1957), Mackworth-Praed & Grant (1952) and Winterbottom (1969), whilst more recently Yosef *et al.* (2002a) gave additional evidence, reporting that 0.9% of migrating *Buteo* buzzards trapped whilst returning to the Palearctic through Eilat were identified as *B. b. menetriesi*. Whilst an extremely small percentage, this amounts to 27 individuals of the 2,892 buzzards trapped over a four year period. Given the observations of ornithologists in the Middle East (Vasil Amanian & Richard Porter per comms.) and the documented individuals passing through Eilat, Israel in migrating flocks of Steppe Buzzard (Yosef *et al.*, 2002a), this may be a plausible theory.

Literature on this race of *B. buteo* is limited, with many authors failing to give descriptions of this taxon's field characters, however Dementiev and Gladkov's (1966) description highlights many similarities between this race and the birds breeding in the Cape. Plumage features are noted as differing from nominate race in the presence of rust-red tones, with brown upperparts featuring broad russet-ochre edging. When abdominal barring occurs in adults, it is in the form of anchor shapes, with the retrices being predominantly russet with pronounced dark crossbars. Mackworth-Praed & Grant (1952) state the young to be "ashy brown; tail ashy brown with some barring", with Dementiev and Gladkov (1966) stating the juveniles have a russet base colour with darker streaks, features that have been seen in juvenile 'mystery buzzards' (Figure 1.2). Both comment that *B. b. menetriesi* is smaller and darker than Long-legged Buzzard *B. rufinus* but more richly coloured than Steppe Buzzard, not dissimilar to the North African race of Long Legged Buzzard *B. r. cirtensis.*

Within Ararat *et. al.* (2011) Dick Forsman is quoted as commenting that the uniformly dark rufous form of *B. b. menetriesi* is the most common; in addition, Dementiev and Gladkov (1966) state that "a small number" are uniformly dark brown, with a black form occurring regularly. It is important to note, however, that based on current knowledge it appears *B. b. vulpinus* and *B. b. menetriesi* are inseparable in the field based on plumage characters. Both taxa appear to occur in a large variety of similar morphs, including uniform rufous and brown, and thus field identification based on plumage features alone is not feasible.

Dementiev and Gladkov (1966) state that *B. b. menetriesi* nests in trees near glades in mountain forests up to 1800 m, hunting in alpine and subalpine meadows. Nests have also been recorded on rock ledges within forests in Armenia (Vasil Ananian, 2011 pers. Comms.), a trait that has been recorded in the 'mystery' buzzards (Curtis & Koeslag, 2007), specifically by a pair of uniformly brown buzzards appearing to fall within the phenotypic variation of both *B. b. menetriesi* or *B. b. vulpinus* (Figure 1.2).

Figure 1.2 'Mystery buzzard' at its nest on a cliff overlooking Newlands Forest, Cape Peninsula 2006. Photo: © Dr. Rob Simmons

Study area

The areas chosen in which to undertake this study are located within the two apparent cores of 'mystery buzzard' distribution in South Africa. The Cape peninsula, including Table Mountain National Park south of Cape Town forms one core, whilst the second reaches from Stellenbosch and the Jonkershoek Valley in the north, to Kleinmond and Betty's Bay in the south (Figure 1.3). The highest densities of breeding buzzards appear to be found within the Elgin valley, an area spreading south and east from the town of Grabouw, and along the eastern side of Table Mountain National Park; thus, the main study effort is concentrated here (Figure 1.4). Figure 1.5 provides a more detailed view of the Elgin Valley, showing public roads from which behavioural and diet and foraging ecology data are collected.

Figure 1.3 Map displaying the location and apparent extent of the 'mystery buzzard' breeding cores within the south-western Cape.

Climate

The climate of the south-western Cape is often described as Mediterranean, and appears to differ little between the two study areas. Cape Town has average day-time temperature of 25.9°C in its hottest month (February), and 15.5°C in its coolest (June), whilst the Grabouw area is slightly cooler, reaching an average of 24.8°C in its hottest month (February) and 15°C in its coolest (June). Rainfall is also similar between areas, with Cape Town receiving an average of 24mm in its driest month (January) and 143mm in its wettest (June), whilst the Grabouw area receives averages of 22mm and 168mm respectively.

Elevation and habitat structure of the two main study areas

Within the Cape Peninsula site, the study was primarily undertaken along the eastern edge of Table Mountain National Park, ranging in altitude from 25m to 420m above sea level. Within the eastern study site centred around Grabouw, elevation ranges from 140m to 600m above sea level. The key focus area of the eastern study site is the Elgin Valley, which ranges in elevation from 140m to 395m.

The Cape Peninsula study area excludes any urban or substantially populous area, being based primarily in Table Mountain National Park, which consists mainly of mountain slopes covered in non-native pine and eucalyptus plantations and areas of fynbos. The site also includes restricted areas of natural forest in places such as Newlands Forest and Kirstenbosch National Botanical Gardens, in contrast to the second study area which is characterised by a heavily agricultural landscape, being predominantly a mix of Apple orchards, vineyards and large commercial pine plantations. There are also areas of open ground bordering the plantations; these are a mixture of areas of fynbos, and areas of grassland. Both study areas are heavily influenced by human activities.

Figure 1.4 Map of the south-western Cape, displaying the areas in which field data collection was undertaken (shaded red)

Figure 1.5 Map displaying a detailed view of the Elgin Valley, including the roads that were driven regularly to collect data

Aims of the study

Based on information gathered, particularly through the Kruckenhauser *et al.* (2004) study, it appears that resolving taxon identity based on just one of genetics or morphology is unlikely to be successful. Therefore, this study aims to explore both of these variables and contrast the evidence gathered in an effort to test each of the hypotheses presented here, with the aim of resolving the identity of the colonising buzzards.

Firstly, I will explore the morphology of the 'mystery buzzards' and compare them to the three candidate taxa in an effort to present an initial identification of the 'mystery buzzards'. I will then explore the genetic structure of the buzzards through microsatellite analysis, with the aim of confirming or clarifying the identities initially determined in Chapter 2. In addition to analysis of genetic and phenotypic traits, a study of the ecology of the buzzards will then also be undertaken. This could potentially provide information as to the viability and likelihood of the colonising buzzards as a partner base for *B. trizonatus,* and the impact this may have on this endemic taxon in terms of its genetic integrity. This information could also potentially reveal traits useful in the identification of the 'mystery buzzards'.

Chapter 2: Assessing the morphology of 'mystery buzzards' in relation to other Old World *Buteo* taxa

Introduction

Phenotypic traits such as morphology and plumage are widely used to explore geographic variation and to aid in our assessment of speciation between taxa (Mayr, 1940; Mayr, 1942; Watson, 2004; Tobias *et al.*, 2010). With the advent of new genetic methods, these techniques have combined to provide further supporting evidence in the investigation into differences between taxa, in line with Mayr's statement that genetic and phenotypic variation, alongside a geographically isolated breeding core, are the key factors to be accounted for when assessing a taxon's validity as a species (Mayr, 1940; Mayr, 1942; Watson, 2004; Tobias *et al.*, 2010).

The usefulness of morphology in clarifying species complexes appears to vary greatly. In some genus', such as the *Phylloscopus* warblers, species are poorly morphologically distinct, and therefore identification is primarily established through genetic evidence (Helbig *et al.,* 1995; Salomon *et al.,* 2003). The *Sylvia* warblers appear to represent an excellent example of the importance of the dual use of phenotypic and genetic methods in the clarification of species complexes (Shirihai *et al*., 2001). For example, the Western Orphean Warbler *Sylvia hortensis* and Eastern Orphean Warbler *Sylvia crassirostris*, once thought to be conspecific, were found to be genetically highly divergent (Shirihai *et al.,* 2001) despite being phenotypically very similar (Shirihai *et al.,* 2001). However, this example is in contrast with the case of the Lesser Whitethroat *Sylvia curruca* superspecies complex, where phenotypic characters were found to be significant in the principle recognition and separation of a number of subspecies (Shirihai *et al*., 2001). Within these phenotypically variable subspecies, *S. c. curruca, S. c. blythi, S. c. halimodendri* and *S. c. margelanica* have subsequently shown evidence of being genetically distinct, and thus probably represent valid species (Shirihai *et al.,* 2001; Olsson *et al*., 2013). Though the status of Lesser Whitethroat requires further study, it does illustrate the importance of morphology and plumage to direct further genetic study.

Similar to the Lesser Whitethroat *S. curruca* superspecies, phenotypic characters appear to play a major role in the principle recognition and separation of Old World *Buteo* taxa (Kruckenhauser *et al.,* 2004). The seminal Kruckenhauser *et al.* (2004) investigation into the speciation and variation of Old World *Buteo*s found morphology to be useful in discriminating taxa, despite a high degree of variation within species. Although this study found significant phenotypic variation between species, further genetic investigation found almost no differentiation between Old World *Buteo* taxa, especially within the *buteo-vulpinus* group (Kruckenhauser *et al.,* 2004). This is particularly relevant to my current study since this is the group to which the candidate taxa in this investigation belong. This study therefore emphasises the importance of the use of phenotypic characters, in particular morphology, in the separation of Old World *Buteo* taxa, especially given the evidence that current genetic methods do not appear to definitively resolve relationships within this group (Kruckenhauser *et al.,* 2004).

Old World *Buteo*s are notoriously difficult to identify in the field (Perrins & Snow, 1998; Hockey *et al.*, 2005; Forsman, 2007), primarily due to their extreme polymorphism and relative similarity (Ferguson-Lees & Christie, 2001; Forsman, 2007). They are also known to hybridise at almost every contact zone, giving rise to much phenotypic diversity (Gjershaug *et al.*, 2006; McCarthy, 2006; Kotyman *et al*, 2008; Corso, 2009; Elorriaga & Muñoz, 2013), further confusing our understanding of variation in the taxa. As such, identification of buzzards outside of their known range must be undertaken with caution, and in the case of extremely similar species, such as *B. b. vulpinus* and Ménétries's Buzzard *B. b. menetriesi* (the Caucasus-breeding, uniform-rufous race of Common Buzzard *B. b. buteo*) which are not currently separable based on plumage features*,* identification must be informed through detailed morphometric and genetic analysis.

As described in the introduction chapter of this thesis, the focal sample of this study is a number of *Buteo* buzzards found in the south-west Cape of South Africa which appear unlike any buzzard species currently known to breed in South Africa. These unidentified buzzards have been colloquially termed 'mystery buzzards'.

In this chapter, I explore the possible identity of individual 'mystery buzzards' through an analysis of their morphology and plumage. This analysis is based on a number of adult and juvenile *Buteo*s in the region which were either trapped near their nests, sampled as chicks or in rehabilitation centres, or were found dead. Though it is currently not thought to be possible to separate *B. b. vulpinus* and *B. b. menetriesi* based on plumage, it is possible to separate *B. trizonatus* from these two taxa, and as such plumage features will be used to identify individual buzzards as either *B. trizonatus* or 'Steppe-type' buzzards. Based on the

Kruckenhauser *et al.* (2004) finding that morphology is significant in the discrimination of Old World *Buteo* taxa, I predict that an analysis of the specimen buzzards' morphology will help reveal the species identity of the 'mystery buzzards' of the Cape.

Methods

Morphometric sampling

Morphometric samples were obtained in four ways: 1) through a constant trapping effort; 2) from injured birds found or brought into a rehabilitation centre; 3) from road casualties; 4) from chicks in nests.

A constant trapping effort was undertaken using a variety of techniques, including traditional Bal chatri and carpet traps, dho-gaza traps (Bub, 1978), and a specially designed remote controlled bow-net. Very little success was achieved in capturing 'mystery buzzards', and as such 19 of 23 individuals used in the morphological analysis were sampled as captive rehabilitated birds or road casualty corpses (Table 2.1). The origins of birds sampled at the rehabilitation centre 'World of Birds' are recorded as 'South-west Western Cape' as more specific location data was not available. In all cases, the sex of individuals was not known.

Measurements

Nine external morphological variables were measured from the 23 individuals. The variables were as follows: tarsus length, middle claw length, hind claw length, middle toe length, hind toe length, culmen depth, culmen length, culmen width and wing chord. These data then allowed the morphometrics of these individuals to be compared with morphological data taken from 19 Old World buzzard taxa (sample sizes displayed in Table 2.2). These particular measurements were chosen as they were found by Kruckenhauser *et al.* (2004) to hold most significance in the separation of Old World *Buteo* taxa.

I compared these measurements taken from the 'mystery buzzards' against reference data collected and supplied by Anita Gamauf and used in Kruckenhauser *et al.* (2004). Measurements used in this study and those collected in Kruckenhauser *et al.* (2004) were identical and followed the methods described by Leisler & Winkler (1991), with each buzzard measured by only one person to avoid observer bias.

Table 2.1 Age, geographical origin and source of 'mystery buzzard' specimens for which morphometric data was recorded.

Specimen	**Age**	**Geographical origin**	**Source**	**Date of sample**
WOB001	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB002	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB003	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB004	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB005	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB006	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB007	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB008	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB009	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB010	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB011	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB012	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB013	Adult	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB014	Juvenile	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
WOB016	Juvenile	South west Western Cape	World of Birds, Hout Bay, Cape Town	25/05/2011
BUIT20091	Juvenile	Buitenverwachting, Tokai, Cape Peninsula	Trapped as fledgling	06/01/2009
BUIT20092	Juvenile	Buitenverwachting, Tokai, Cape Peninsula	Trapped as fledgling	06/01/2009
REST2009	Juvenile	Restanwold Farm, Grabouw, Western Cape	Injured fledgling discovered	09/02/2009
SWART2008	Adult	Darling, Western Cape	Adult trapped near its nest	29/02/2008
ZONN2008	Juvenile	Zonnestraal Farm, Cape Peninsula	Fledgling trapped near its nest	20/03/2008
CONST052012	Juvenile	Constantia, Cape Town	Road-kill corpse	05/05/2012
WC062012	Juvenile	Yzerfontein, Western Cape	Road-kill corpse	15/06/2012
TOK052012	Juvenile	Tokai, Cape Town	Road-kill corpse	18/05/2012

The reference data (Kruckenhauser *et al.*, 2004) used for the 19 Old World *Buteo* species was collected from skin specimens, which are known to suffer a degree of shrinkage in soft tissue (Winker, 1993). This was corrected for by comparing the average wing chord length of *B. b. vulpinus* museum specimens (n=10) used in Kruckenhauser *et al.* (2004) with live specimens caught on migration in Eilat, Israel (n= 3,949, R. Yosef, unpublished data).

From this comparison, I found a 2.2% shrinkage level between live and museum specimens, and all live bird wing chord measurements were adjusted accordingly to create a data set which can be compared with museum skins (Winker, 1993), as was required by this study. Green (1980) found similar levels of shrinkage in a number of species, including Ringed Plover *Charadrius hiaticula* (2.7%) and Dunlin *Calidris alpina* (2.2%).

Table 2.2 Sample size of each of the 19 Old World *Buteo* taxa, against which the 'mystery buzzards' are assessed. Adapted from Kruckenhauser *et al*. (2004; Table 1).

Taxon	**Sample size**
B. b. buteo	11
B. b. hispaniae	5
B. b. harterti	5
B. b. insularum	5
B. b. arrigonii	3
B. b. rothschildi	3
B. b. menetriesi	10
B. b. vulpinus	6
B. b. socotrae	2
B. b. bannermani	3
B. rufinus rufinus	4
B. r. cirtensis	3
B. oreophilus	4
B. trizonatus	4
B. b. japonicus	7
B. b. toyoshimai	2
B. b. refectus	4
B. hemilasius	4
B. brachypterus	3

Plumage

As previously stated, though it does not currently appear possible to separate *B. b. vulpinus* and *B. b. menetriesi* based on plumage features, it does remain possible to separate *B. trizonatus* from these two taxa, collectively termed ‘Steppe-type’ buzzards. The field identification issues surrounding *B. trizonatus* and ‘Steppe-type’ buzzards in South Africa are well documented (Hockey *et al.,* 2005) however *B. trizonatus* can be identified by its characteristic ‘blob-like’ ‘tear-drop’ abdominal and breast spotting pattern, which in juveniles can be sparse enough to appear almost entirely white. Steppe-type buzzards are highly polymorphic but in their light morphs, the only morphs likely to be confused with *B. trizonatus*, they typically feature heavy horizontal abdominal barring, contrasting with a uniform ‘bib’. Juvenile *B. b. vulpinus* typically show heavy vertical breast and abdominal streaking, rather than spotting as seen in *B. trizonatus*. Both have a white breast ‘U’, which though variable in *B. b. vulpinus* is always present and appears more prominent in *B. trizonatus* (Hockey *et al.,* 2005; Clark, 2007).

It must be noted that separation of *B. trizonatus* and light-morph ‘Steppe-type’ buzzards is still challenging at times and will not always be possible, however *B. trizonatus* is currently believed to be monomorphic, making it easily diagnosable from uniform-morph ‘Steppe-type’ buzzards (although see Chapter 3). Morphometric and genetic characters, however, remain a more readily quantifiable and reliable method of separating the taxa. As such, inference of identity from plumage as either ‘Steppe-type’ buzzard or *B. trizonatus* will only be applied to inform identification if a buzzard sampled in the Western Cape falls within an area of overlapping morphology.

Statistical analyses

Using the Kruckenhauser *et al.* (2004) data from 19 Old World *Buteo* taxa, and data from 23 buzzards sampled in the Cape, I constructed a Discriminant Component Analysis using nine morphometric characters determined to be useful in the separation of Old World *Buteo* taxa (Kruckenhauser *et al.,* 2004). The nine morphometric characters were analysed using the ‘classical discriminant analysis’ function of the program MyStat (SYSTAT Inc., 2009), and were computed with the given group sizes for each taxon. The canonical score read-out was also requested.

From the canonical score read-out, I then constructed a scatter chart by plotting the first two discriminant components, which together accounted for 80% of the total morphometric variation (as detailed by the 'cumulative proportion of total dispersion'). This displayed the taxon-groupings of the 19 Old World *Buteos*, and the relative positioning of the 'mystery buzzards' in two dimensional space. This graph also displays the variation in morphology within each of the Old World *Buteo* taxa.

Having established the relative morphological positioning of the 'mystery buzzards' within the entire breadth of the Old World *Buteo*s, I then removed the 16 taxa not considered potential candidates in this investigation from the graph. This gave a clearer view of the mystery buzzards' morphology in comparison to the candidate taxa.

Results

A discriminant component analysis (DCA) was performed on the morphometric data I collected from the sampled buzzards (Table 2.1), together with the data from the Kruckenhauser *et al.* (2004) study. This DCA used the nine morphometric variables previously found to be significant in the separation of Old World *Buteo* species (Kruckenhauser *et al.*, 2004), which were also measured in this study. Using the scores from each sample we can then compare all the Western Cape individuals in morphological space relative to samples from the other 19 Old World *Buteo* taxa (Figure 2.1). Taxa that were originally used in Kruckenhauser *et al.* (2004), but that were not considered as candidates in this investigation have been removed from the graph.

The first axis from the DCA described 66% of total variation and was most influenced by wing chord and culmen width. The second axis described 14% of total variation and was most influenced by middle toe length, wing chord and culmen length.

It is clear from Figure 2.1 that there is considerable overlap in the morphology of the candidate buzzard taxa. However, nineteen (82%) of the twenty-three 'mystery buzzards' are shown to sit within or extremely close to the distinct morphospace of a single taxon, with just four laying in a zone of overlapping morphology. Specimens falling within or closest to the morphospace of the resident *B. trizonatus* (n=4) and abundant migrant *B. b. vulpinus* (n=8) account for 52.1% (n=12) of the total buzzards sampled. A further 30.4% (n=7) fall within the distinct morphospace of *B. b. menetriesi*, and four buzzards fall within an overlap zone created by *B. b. menetriesi, B. b. vulpinus* and *B. trizonatus*.

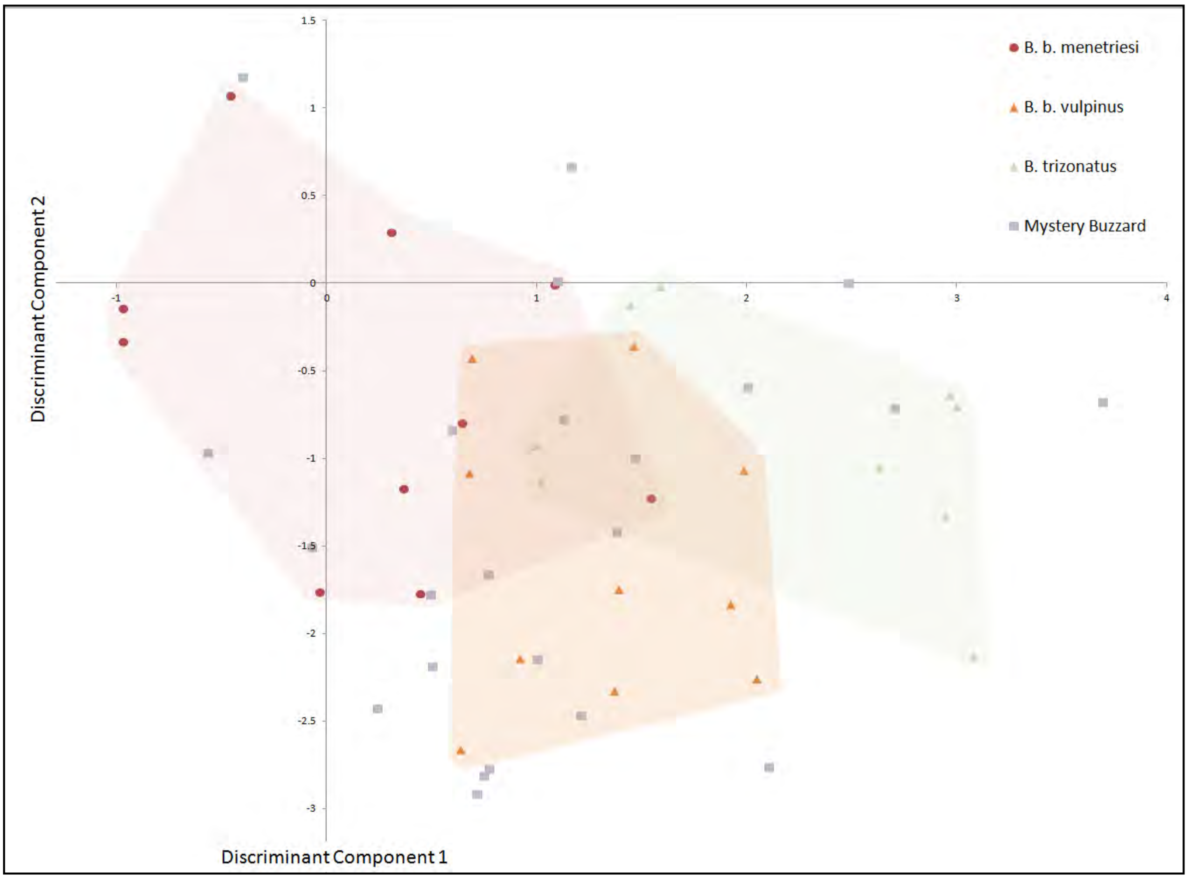

Figure 2.1 Discriminant Component Analysis displaying buzzards sampled in the Western Cape between February 2008 and May 2012 plotted in morphological space relative to the defined morphospace area occupied by 19 Old World *Buteo* taxa, using 9 morphometric variables considered key in the separation of taxa. Taxa not considered candidates in this investigation have been removed.

Table 2.3 Taxon identification of sampled buzzards based on matches made to candidate taxa in their morphology, and their plumage match to either Steppe-type buzzards (i.e. *B. b. vulpinus* OR *B. b. menetriesi*) or *B. trizonatus*.

Specimen	**Morphology match**	**Plumage match**
WOB001	*B. b. menetriesi*	Steppe-type buzzard
WOB002	*B. b. vulpinus*	Steppe-type buzzard
WOB003	*B. b. menetriesi*	Steppe-type buzzard
WOB004	*B. b. menetriesi*	Steppe-type buzzard
WOB005	Overlap zone: *B. b. vulpinus, B. trizonatus* and *B. b. menetriesi*	Steppe-type buzzard
WOB006	*B. b. vulpinus*	Steppe-type buzzard
WOB007	*B. b. menetriesi*	Steppe-type buzzard
WOB008	*B. b. vulpinus*	Steppe-type buzzard
WOB009	*B. b. vulpinus*	Steppe-type buzzard
WOB010	*B. b. vulpinus*	Steppe-type buzzard
WOB011	*B. trizonatus*	*B. trizonatus*
WOB012	Overlap zone: *B. trizonatus, B. b. vulpinus* and *B. b. menetriesi*	*B. trizonatus*
WOB013	*B. b. menetriesi*	Steppe-type buzzard
WOB014	*B. b. vulpinus*	Steppe-type buzzard
WOB016	*B. trizonatus*	Steppe-type buzzard
BUIT20091	*B. b. menetriesi*	Steppe-type buzzard
BUIT20092	*B. b. menetriesi*	Steppe-type buzzard
REST2009	*B. b. trizonatus*	Steppe-type buzzard
SWART2008	*B. b. vulpinus*	Steppe-type buzzard
ZONN2008	Overlap zone: *B. b. trizonatus, B. b. vulpinus* and *B. b. menetriesi*	Steppe-type buzzard
CONST052012	*B. trizonatus*	Steppe-type buzzard
WC062012	Overlap zone: *B. b. vulpinus* and *B. b. menetriesi*	Steppe-type buzzard
TOK052012	*B. b. vulpinus*	Steppe-type buzzard

Discussion

Kruckenhauser *et al.* (2004) determined that there were notable differences between taxa in terms of their morphology, and although this variation was not totally discrete they suggested that these morphological features could be useful to separate out different taxa. Aside from Kruckenhauser *et al.* (2004), little work including a morphological component appears to have been undertaken to clarify the phenotypic differentiation of the Old World *Buteo*s. However, many identification field guides exist that rely heavily on plumage traits to separate

Buteo species (Perrins & Snow, 1998; Ferguson-Lees & Christie, 2001; Hockey *et al.,* 2005; Forsman, 2007). Though these guides are designed to be as comprehensive and detailed as possible, separation of certain little-known taxa using plumage features alone appears to remain impossible based on our current understanding. Pertinently, this applies to the separation of *B. b. vulpinus* and *B. b. menetriesi*, and as such morphology plays a particularly key role in the separation of these taxa. It must be noted however, that *B. trizonatus* remains routinely diagnosable from 'Steppe-type' buzzards (i.e. *B. b. vulpinus* and *B. b. menetriesi*) in its plumage.

Using the aforementioned 9 key morphometric characters, it was possible to assign sampled buzzards to the single candidate taxon to which they were most similar in all but four cases.

Of the 23 'mystery buzzard' specimens analysed, 15 were sampled as captive rehabilitated birds and so had little known history, and three were collected as corpses. As I can't be certain of the previous breeding status of these buzzards, it is not possible for those matching *B. b. vulpinus* to cast light on the identity of the colonising buzzards as they may have occurred as typical summer migrants, and not as resident breeding birds. As such, of the buzzards sampled at rehabilitation centres only those specimens falling within the morphospace of the taxa not previously believed present in South Africa are of particular interest.

Birds with morphology matching the known *Buteo*s of South Africa: Steppe Buzzard *B. b. vulpinus* and Forest Buzzard *B. trizonatus*

Of the 23 specimens analysed, the majority (52.1%, n=12) matched closest with *B. trizonatus* (n=4) or *B. b. vulpinus* (n=8), sitting in the distinct morphospace of these taxa. Given that these are the only two *Buteo* taxa in the *buteo-vulpinus* group that are known to occur in Southern Africa, this is the result one would expect. Interestingly, buzzard REST2009 was sampled as an injured fledgling, and though it shows morphology most similar to *B. trizonatus*, it was deemed to display plumage more similar to the 'Steppe-type' buzzards. This could, however, feasibly be because of undeveloped plumage due to its extremely young age.

In addition to the 12 'mystery buzzards' placing in or extremely close to the distinct morphospace of *B. b. vulpinus* and *B. trizonatus*, four placed within the overlap zone between these two taxa and *B. b. menetriesi*. WOB012 falls within the zone of overlapping morphology of all three candidate taxa but has plumage most similar to that of *B. trizonatus*, suggesting that it represents *B. trizonatus.* The remaining three appear to be 'Steppe-type' buzzards, which cannot be identified to taxon level based on their plumage features. As these individuals are not significantly separated from *B. b. vulpinus* morphologically, appearing within the spectrum of variation for this taxon, there is no reason to suspect they are not *B. b. vulpinus*, the most likely candidate taxon.

Buzzards with morphology matching *B. b. menetriesi*

Of the sampled buzzards, seven (30%) were demonstrated to display morphology most similar to *B. b. menetriesi*. Of these seven, five were shown to be far removed from both *B. trizonatus* and *B. b. vulpinus*. The remaining two place close to the zone of overlapping morphology between *B. b. menetriesi* and *B. b. vulpinus*, however they appear remarkably similar in their morphology to two of the *B. b. menetriesi* specimens used in the Kruckenhauser *et al.* (2004) investigation.

Before drawing any conclusions on the presence of *B. b. menetriesi* in South Africa from this data, however, we must take into account the relatively unknown nature of *B. b. menetriesi*. Due to the impact sexual dimorphism may have on the morphometric variation of a taxon, it is not unreasonable to speculate that the 'mystery buzzards' falling far removed from the morphospace of *B. trizonatus* and *B. b. vulpinus* are in fact simply particularly large female *B. b. vulpinus*. The observed plumage of these large buzzards would seemingly eliminate the apparently-monotypic *B. trizonatus* as a candidate in their identification, based on our current understanding of the taxon's plumage variability (although see Chapter 3). Similarly, however, those falling close to the overlap zone with *B. b. vulpinus* could just as feasibly represent small male *B. b. menetriesi*, as is supported by their placement extremely close to two true *B. b. menetriesi* specimens from Kruckenhauser *et al.* (2004).

Given that the extent of variation in morphology of *B. b. menetriesi* is little known, it is clearly premature to speculate on the existence within the Western Cape of buzzards appearing to represent *B. b. menetriesi*, based solely on morphological data. However, it remains intriguing that there are a number of buzzards occurring in the Western Cape that are distinctly more similar to *B. b. menetriesi* than *B. trizonatus* or *B. b. vulpinus* in their morphology. Perhaps, however, a simpler explanation is that the full breadth of morphological variation in *B. b. vulpinus* has not been accounted for here, for example through discrepancies caused by sexual dimorphism. With Yosef *et al.* (2002a) reporting *B.*

b. menetriesi migrating through Eilat from Africa among *B. b. vulpinus*, determined through morphometric analysis during trapping efforts, it is in theory feasible that *B. b. menetriesi* could occur in Southern Africa, and it therefore cannot be ruled out as a potential taxon candidate for the 'mystery buzzards' in this region.

Conclusions

The taxa composition of the sampled buzzards within the study area is clearly complex. Buzzards matching *B. b. vulpinus* and *B. trizonatus* in their morphology were the most common, as would be expected given that these are the only two small *Buteo* species traditionally believed to be found in South Africa. The high number of buzzards sampled in the Western Cape considered to represent *B. b. menetriesi* or *B. b. vulpinus*, a species previously considered a non-breeding summer migrant, is extremely interesting. This includes three buzzards sampled as fledglings, and one as an adult attending a nest (see Table 2.1), and supports the hypothesis that *B. b. vulpinus*, or 'Steppe-type' buzzards, have colonised the Cape. Buzzards identified as 'Steppe-type' buzzards have also been observed breeding with *B. trizonatus* and successfully rearing young (see Chapter 4), which therefore provides, for the first time, evidence of hybridisation between the two taxa in the Western Cape.

Of particular interest are a large number of buzzards which are tentatively identified as *B. b. menetriesi* through an assessment of their morphometric characters. Whilst these identifications are made with considerable caution due to the traditionally unknown presence of *B. b. menetriesi* in South Africa, the morphological data from this study together with the potential for the *B. b. menetriesi* to occur as a migrant (Yosef *et al.*, 2002a) suggest that this taxon should not be discounted entirely as a candidate taxa for the 'mystery buzzards'.

Given the confusion and lack of clarity surrounding the separation of *B. b. menetriesi* and *B. b. vulpinus*, particularly based on plumage features, any identification of *B. b. menetriesi* in South Africa would need to be made with caution, and only with supporting morphometric and genetic data. Field identification of *B. b. menetriesi* based on plumage features does not currently seem possible.

Chapter 3: Analysing the genetic signature of the 'mystery buzzards' in relation to other Old World *Buteo* taxa

Introduction

Genetic variation has long been a key consideration when assessing species validity. Together with phenotypic traits, such as morphology and plumage, and an isolated breeding core, these three variables form the basis for assessing and recognising species (Mayr, 1940; Mayr, 1942; Tobias *et al.,* 2010).

As previously discussed in Chapter 2, the usefulness of genetic approaches in clarifying the species-composition of certain genera is unquestionable. In some cases, species are poorly differentiated phenotypically and genetic approaches are paramount in unravelling the complex, such is the case of the *Phylloscopus* warblers (Helbig *et al.,* 1995; Salomon *et al.*, 2003) and a number of the *Sylvia* warblers (Shirihai *et al.,* 2001). In the case of the Orphean Warblers (*Sylvia hortensis* and *S. crassirostris*), despite being phenotypically extremely similar, the Eastern and Western geographically isolated populations were found to be genetically highly divergent (Shirihai *et al.,* 2001). Similarly, in the European chiffchaffs, the most geographically separated populations of Iberian *P. ibericus ibericus* (south-west Spain and southern Portugal) and Common Chiffchaff *P. collybita* (UK & Brittany) were shown to display extremely similar phenotypic characters (Salomon *et al.,* 2003), despite being genetically divergent (Helbig *et al.,* 2008).

The use of genetic methods is clearly critical in revealing the relationships between and indeed within species. Such studies are often guided by the discovery of variation in the phenotypic traits or breeding ecology of a single geographic population of a species. A case in point are members of the Band-rumped Storm Petrel *Oceanodroma castro* complex, where studies initiated following the discovery of hot and cold season breeding populations on some island groups revealed substantial genetic variation between the two populations, as well as differences in morphology, moult chronology and vocalisations (Friesen, 2007; Howell *et al.,* 2010). These findings supported the elevation of the Azorean hot season breeding petrels to full species status as Monteiro's Storm Petrel *Oceanodroma monteiroi* (Bolton *et al.,* 2008). Similarly, in the case of the Lesser Whitethroat *Sylvia curruca* complex, studies were initiated following the recognition of substantial phenotypic variation across the species' range. Such studies discovered that *S. c. curruca, S. c. blythi, S. c. halimodendri* and *S. c.*

margelanica show evidence of being genetically distinct, and probably represent valid species (Shirihai *et al.,* 2001; Olsson *et al*., 2013). As such, it is important to acknowledge that none of the three precursors to species validity should be analysed alone, instead, each study should combine assessment of all of these variables. With the continual technological advances of the 21st century, it seems that previously unrecognised and cryptic species will continue to be discovered through genetic study.

It is well established that the Old World *Buteo*s are genetically extremely similar, especially in the *buteo-vulpinus* complex investigated in this study. They are also a notoriously difficult group to separate in the field in terms of their phenotypic characters, due to their extreme plumage polymorphism and similarity among taxa (Kruckenhauser *et al.,* 2004; Perrins & Snow, 1998; Hockey *et al*., 2005; Forsman, 2007). This is probably due to their status as a relatively taxonomically-young group of raptors, and through prolific hybridisation at almost every overlap zone, resulting in vast phenotypic variation (Kruckenhauser *et al.,* 2004; Gjershaug *et al*., 2006; McCarthy, 2006; Kotyman *et al*, 2008; Corso, 2009; Elorriaga & Muñoz, 2013).

In this chapter, I aim to undertake a study of the genetic character of a number of buzzards sampled in the Western Cape, in an effort to reveal the identity of the 'mystery buzzards'. Despite the established difficulty with which the *buteo-vulpinus* complex is differentiated genetically, it is hoped that microsatellite analysis will successfully reveal the taxon composition of the buzzards of the Western Cape, casting light on their identity and inherent origin.

Methods

Sample collection

Thirty-three buzzards were analysed in this component of the study (Table 3.1), 26 of which were sampled in the Western Cape and seven as tissues with associated vouchers at the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley. The seven samples from the MVZ included six known *B. rufofuscus* and one known *B. b. vulpinus.* The *B. rufofuscus* samples were included to test the accuracy of the STRUCTURE taxa groupings, whilst the *B. b. vulpinus* provided a pure *B. b. vulpinus* signature to test the 'mystery buzzards' against. Of the samples obtained in South Africa, 19 were taken from captive rehabilitated birds at Eagle Encounters in Stellenbosch and World of Birds in Hout

Bay, Cape Town. Four of the remaining birds were sampled as chicks from nests on the Cape Peninsula, and three were caught using traditional Bal-Chatri traps near Cape Agulhas.

Blood samples were taken by sterilising and then piercing the brachial vein with a 21 gauge needle, after which two capillary tubes of blood were collected and transferred to containers of lysis buffer. Samples were then stored at c.5°C until transfer to UC Berkeley (Owen, 2011).

Three of the 26 buzzards sampled in the Western Cape, three were captured in the austral summer at Cape Agulhas, in typical habitat for migratory *B. b. vulpinus,* away from any suitable breeding habitat, and appeared most like this taxon in their appearance (Figure 3.1). These samples were taken to provide a reliable example of apparently genetically pure *B. b. vulpinus*. Confirmed *B. trizonatus* proved much more difficult to capture, and despite extensive efforts in the core of their range near Knysna, none were successfully captured. Due to the difficulty in obtaining a genetic sample of *B. b. menetriesi* and *B. r. cirtensis*, these two taxa were not included in the analysis.

Figure 3.1 Buzzards SB001 (above) and SB003 (below) sampled as pure *B. b. vulpinus* near Cape Agulhas. SB002 is not shown due to the bird being released before a comparable photo could be taken.

Table 3.1 Sample type, age, geographical origin and date of all buzzards sampled for genetic analysis

Specimen	Sample type	Taxon	Age	Location	Date
EE001	Blood	Unknown	Adult	Eagle Encounters, Stellenbosch, WC	18/03/2011
EE002	Blood	Unknown	Adult	Eagle Encounters, Stellenbosch, WC	11/01/2012
EE1116	Blood	Unknown	Adult	Eagle Encounters, Stellenbosch, WC	11/01/2012
WOB001	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB002	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB003	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB004	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB005	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB006	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB007	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB008	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB009	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB010	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB011	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB012	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB013	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB014	Blood	Unknown	Juvenile	World of Birds, Hout Bay, WC	25/05/2011
WOB015	Blood	Unknown	Adult	World of Birds, Hout Bay, WC	25/05/2011
WOB016	Blood	Unknown	Juvenile	World of Birds, Hout Bay, WC	25/05/2011
BUIT20091	Blood	Unknown	Juvenile	Buitenverwagten Farm, Cape Town, WC	06/01/2009
BUIT20092	Blood	Unknown	Juvenile	Buitenverwagten Farm, Cape Town, WC	06/01/2009
CF001C	Blood	Unknown	Juvenile	Chart Farm, Cape Town, WC	28/11/2011
RM001	Blood	Unknown	Juvenile	Rhodes Memorial, Cape Town, WC	09/01/2012
SB001	Blood	*B. b. vulpinus*	Juvenile	Cape Agulhas, WC	24/01/2012
SB002	Blood	*B. b. vulpinus*	Juvenile	Cape Agulhas, WC	24/01/2012
SB003	Blood	*B. b. vulpinus*	Juvenile	Cape Agulhas, WC	24/01/2012
GO265	Tissue	*B. rufofuscus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	
480	Tissue	*B. rufofuscus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	
517	Tissue	*B. rufofuscus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	
527	Tissue	*B. rufofuscus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	
566	Tissue	*B. rufofuscus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	
625	Tissue	*B. rufofuscus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	
JF355	Tissue	*B. b. vulpinus*	Adult	Museum of Vertebrate Zoology, Berkeley, CA	

Approximately 25μL of blood or 20μg of tissue was used to isolate DNA following the purification of total DNA from animal tissues using a Qiagen DNeasy kit (Qiagen Inc.). The extracted DNA was then stored at -80°C. All remaining tissue samples and extracted DNA is permanently stored at the Museum of Vertebrate Zoology.

Genetic analysis

To determine the taxon-assignment of the sampled buzzards, a multi-step microsatellite analysis was undertaken using the program STRUCTURE 2.3 (Pritchard *et al.,* 2000). STRUCTURE has been found to be efficient in identifying population structure and detecting hybridisation within populations (Vähä and Primmer, 2006; Pons *et al.,* 2014). For species as shallowly-divergent as the Old World *Buteo*s, microsatellites prove useful in identifying genetic variation and introgression within populations.

Each of the sampled birds was genotyped for 18 polymorphic microsatellite loci, designed for *Buteo swainsoni* (Hull *et al.,* 2007): BswA110, BswA302, BswA303, BswA312, BswA317, BswB111, BswB220, BswB221, BswD107, BswD210, BswD220, BswD223, BswD234, BswD235, BswD310, BswD313, BswD327, BswD330. Development of new species-specific microsatellite primers is expensive and time-consuming and as such newly-developed primers are often tested, successfully, for cross-specific amplification on related species (Moore *et al.,* 1991; Estoup *et al.,* 1993; Zardoya *et al.,* 1996; Li *et al.,* 1997; Ishibashi *et al.,* 2000; Galbusera *et al.,* 2000). The primers used in this investigation were tested for cross-amplification with seven *Buteo* species: *B. regalis, B. lagopus, B. jamaicensis, B. albicaudatus, B. galapagoensis, B. platypterus* and *B. lineatus* (Hull *et al.,* 2007). Interestingly, Galbusera *et al.* (2000) found an 84% success rate of cross-amplification in non-closely related passerines of 13 species representing 10 families, using 40 microsatellite markers developed in 16 species representing 11 families, suggesting that cross-amplification may not be limited to closely-related species.

PCR reactions included 1.0µL of extracted DNA, 0.6µL of each primer (10µM), 1.0µL of 10X Invitrogen Taq Reaction Buffer (Invitrogen Inc.), 0.3 – 0.5µL of 50mM $MgCl_2$, 0.5µL of BSA (10mg/ml), 0.25µL of dNTPS (10mM each dNTP), and 0.12µL of Taq DNA polymerase and ddH_2O to make up a total of 10µL reaction volume. Optimised PCR conditions for the *Buteo* samples analysed were as follows: 3 minutes (min.) denaturation at 94°C, 30 cycles of 45 seconds (s) at 94°C, 30s at 52 – 56°C, and 45s at 72°C, followed by a final extension of 30 minutes at 72°C.

STRUCTURE 2.3 runs a multi-locus Bayesian assignment method to determine the most likely number of populations (K) present among the individuals scored. Firstly, all of the adult birds (n=20) were combined into one data set and STRUCTURE was run using the admixture model with no prior population information provided. This model allowed us to examine whether there were groups of taxa recovered by the assignment analyses. Since adult birds are more reliably assigned to species, we used these taxa as a “guide” in an attempt to assign birds of uncertain morphology into taxonomic categories. The model was run for 10^6 iterations after a burn-in period of 1×10^5 for each value of K (K=1 – 7, each K repeated 5 times).

The output for the first step was visually examined for the presence of consistent groupings of individuals for each value of K, as well as correlation between the assigned groups and morphological taxa identification, as determined in Chapter 2. Consistently identified groups were then used to select a subset of adults that were assigned to putative population groups for *B. b. vulpinus, B. b. menetriesi, B. trizonatus* and *B. rufofuscus,* informed by morphology data gathered in Chapter 2.

STRUCTURE was run for a second time using the subset of assigned adults to provide prior information for the model. This time the USEPOPINFO model was run, with the assigned adults as "learning samples" for the model. The USEPOPINFO model with "learning samples" specifically uses individuals from known clusters to help create a more informed model that helps to assign the remaining individuals in the data set. The model was run for 1 x 10^6 iterations with 5 x 10^4 burn-in for each K value (K=3 – 5, 5 iterations each).

Data from the final runs was then examined, and a bar plot of the estimated membership coefficients for each individual to a cluster was created for K=5.

Results

The output from the STRUCTURE analyses (Figure 3.2) assigned all 33 buzzard samples included in the analysis. The *B. rufofuscus* test samples clearly group together, signified as yellow here, indicating an accurate assignment of populations.

Taking samples SB001, SB002, SB003 and JF355 as pure *B. b. vulpinus*, determined through morphological traits and seasonal location data, it can be ascertained that *B. b. vulpinus* is displayed as a red signature here. Similarly, buzzards WOB011 and WOB012 appear typical of *B. trizonatus* in their phenotypic traits, and buzzard RM001 was sampled as a chick on the Cape Peninsula with apparently typical *B. trizonatus* parents. Using these birds as a benchmark for recognising the genetic signature of *B. trizonatus*, it would appear that this taxon is represented by blue.

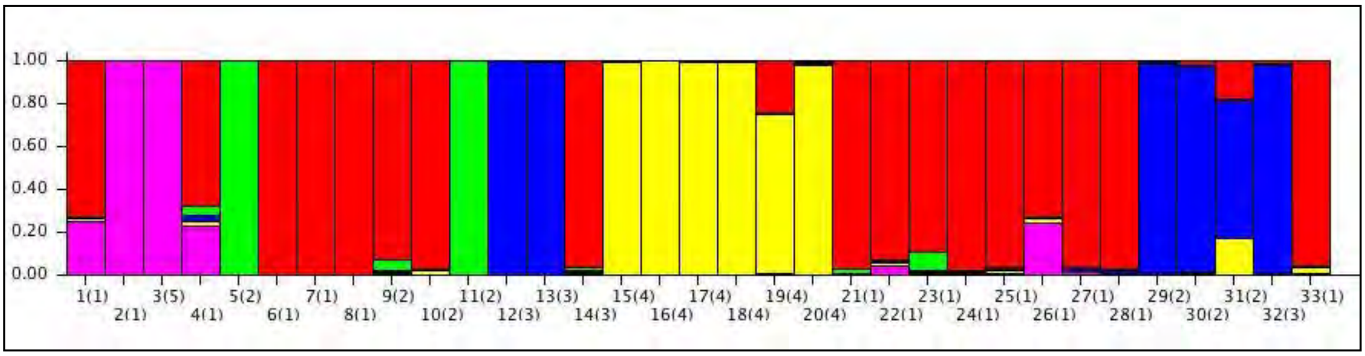

Figure 3.2 Population assignment graph outputted by STRUCTURE, detailing population assignment of the sampled buzzards. Yellow appears to represent *B. rufofuscus, r*ed appears to represent *B. b. vulpinus,* and blue appears to represent *B. trizonatus.* Pink and green signatures are unidentified. Further information can be found in Table 3.2.

Table 3.2 STRUCTURE graph number, specimen code, and genetic and morphology matches of buzzards analysed in this component of the study.

STRUCTURE graph number	Specimen code	Genetic match	Morphology match	Notes
1	EE002	*B. b. vulpinus*	N/A	Morphology data not available
2	EE1116	Unknown	N/A	Morphology data not available
3	EE001	Unknown	N/A	Morphology data not available
4	WOB002	*B. b. vulpinus*	*B. b. vulpinus*	
5	WOB003	Unknown	*B. b. menetriesi*	
6	WOB006	*B. b. vulpinus*	*B. b. vulpinus*	
7	WOB008	*B. b. vulpinus*	*B. b. vulpinus*	
8	WOB009	*B. b. vulpinus*	*B. b. vulpinus*	
9	WOB007	*B. b. vulpinus*	*B. b. menetriesi*	
10	WOB001	*B. b. vulpinus*	*B. b. menetriesi*	
11	WOB005	Unknown	*B. b. vulpinus*	
12	WOB011	*B. trizonatus*	*B. trizonatus*	
13	WOB012	*B. trizonatus*	*B. trizonatus*	
14	WOB015	N/A	*B. trizonatus*	Plumage typical of *B. trizonatus*
15	GO265	*B. rufofuscus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology
16	480	*B. rufofuscus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology
17	517	*B. rufofuscus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology
18	527	*B. rufofuscus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology
19	566	*B. rufofuscus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology
20	625	*B. rufofuscus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology
21	WOB004	*B. b. vulpinus*	*B. b. menetriesi*	
22	WOB010	*B. b. vulpinus*	*B. b. vulpinus*	
23	WOB013	*B. b. vulpinus*	*B. b. menetriesi*	
24	SB001	*B. b. vulpinus*	*B. b. vulpinus*	Collected on Agulhas Plains as pure *B. b. vulpinus*
25	SB003	*B. b. vulpinus*	*B. b. vulpinus*	Collected on Agulhas Plains as pure *B. b. vulpinus*
26	SB002	*B. b. vulpinus*	*B. b. vulpinus*	Collected on Agulhas Plains as pure *B. b. vulpinus*
27	WOB014	*B. b. vulpinus*	*B. b. vulpinus*	
28	WOB016	*B. b. vulpinus*	*B. b. vulpinus*	
29	BUIT20091	*B. trizonatus*	*B. b. menetriesi*	Uniform rufous parents
30	BUIT20092	*B. trizonatus*	*B. b. menetriesi*	Uniform rufous parents
31	CF001C	*B. trizonatus*	N/A	Morphology data not collected from nest-bound chick. Uniform rufous parents.
32	RM001	*B. trizonatus*	N/A	Morphology data not collected from nest-bound chick
33	JF355	*B. b. vulpinus*	N/A	Tissue with voucher, Museum of Vertebrate Zoology

In addition to the signatures of *B. rufofuscus, B. b. vulpinus* and *B. trizonatus*, there appear to be two additional unknown genetic signatures, displayed by EE1116 and EE001 as pink, and WOB003 and WOB005 as green.

Table 3.2 details the genetic taxon-assignment of each of the sampled buzzards, together with their phenotypic taxon-assignment. Of the 23 buzzards sampled in the Cape, excluding those collected as *B. b. vulpinus* at Agulhas, twelve have matching genetic and phenotypic characters identifying them as *B. b. vulpinus* (n=10) or *B. trizonatus* (n=2).

Of the five buzzards for which phenotype data was not available due to data being collected by other people before my arrival, one matched *B. b. vulpinus* (EE002) genetically, whilst two matched *B. trizonatus* (RM001 and CF001C). One of the latter buzzards (RM001) was born to parents appearing typical of *B. trizonatus,* whilst the other (CF001C) was born to parents that were entirely uniform rufous. Two buzzards (EE1116 and EE001), which were sampled before my arrival in South Africa and for which no phenotypic data was collected, appear to represent a further, unidentified taxon.

Eight buzzards have conflicting phenotypic and genetic matches. Buzzards WB001, WOB004, WB007 and WOB013, though deemed to match *B. b. menetriesi* most closely in their phenotype due to their large morphology, were found to match *B. b. vulpinus* genetically. Similarly, buzzards BUIT20091 and BUIT20092 were deemed to most closely match *B. b. menetriesi* in their phenotype, featuring the large morphology of this taxon, however genetically they unexpectedly appear to be a match for *B. trizonatus*.

Finally, buzzards WOB003 and WOB005 were considered to match *B. b. menetriesi* and *B. b. vulpinus* in their phenotypes, respectively, but appear to feature a second unidentified genetic signature. They are represented by the green signature in Figure 3.2.

Interestingly, there appears to be a general lack of introgression. For example there is no evidence to suggest any of the sampled buzzards are F1 hybrids however, as displayed in Figure 3.2, there does appear in a number of cases to be the suggestion of possible past introgression, and as such some of the buzzards may be backcrosses.

Discussion

Kruckenhauser *et al.* (2004) concluded that due to their very recent divergence, the Old World buzzards of the *buteo-vulpinus* complex could not be unequivocally separated genetically. Little further work appears to have been undertaken on this group using modern next-gen genetic methods, and the taxonomic status of many taxa remains unclear.

Using 18 polymorphic microsatellite loci designed for *Buteo swainsoni* (Hull *et al.,* 2007), I was able to clarify the genetic identity of all but four of the 26 buzzards sampled in the Western Cape, with taxon groups appearing to separate reliably.

Buzzards matching the traditional small *Buteo*s of South Africa: Steppe Buzzard *B. b. vulpinus* and Forest Buzzard *B. trizonatus*

As would be expected, the majority of buzzards sampled (n=15; 65%) were a genetic match for either *B. b. vulpinus* or *B. trizonatus*, with twelve of the birds possessing consistent genetic and morphological taxon designations.

Interestingly, two buzzards displaying phenotypic characteristics most like *B. b. menetriesi* (WOB004 and WOB013) were a genetic match for *B. b. vulpinus*. These birds do not appear 'typical' of *B. b. vulpinus* in their phenotype. Buzzards WOB004 (Appendix 1, buzzard 4) and WOB013 (Appendix 1, buzzard 13) are much larger than would be expected of *B. b. vulpinus*, and are more similar to the *B. b. menetriesi*. It is worth noting that the morphometric separation of the candidate species can in some cases be a matter of millimetres (See Chapter 2), and as such the larger size of WOB004 and WOB013 could perhaps be explained by incorrect measurements being taken, or perhaps sexual dimorphism. For example, in the extremely closely related *B. b. buteo*, females are 5-10% taller and 27-30% heavier than males (Perrins & Snow, 1998).

A further four of the buzzards sampled showed a genetic match with either *B. b. vulpinus* or *B. trizonatus*. One of the samples came from a buzzard (EE002) for which no phenotypic data is available, and so no further information or conclusions can be drawn other than that it does not, genetically, represent an unexpected taxon. One other buzzard has no phenotypic data, due to being sampled as a chick from a nest on the Cape Peninsula. This buzzard, RM001, shows a distinct genetic signature matching *B. trizonatus*, and was born to a pair of buzzards that appeared typical of this taxon in their plumage. As such, it appears most reasonable that it is identified as *B. trizonatus*.

The two remaining buzzards, WOB001 and WOB007, displayed genetic signatures matching *B. b. vulpinus* but were deemed to most closely match *B. b. menetriesi* morphologically. Buzzards WOB001 (Appendix 1, buzzard 1) and WOB007 (Appendix 1, buzzard 7) both feature the large morphology associated with *B. b. menetriesi*. Due to the absence of a pure *B. b. menetriesi* genetic sample as a benchmark in this study, the potential presence of this taxon cannot be unequivocally assessed, however the extremely strong genetic match for *B. b. vulpinus* in both birds is interesting. The remarkable similarity of these buzzards to two true *B. b. menetriesi* samples suggests that these birds could represent *B. b. menetriesi*, however as they still place close to the morphospace of *B. b. vulpinus,* and appear to be a strong genetic match for this taxon, it is perhaps reasonable to suggest that these birds are in fact *B. b. vulpinus*. WOB007 appears to show an extremely small genetic influence from the unidentified signature designated as green in Figure 3.2.

Atypical juvenile buzzards with conflicting genetic and morphometric matches

Three of the young buzzards sampled on the Cape Peninsula were of particular interest and displayed a quite unexpected genetic result. Two sibling buzzards (BUIT20091 and BUIT20092; Appendix 1, buzzards 17 and 18) were sampled as recently fledged juveniles. Despite being recently fledged, both buzzards possessed morphology most similar to *B. b. menetriesi*, being large, long winged and long tailed. In fact, the morphology of BUIT20092 is almost identical to that of a true *B. b. menetriesi* sample used in the Kruckenhauser *et al.* (2004) study. Buzzard CF001C was sampled as a nest-bound chick, and as such no comparable morphometric measurements were obtained. This bird was born to a pair of buzzards that were entirely uniform rufous with no hint of any abdominal spotting, breast U or defined bib. All three buzzards unexpectedly revealed an extremely strong genetic match for *B. trizonatus*.

Given that *B. trizonatus* is traditionally believed to be monotypic, and phenotypically dissimilar to these buzzards, this result is puzzling. With a number of the sampled buzzards in this component of the study appearing phenotypically typical of *B. trizonatus* sharing the same genetic signature (blue in Figure 3.2), that is not present in these juveniles, it seems unlikely that the signature of *B. trizonatus* has been misidentified. However, if this result is indeed correct, then it could have serious implications for the understanding and subsequent field identification of *B. trizonatus*.

It has long been understood that *B. trizonatus* is monotypic (Hockey *et al*., 2005), as would seem logical if the theory that this taxon evolved from Mountain Buzzard *B. oreophilus*, which is also monotypic, is to be accepted (Siegfried, 1969). However, it would appear an interesting coincidence that the first instances of atypically uniformly plumaged buzzards breeding in the south-west Cape, in the late 1970s and early 1980s, coincides with the initial colonisation of the Western Cape by *B. trizonatus* (Boshoff *et al.*, 1983). Based on the strong genetic match for *B. trizonatus* found in these uniformly rufous buzzards, it would perhaps be reasonable to speculate that there is in fact, although rare, a uniform morph of *B. trizonatus*. Unless this apparent morph of *B. trizonatus* differs from the traditionally recognised 'light' morph in its morphology, however, this would not explain the morphology of these birds, which at least in the case of the BUIT2009 siblings is almost identical to *B. b. menetriesi*.

Although, quite remarkably, it appears that there could indeed be a uniform morph of *B. trizonatus*, the morphometrics of the sampled buzzards do not appear to support this conclusion. Without further study of the uniform buzzards of the south-west Cape, and in particular these individuals, no firm conclusions can be drawn from this evidence.

Unidentified genetic signatures

Aside from the presence of *B. b. vulpinus* and *B. trizonatus*, as was expected, the study also revealed two unidentified genetic signatures. The first was possessed by buzzards EE001 and EE1116. Unfortunately, these samples were collected prior to my arrival in South Africa and without accompanying images or morphometric measurements. Frustratingly, no conclusions can be drawn from these birds other than that they appear to represent a taxon of *Buteo* other than the expected *B. b. vulpinus* and *B. trizonatus*.

The second unidentified signature was discovered in buzzards WOB003 (Appendix 1, buzzard 3) and WOB005 (Appendix 1, buzzard 5). As displayed in Chapter 2, the morphology of these buzzards places WOB003 firmly in the morphospace of *B. b. menetriesi* and WOB005 in the overlap zone of *B. b. vulpinus, B. trizonatus* and *B. b. menetriesi*. Given the relatively large morphology and strong unidentified genetic signature of WOB005, it is perhaps reasonable to theorise that this individual could represent *B. b. menetriesi*. The morphology of this bird places it within the known variation of *B. b. menetriesi*, and given that *B. b. vulpinus* and *B. trizonatus* appear clearly defined genetically, the genetic character of this bird would appear to truly signify a taxon previously unknown from South Africa. It would appear that WOB005 may present a strong case for identification as *B. b. menetriesi*.

With morphology well-removed from *B. b. vulpinus* and *B. trizonatus* and a genetic signature that is unrecognised and seemingly neither of the small *Buteo*s traditionally known from South Africa, it would appear that WOB003 presents another interesting case for the presence of *B. b. menetriesi* in South Africa. This is especially true, given that both buzzards sharing this genetic signature have supporting evidence that indicates *B. b. menetriesi*.

As no genetic samples of confirmed *B. b. menetriesi* were included in the analysis here, at this stage it is not possible to say with certainty whether the observed signature is in fact this taxon. However, the weight of evidence does seem to indicate that this could be the case.

Conclusions

It remains apparent that the taxon-composition of the buzzards of the Western Cape is complex. Whilst the majority of sampled buzzards proved a genetic match for *B. b. vulpinus* or *B. trizonatus*, there is strong evidence that there may indeed taxa present in the Cape that appear to be neither of these traditionally-present buzzards. The results of this genetic investigation point toward the presence of two taxa previously unknown from the Cape, with supporting morphology and plumage evidence indicating that one of these may be *B. b. menetriesi*, as I have made the case for in Chapter 2. With a lack of supporting phenotypic data, the second genetic signature remains unresolved.

In addition to the apparent discovery of *Buteo* taxa previously unknown from the region, genetic results presented in this chapter indicate that some uniformly-rufous juveniles, born to uniformly-rufous parents, are a strong genetic match for *B. trizonatus*; a taxon that is understood to be monotypic and quite unlike the buzzards described here. The logical supposition would be that there is a previously undescribed and uncommon uniform morph of *B. trizonatus,* however the meristic characters of the sampled buzzards would appear to contradict this theory.

Further study of the taxon-composition of the Western Cape buzzards will clearly be required before any firm understanding of the complex dynamics is achieved. At this point, it would appear that *B. b. vulpinus* and *B. trizonatus* continue to be the most common buzzards in the Cape, with potentially a further two unidentified *Buteo* taxa being present with unknown regularity and abundance.

Chapter 4: The foraging ecology, diet and nesting behaviour of 'mystery buzzards' in the South-western Cape

Introduction

Traditionally, ecology was rarely used to assess the specific validity of a taxon as genetic and phenotypic variation has taken precedent in the assessment of species boundaries (Mayr, 1940). Increasingly, however, differences in ecology between populations of species' are being investigated with surprising results. For example, in the Band-rumped Storm Petrel complex it has been recognised that numerous island populations have hot and cold season breeding populations, which have subsequently been shown to differ in their morphology, moult chronology and vocalisations (Friesen, 2007; Robb *et al.,* 2008; Howell *et al*., 2010). In the case of the Azorean breeding populations, significant genetic variation has been recognised and elevation of the hot season breeders to species status as Monteiro's Storm Petrel *Oceanodroma monteiroi* has been proposed as a result of studies initiated following the recognition of intriguing aspects of the population's ecology (Bolton *et al.,* 2008; Robb *et al.,* 2008). Evidently, variation in the ecology of populations can help highlight situations which may merit further investigation, which in some cases may prove to reveal currently unrecognised cryptic taxa.

Genetic dilution through widespread hybridisation is in some cases a major threat to the continued existence of a species (Rhymer & Simberloff, 1996; Huxel, 1999), as is the situation with the Black Stilt *Himantopus novaezelandiae*, a critically endangered wader found in the Mackenzie Basin of New Zealand (Wallis, 1999; Robertson & Heather, 2005). The decline of the Black Stilt has been exacerbated by the colonisation of the White-headed Stilt *Himantopus leucocephalus,* with which it shares extremely similar courtship behaviour, giving rise to widespread hybridisation (Pierce, 1996). In situations where a pure Black Stilt mate is not available, one of the now numerous dark-plumaged hybrid stilts is chosen as a mate; where one of these hybrid birds is not present, breeding takes place with White-headed Stilt (Pierce, 1996). This has given rise to vast phenotypic diversity, and has in part led to the near collapse of the species.

Similarly, the dire situation faced by the White-headed Duck *Oxyura leucocephala* is, in part, a result of widespread hybridisation with introduced Ruddy Duck *Oxyura jamaicensis* (Muñoz-Fuentes *et al.*, 2006). Following a severe bottleneck in White-headed Duck, the rapid establishment of introduced Ruddy Duck from just 7 individuals has resulted in hybridization across the range of the White-headed Duck, resulting in the forecast that without effective control of Ruddy Ducks, genetic introgression will compromise the continued existence of the White-headed Duck as a genetically and evolutionarily distinct species (Muñoz-Fuentes *et al.*, 2006).

As discussed in the introduction chapter of this thesis, under our term 'mystery buzzard' we hypothesise that there may be up to three candidate taxa which are now resident and breeding in South Africa; these are *B. b. vulpinus*, *B. b. menetriesi* and *B. trizonatus*. A comparison of the ecology of these different taxa with the ecology of our 'mystery' buzzards may provide some information on the weight of evidence as to the likely candidate species. In addition, it may reveal the levels of potential compatibility and indeed competition that the other candidate taxa may have with the resident endemic *B. trizonatus.*

This chapter aims to review the breeding ecology of the 'mystery' buzzards and assess the potential of this endemic taxon as a viable reproductive partner base for the 'mystery' buzzards. I first undertake a review of the published literature to describe what is known about the foraging ecology, diet and nesting behaviour of the three candidate taxa. I then explore the foraging behaviour of the buzzards in my study area from observations gathered in 2011 and 2012, describing their main modes of hunting and diet, together with their nesting behaviour.

Methods

Review methods

A literature search was undertaken to establish the diet, foraging behaviour and nesting behaviour of the candidate taxa in this study. This was undertaken using the search engines Google Scholar, Searchable Ornithological Research Archive (SORA), Web of Science and, for the nesting and foraging behaviour, by using a number of key texts describing these traits. For an effective literature search I used the candidate taxa names, both common and species (Steppe Buzzard *B. b. vulpinus,* Ménétries's Buzzard *B. b. menetriesi* and Forest Buzzard *B. trizonatus*), in combination with the search terms: diet, prey, ecology, nesting behaviour, nesting ecology, foraging behaviour, foraging ecology.

Foraging ecology and diet

To investigate the foraging behaviour and diet of the 'mystery buzzards' I used a basic observation system, whereby during the breeding season (September 2011 – March 2012) I drove a fixed route opportunistically stopping whenever a buzzard was sighted within ca.300m of the vehicle. I would then watch the buzzard from the vehicle with 8.5x42 binoculars for at least thirty minutes, or until it flew out of sight, observing the proportion of time the bird was engaged in different behaviours by recording its behaviour every 3 minutes. The time spent engaged in foraging behaviour was then estimated by excluding other behaviours, such as flying, preening and interacting. The foraging behaviours were classified as: 1) Perch hunting, where the buzzard would be perched and actively scanning the ground for prey; 2) Hovering, where the buzzard would be actively 'hovering', or hanging in the wind whilst scanning the ground; 3) Walking on the ground, taking prey on foot. Whenever any successful capture attempt was made, I tried to identify the prey item using optical and photographic equipment. Identifiable prey items were documented to the level of mammal, bird, invertebrate, reptile or amphibian, and where possible to species level. Prey items and remains in nests were identified and recorded during single visits that were made to ring and sample blood from the chicks.

Details of the diet and foraging behaviour of the five candidate taxa can be found in tables 4.1 and 4.2 respectively.

Nesting ecology

Nests were found by observing suspected, suitable and past-season nest sites. At sites where buzzards appeared active, the points at which they entered the plantation/trees were determined and attempts were made to watch their flight path through the forest, both from afar and from the edge of the area of trees. This area was then searched on foot by walking transects parallel to the edge of the plantation, progressing into the plantation by 10 metres after each transect. Often I would be harassed by loudly calling and dive-bombing buzzards, allowing me to determine the nest was close. I would then narrow my search to within a radius of ca.30 metres.

Records of any buzzards, including *B. trizonatus*, nesting in the study areas over a 10 year period between 2002 and 2012 were compiled from a combination of field work and past season records (Martin & Walton, 2011, unpublished data). The information concerning the nest site was then collated, specifically the location, the species of tree used and whether the tree utilised was alone or within a small stand, large plantation or single-depth row of trees. Small stands were classified as covering less than a hectare in area, whilst large commercial plantations in the study area cover a hectare or more of land.

In as many instances as possible, plumage descriptions of the buzzards attending each nest were also collected. These descriptions were then matched against the plumage descriptions of *B. trizonatus* and 'Steppe-type buzzards' (i.e. the inseparable *B. b. vulpinus* and *B. b.* menetriesi) outlined in Chapter 2 to tentatively identify each buzzard in an effort to reveal any apparent hybridisation within the study area, and to further inform our knowledge of the apparent colonisation of the Western Cape by 'Steppe-type buzzards'. These records were made by four individuals and were centred on the main study area of the Elgin Valley and along the Cape Peninsula (see Chapter 1: Introduction).

Results

Literature review

There appear to be some substantial knowledge gaps in the diet of the buzzards considered in this study, with little or no detailed diet information available for *B. b. vulpinus* and *B. b. menetriesi*, and just one study that gives detailed information on the diet of *B. trizonatus* (Palmer *et al.,* 1985), as shown in Table 4.1.

A review of key texts suggests that *B. b. vulpinus* and *B. b. menetriesi* both primarily feed on small rodents, with reptiles, birds and invertebrates playing lesser roles in their diet (Dementiev & Gladkov, 1966; Adamian and Klem, 1999; Hockey *et al.,* 2005). *Buteo* buzzards are, however, extremely adaptable and likely change their diet to adapt to the availability of different prey types, in keeping with the alternative prey hypothesis which suggests that predators alter their diet according to prey type and abundance, especially in predators with a strong preference for prey that fluctuates in numbers (Reif *et al.,* 2001). For example, in *B. b. buteo* the importance of birds in their diet ranges significantly, from just 2% of the diet in a Spanish population (Tapia *et al.,* 2007*)* to 47% in a British population (Graham *et al.,* 1995). Similarly, reptiles vary from making up just 5.8% of the diet in a study of Finnish *B. b. buteo,* to 30.4% in a study of a Spanish population (Zuberogoitia *et al.,* 2006).

Table 4.1: Collation of candidate taxa diet studies illustrating the percentage of diet that each class of animal represents

Taxon	**Study area**	**Methods**	**Sample size**	**Diet %** **Bird**	**Mammal**	**Amphib.**	**Reptile**	**Invert.**	**Study**
B. b. vulpinus	*Detailed diet information unavailable*			Primarily small rodents; also lizards, snakes, small or young birds, and insects. Also takes road kill.					Dementiev & Gladkov, 1966 Adamian & Klem, 1999 Hockey *et al.*, 2005
B. b. menetriesi	*Detailed diet information unavailable*			Primarily small rodents; also lizards, snakes, small birds, and insects including Cicadas					Dementiev & Gladkov, 1966
B. trizonatus	South Africa	Nest prey remains	4 years, 6 nests, 21 prey remains	14.2%	23.8%	0%	28.5%	33.3%	Palmer *et al.,* 1985

Table 4.2 displays the known foraging behavioural traits of the candidate buzzards. All of the buzzards appear to be primarily perch-hunters, however only *B. trizonatus* is not known to also employ soaring, hovering and hunting on foot to a lesser degree. Information for *B. b. menetriesi* and *B. trizonatus* is again sparse and mainly based on anecdotal evidence, however it appears that foraging behaviour is widely shared among the taxa.

The nesting behaviour of the candidate taxa is extremely similar, as shown in Table 4.3. *B. trizonatus* is the only taxon for which cliff nesting has not been recorded, with all appearing to prefer trees, specifically within forests. Clutch sizes are similar, with *B. b. vulpinus* and *B. b. menetriesi* laying between 2 and 4 eggs per clutch, and *B. trizonatus,* on limited evidence, appearing to lay only 2 eggs.

Table 4.2: Summary of the foraging behaviour of the candidate taxa compiled from literature

	Foraging behaviour				**Detailed information**	**Source**
	Perch hunting	Soaring and quartering	Hovering	On foot		
B. b. vulpinus	Yes	Yes	Yes	Yes	Utilises perch hunting and hovering as primary foraging means. Soaring and quartering used to lesser extent. Recorded 'walking' to forage for locusts.	Dementiev & Gladkov, 1966 Perrins & Snow, 1998 Ferguson-Lees & Christie, 2001
B. b. menetriesi	Yes	Yes	Yes	Yes	Primarily a perch hunter, though hovering has been recorded. Information sparse.	Dementiev & Gladkov, 1966 V. Ananian, per comms.
B. trizonatus	Yes	Information unavailable	Information unavailable	Information unavailable	Hunts mainly from perch within forest, dropping on to prey.	Palmer *et al.,* 1985 Hockey *et al.,* 2005

Table 4.3: Summary of the nesting behaviour of the candidate taxa compiled from literature

	Nest siting	**Description of nest**	**Cliff nesting**	**Clutch size**	**Description of egg**	**Source**
B. b. vulpinus	Forest edge	Platform of sticks; cup lined with bark, moss and down. Usually covered with green twigs; usually 8-12m above ground.	Only one incidence found.	2-3	Eggs whitish green with chestnut-brown and deep violet-brown speckling	Dementiev & Gladkov, 1966
B. b. menetriesi	Trees in forests near glades	Information unavailable	Nests occasionally found on rock ledges	2-4	Information unavailable	Dementiev & Gladkov, 1966 V. Ananian, per comms.
B. trizonatus	Forest interior	Platform of sticks; cup lined with green leaves. Placed 9-30m above ground.	Not recorded	2	Eggs greenish-white, variably marked red, rust brown and grey.	Hockey *et al.,* 2005 Palmer *et al.,* 1985

Diet

Between July 2011 and June 2012, I recorded 37 prey items from observations of buzzards making kills (n=29), from prey remains (n=3) and from pellets recovered from nests (n=5). I was able to identify all of these to at least main taxonomic group. Table 4.4 reports the recorded prey types, the number of each type, and the percentage of total observed diet that each type comprises.

Table 4.4: Diet of the 'mystery buzzards', including recorded prey types, number of instances this type of prey was recorded and the percentage of instances this comprises. Derived from observed kills, prey remains in nests, and pellets recovered from nests.

Type of prey	**Kills**	**Prey remains**	**Pellets**	**Percentage of total instances recorded**
Small rodents	15	2	5	59.4%
Locust/Grasshopper	7	0	0	18.9%
Snake	3	0	0	8.1%
Lizard	2	0	0	5.4%
Bird	1	0	0	2.7%
Freshwater Crab	0	1	0	2.7%
Worm	1	0	0	2.7%
Total:	29	3	5	

From observations of successful kills and remains found in nests, small rodents were found to form the majority of the buzzards' diet (59.4%), with large locusts and grasshoppers forming the next largest proportion at 18.9%. Of the 22 rodent prey items, nine were identified to species or family level. These were Four-Striped Mouse *Rhabdomys pumilio* (n=5), Cape Molerat *Georychus capensis* (n=2), and elephant shrew of unidentified species (n=2).

Reptiles made up a further 13.5% of the observed kills. One of the predated snakes was identified as a Spotted Skaapsteker *Psammophylax rhombeatus*, and of the Lizards caught one was identified as a Southern Rock Agama *Agama atra*. Only one bird-predation event was witnessed and was of a Grey-winged Francolin *Scleroptila africanus* that was caught in thick fynbos vegetation.

A number of insect parts were found in the collected pellets, however given the difficulty with which invertebrates are identified from just small fragments and the lack of complete specimens or recognisable features to denote number of animals present (e.g. pairs of wing casings), an estimate of the number of insects present in the pellets was not possible, nor were any species identified.

Foraging behaviour

Between September 2011 and March 2012 a total of 117 hours were spent observing buzzards and recording behaviour, primarily in the Elgin study area. Of these 117 hours, an estimated 40% (ca.47 hours) was spent engaged in foraging behaviour by either scanning for prey, perch hunting, hovering or hunting on foot. The remainder of the time was spent in non-foraging activities such as preening, interacting and flying. Table 4.5 displays the proportion of time for which each foraging method was recorded.

Table 4.5: Proportion of foraging behaviour engaged in by buzzards in the study area, based on ca.47 hours of observed foraging behaviour

Foraging method	Proportion of time engaged in method
Perch hunting	99.4%
Hovering	0.4%
Hunting on foot	0.2%

Evidently, the buzzards of the Elgin valley spend the vast majority of their time hunting from perches, predominantly using vineyard poles, orchard poles and fruit trees in orchards.

Nesting ecology

Between 2002 and 2012, all but one of the nests (n=45) found were situated in non-indigenous trees, ranging from an isolated single tree to large commercial plantations of Monterey Pine *Pinus radiate.* The single outlying record was a nest situated on a rock ledge above Kirstenbosch National Botanical Gardens on the Cape Peninsula in 2002.

Table 4.6: Number of buzzard nests, where location was known, per season from 2002 to 2012 in each of the study areas

Study area	**Number of nests per breeding season**										
	2002/03	2003/04	2004/05	2005/06	2006/07	2007/08	2008/09	2009/10	2010/11	2011/12	**Total nests**
Cape Peninsula	2	1	0	1	0	0	3	4	6	8	25
Elgin Valley	0	0	0	1	2	6	3	3	0	5	20
Total:	2	1	0	2	2	6	6	7	6	13	45

Of the 45 nest records, all but five were independent, with at least one 'new' buzzard per pair attending a new nest at a different site over subsequent seasons. Clifford's Wood in Elgin (34°10'21.57 S 19°02'09.38 E) was occupied by the same breeding pair of buzzards in the 2005/06, 2006/07 and 2007/08 seasons, whilst Glen Brae, also in Elgin (34°13'02.81 S 19°05'21.85 E) played host to a nest used in the 2007/08 breeding season, which was re-used in the 2008/09 season.

Table 4.7 displays the nest site choice of the 45 'mystery buzzard' breeding records, where the nest site was known.

Table 4.7: Nesting location of buzzards within the study area in terms of situation, specifically tree species chosen, between 2002 and 2012 across both the Cape Peninsula and Elgin Valley study sites

Nest location	**Frequency**	**Percentage**
Monterey Pine *Pinus radiata*	34	75.5%
Maritime Pine *Pinus pinaster*	5	11.1%
Tasmanian Blue Gum *Eucalyptus globulus*	3	6.6%
Australian Blackwood *Acacia melanoxylon*	1	2.2%
Deodar *Cedrus deodara*	1	2.2%
Rock ledge	1	2.2%

The majority (86%) of nests were found in *Pinus* sp., with 75% of the total nests being located in Monterey Pine *Pinus radiata*. Of 44 nests found in trees, none have been in indigenous species.

Table 4.8: Nest site selection of buzzards in the Cape Peninsula and Elgin Valley study areas between 2002 and 2012 in terms of tree location

Nesting location type	Number of nests	Percentage
Isolated stand of trees	18	48.6%
Large commercial Pine plantation	14	37.8%
Single-depth row of trees	4	10.8%
Isolated single tree	1	2.7%

As Table 4.8 displays, of the 37 records of nesting where the location of the tree was also recorded, 48% of nests were situated in small stands (less than one hectare), whilst 37% were situated in commercial pine plantations of more than one hectare. A total of 10% of nests were located in single-depth rows of Pines, whilst one nest (2.7%) was located in an isolated single Monterey Pine *Pinus radiata* ±100m from the nearest stand of trees.

Tables 4.9 and 4.10 display the details of 45 buzzard nests from across the study area between 2002 and 2011 where descriptions of the attending adult buzzards were collected. In just 11.1% of nesting records (n=5) were both attending adult buzzards considered to show plumage consistent with identification as *B. trizonatus*. This is in contrast to the 64.4% of nest records (n=29) where both attending adult buzzards were considered to show plumage consistent with identification as ‘Steppe-type’ buzzards. In 24.4% of recorded nests (n=11) the attending adult buzzards were considered to consist of one *B. trizonatus*, and one ‘Steppe-type’ buzzard.

Table 4.9 Name, year and location of buzzard nests within the Elgin Valley between 2002 and 2011, with identification of attending adult buzzards as either ‘Steppe-type buzzard’ or *B. trizonatus*, based on plumage features

Nesting site	**Year**	**Location**		**Buzzard 1**	**Buzzard 2**
Clifford’s Wood	2005	34°10’17 S	19°02’16 E	‘Steppe-type’	‘Steppe-type’
Clifford’s Wood	2006	34°10’08 S	19°02’32 E	‘Steppe-type’	‘Steppe-type’
Clifford’s Wood	2007	34°10’21 S	19°02’07 E	‘Steppe-type’	‘Steppe-type’
Clifford’s Wood	2008	34°10’15 S	19°02’08 E	‘Steppe-type’	‘Steppe-type’
Clifford’s Wood	2009	34°10’16 S	19°02’04 E	‘Steppe-type’	‘Steppe-type’
High Rising	2007	34°12’06 S	19°06’16 E	‘Steppe-type’	‘Steppe-type’
Highlands East	2011	14°16’41 S	19°06’33 E	‘Steppe-type’	‘Steppe-type’
Highlands	2011	34°16’00 S	19°94’23 E	‘Steppe-type’	‘Steppe-type’
Highlands West	2011	34°16’00 S	19°04’23 E	‘Steppe-type’	‘Steppe-type’
High Rising West	2011	34°11’51 S	19°06’11 E	‘Steppe-type’	‘Steppe-type’
High Rising East	2011	34°12’16 S	19°07’18 E	‘Steppe-type’	‘Steppe-type’
Valley Road 1	2011	34°14’06 S	19°05’31 E	*B. trizonatus*	‘Steppe-type’
Valley Road 2	2011	34°14’30 S	19°05’58 E	‘Steppe-type’	‘Steppe-type’
Smarag	2011	34°13’17 S	19°04’54 E	‘Steppe-type’	‘Steppe-type’
Mardale	2011	34°11’30 S	19°03’11 E	‘Steppe-type’	‘Steppe-type’
Applethwaite 1	2011	34°11’30 S	19°03’11 E	‘Steppe-type’	‘Steppe-type’
Applethwaite 2	2011	34°11’30 S	19°01’30 E	‘Steppe-type’	‘Steppe-type’
Casey’s Ridge	2011	34°11’51 S	19°00’40 E	*B. trizonatus*	‘Steppe-type’
Nuwebergdam	2011	34°05’28 S	19°94’98 E	*B. trizonatus*	*B. trizonatus*
Hottentots Holland North	2011	34°05’22 S	19°94’29 E	‘Steppe-type’	*B. trizonatus*
Hottentots Holland South	2011	34°05’49 S	19°03’08 E	*B. trizonatus*	*B. trizonatus*
Theewaterskloof	2011	33°59’24 S	19°11’92 E	‘Steppe-type’	‘Steppe-type’
Helderberg North	2011	34°03’54 S	18°52’15 E	‘Steppe-type’	‘Steppe-type’
Helderberg South	2011	34°03’54 S	18°52’15 E	‘Steppe-type’	‘Steppe-type’

Table 4.10 Name, year and location of buzzard nests within the Cape Peninsula study area between 2002 and 2011, with identification of attending adult buzzards as either 'Steppe-type buzzard' or *B. trizonatus*, based on plumage features

Nesting site	Year	Location		Buzzard 1	Buzzard 2
Rhodes Memorial	2009	33°56'42 S	18°27'28 E	*B. trizonatus*	'Steppe-type'
Rhodes Memorial	2010	33°56'25 S	18°26'49 E	*B. trizonatus*	'Steppe-type'
Rhodes Memorial	2011	33°56'27 S	18°26'51 E	*B. trizonatus*	*B. trizonatus*
Eastern Slopes	2010	33°56'49 S	18°27'37 E	'Steppe-type'	'Steppe-type'
Eastern Slopes	2011	33°57'01 S	18°27'50 E	'Steppe-type'	'Steppe-type'
Newlands Forest	2011	33°58'34 S	18°26'40 E	'Steppe-type'	'Steppe-type'
Tokai	2011	34°02'53 S	18°24'54 E	'Steppe-type'	'Steppe-type'
Chart Farm	2011	34°00'14 S	18°26'45 E	'Steppe-type'	'Steppe-type'
Higher Tokai Forest	2002	34°03'04 S	18°24'25 E	*B. trizonatus*	'Steppe-type'
Higher Tokai Forest	2003	34°03'04 S	18°24'45 E	'Steppe-type'	'Steppe-type'
Naked Lady	2005	34°02'41 S	18°24'06 E	'Steppe-type'	*B. trizonatus*
Northern Border	2007	34°02'28 S	18°23'49 E	*B. trizonatus*	'Steppe-type'
Higher Tokai Forest	2010	34°03'25 S	18°24'16 E	*B. trizonatus*	'Steppe-type'
Tokai Arboretum	2010	34°03'51 S	18°24'18 E	'Steppe-type'	'Steppe-type'
Glen Dirk	2010	33°59'45 S	18°26'42 E	*B. trizonatus*	'Steppe-type'
Lower Tokai	2008	34°03'02 S	18°25'52 E	*B. trizonatus*	'Steppe-type'
Lower Tokai	2009	34°03'13 S	18°25'51 E	*B. trizonatus*	*B. trizonatus*
Nova Zonnestraal	2009	34°00'18 S	18°26'48 E	'Steppe-type'	'Steppe-type'
Pagasvlei Greenbelt	2009	34°01'54 S	18°25'44 E	'Steppe-type'	'Steppe-type'
Window Ravine	2006	33°58'37 S	18°25'22 E	'Steppe-type'	'Steppe-type'
Zonnestraal	2008	34°00'35 S	18°27'15 E	*B. trizonatus*	*B. trizonatus*

Discussion

Foraging ecology and diet

As seen in Table 4.4, though the diet of buzzards within the study areas during the breeding season is varied, the component of small mammals is largest, accounting for 59.4% of the total observed diet. Interestingly, the invertebrate component holds the next largest component, with 18.9% of the observed diet provided by locusts and grasshoppers. As shown in Table 4.1, the only other study with such a large invertebrate component is that of Palmer *et al.* (1985) concerning *B. trizonatus*. Whilst there is little detailed information on the diet of *B. b. vulpinus* at the breeding grounds, from field observations in South Africa (i.e. during the non-breeding season) they are commonly seen foraging for locusts and grasshoppers on the ground and from perches, with large congregations having been seen to occur where invertebrate swarms are located (Per obs.; Siegfried, pers. comm.). This agrees with the alternative prey hypothesis, which suggests that predators alter their diet according to prey type and abundance, especially in predators with a strong preference for prey that fluctuates in numbers (Reif *et al.,* 2001). No small mammal trapping was undertaken to assess the abundance of small mammals in the study areas in order to explain the large diet component this class represents, however it appears that the diet of the *Buteo*s is indeed highly adaptable, with Reif *et al.* (2001) concluding that buzzards are able to shift their diet in line with the alternative prey hypothesis. Therefore it would perhaps be reasonable to assume that the proportion of small mammals taken by buzzards in the study areas is due to an abundance of this prey type, with a shift to invertebrate prey being made as and when opportunity and abundance is favourable.

The foraging behaviour of the studied buzzards is interesting. Whilst very little information is available for *B. b. menetriesi*, it appears that foraging behaviour is largely shared by all of the candidate taxa. All employ perch hunting as their primary foraging technique, however *B. b. vulpinus* also appears to regularly forage on foot for invertebrates.

The Elgin valley contains a vast abundance of vineyard poles, orchard supports, telephone poles, fences and boundary markers, creating a theoretically perfect habitat for perch hunting raptors. It is no surprise then that buzzards in this environment utilised perch hunting 99.4% of the recorded time. In fact, just three observations were made of birds not employing this method. Two instances accounting for a total of 0.2% were of birds of typical *B. b. vulpinus* appearance observed foraging on foot, with one foraging for worms in a field being actively ploughed and the other taking locusts by running after them in a field. The third instance involved successful foraging through hovering by a bird of entirely dark brown appearance, which hung in a strong wind before dropping to the ground and successfully capturing a medium sized rodent of unknown identity. Interestingly, the buzzard then proceeded to consume parts of the rodent on the wing before drifting out of sight.

Given that this was the only example of hunting through hovering in 117 hours of detailed observation, and indeed a year of incidental observation, it is perhaps reasonable to assume that this was opportunistic rather than demonstrative of a favoured method. One pair that was observed extensively, and whose territory consisted of an area of recently cleared pine plantation, was not observed to engage in any foraging through hovering despite the comparative lack of available perch sites. Rather, they appeared to utilise the sparse and widely scattered remaining perch sites to hunt in the same areas repeatedly. Thus, hovering does not appear to be a key foraging method in the buzzards that occupy the study area, with perch hunting being employed where possible.

Given that ploughed fields are irregular in the area, and the majority of the land appears to be given to apple orchards and vineyards, perch hunting would appear the most effective and energy efficient method of foraging. Only rarely does there appear to be the opportunity for hunting worms in ploughed fields, and as such they are not sought with the regularity as is documented in the British population of *B. b. buteo* during winter*,* for example (Perrins & Snow, 1998). Even during the wet winter months, when worms would theoretically more often be drawn to the surface by rain, they do not appear to make up any substantial percentage of the buzzards' diet. Locusts on the other hand appear to be a key diet component in the summer months when there is an abundance of this prey type, again as is in keeping with the alternative prey hypothesis.

Given this evidence, it can be said that the buzzards inhabiting the study area primarily feed on small mammals through perch hunting, though they will supplement their diet with various invertebrates, reptiles and even birds when the opportunity arises, and engage in ground foraging where required, though rarely do they forage by hovering.

Nesting ecology

The breeding ecology of buzzards in the south-western Cape was found to be as was expected. In terms of nest site location, it was expected that the majority of nests would be in alien trees, given the lack of indigenous forest now present in the region. Indeed, all but one of the observed nests over a ten year period were found to be in trees, and of those in trees all were in non-indigenous species. The majority (86%) were found in *Pinus* sp., predominantly Monterey Pine *Pinus radiata* patches under a hectare in size (48%). Plantations over a hectare in size also accounted for a substantial amount of nest sites (37%). Given the abundance of large commercial pine plantations surrounding Elgin, and the small patches of pine and gum within the valley, there appears to be extremely little indigenous forest left to be utilised as potential nest sites, and as such the buzzards appear to have little choice for nest sites. A similar situation is found on the Cape peninsula, where vast plantations and patches of pine skirt the mountains, providing the majority of possible nesting locations.

The single outlying record is that of a pair of uniformly brown buzzards observed nesting on a rock ledge above Kirstenbosch National Botanical Gardens in 2002. This is particularly interesting as cliff nesting is as-yet unrecorded in *B. trizonatus*, but is observed occasionally in *B. b. vulpinus* and *B. b. menetriesi* (Table 4.3). This nest site choice, combined with the phenotypic characters of the attendant buzzards would appear to indicate that *B. trizonatus* was not involved in this instance, however due to cliff nesting being known from both of the other candidate taxa, and the inseparability of *B. b. vulpinus* and *B. b. menetriesi* based on plumage features, no further evidence can be drawn as to the identity of buzzards in this case based on ecology alone. To date this is the only record of cliff nesting in South Africa, though a single further instance has been suspected (per obs.) but not proven, due to difficult to access terrain in the heart of the Hottentots-Holland Nature Reserve.

With regard to the apparent taxon composition of buzzards breeding in the Western Cape, it appears clear that the majority of nests now belong to 'Steppe-type' buzzards. 64.4% (n=29) of recorded nesting efforts across the study areas between 2002 and 2011 involved buzzard pairs in which both adult appeared most similar to *B. b. vulpinus,* or perhaps *B. b. menetriesi* given that the two are currently un-diagnosable based on plumage features. The study areas hold abundant suitable habitat for nesting buzzards, and given that *B. trizonatus* has never been common in the area (Boshoff, 1997a; Hockey *et al.,* 2005) it seems likely that the colonising 'Steppe-type' buzzards will have faced little or no competition for territory from *B. trizonatus*, allowing a rapid and widespread colonisation.

Interestingly, 24.4% (n=11) of recorded nests were found to be occupied by apparent mixed buzzard pairs consisting of one *B. trizonatus* and one 'Steppe-type' buzzard. Given that *B. trizonatus* is diagnosable from *B. b. vulpinus* and *B. b. menetriesi* based on its plumage, it seems that this presents firm evidence of hybridisation of buzzards within the south-western Cape. With just 5 pairs found in the study area in which both buzzards were identified as *B. trizonatus,* it would appear that in the south-western Cape at present mixed pairings outnumber pure *B. trizonatus* pairings*,* perhaps due to *B. trizonatus* facing difficulties finding a conspecific mate (i.e. the 'Allee Effect' - Short, 1969; Helbig *et al*, 2005). Given the abundance of the 'Steppe-type' buzzards, and the natural scarcity of *B. trizonatus*, it appears likely that the future of *B. trizonatus* as a genetically-distinct species in the south-western Cape is under threat.

Conclusion

The adaptability of the *Buteo*s is perhaps a key factor in the success of the genus in terms of their global presence, being present on all contents but Oceania and Antarctica (Del Hoyo *et al.*, 1994). It is therefore no surprise that there appears to be great variation and adaptability in the ecology of each of the candidate taxa considered in this investigation, with no known taxon-defining ecological traits. For this reason, it is unlikely that any facet of the ecology studied here is able to provide firm evidence or information as to the specific identity of the 'mystery' colonising buzzards. However, the information detailed here serves as documentation of the ecology of these colonising buzzards, and their potential as a viable partner base for *B. trizonatus*.

Though the evidence gathered through this study of the ecology of the buzzards breeding in the south-western Cape is unable to cast light on their specific identity, it has been established that their ecology differs very little from the endemic *B. trizonatus*, and indeed from any of the candidate taxa. Although specific ecological traits can be seen within the population, such as the preference of *Pinus* sp. as nest sites and small rodents as prey, it must be remembered that the areas of the south-western Cape that these birds inhabit is a radically altered landscape, especially so in Elgin, and could scarcely be described as natural. As such, the inhabiting buzzards would be expected to have adapted to their environment, as has been seen in *B. trizonatus,* which has successfully adapted to nesting in the abundant alien tree species (Hockey *et al.*, 2005).

Apparent widespread hybridisation between buzzard taxa across the south-west Cape has been discussed previously in Chapter 2 of this thesis, and the ecology of the colonising buzzards plays a great part in whether this continues and progressively spreads. Whilst there appear to be no postzygotic genetic barriers to successful hybridisation, given the offspring previously produced in the Cape by apparent mixed-taxon pairings, there also appear to be no prezygotic barriers in terms of their ecology. Though *B. trizonatus* differs from the 'mystery buzzards' in that it does not to our knowledge nest on cliffs, just 2% (n=1) of recorded 'mystery buzzard' nests have involved this choice of nest site, with the vast majority (98%) of nests being found in non-indigenous forest.

Though display behaviour is not studied here, given the widespread hybridisation amongst the genus (Gjershaug *et al*., 2006; McCarthy, 2006; Kotyman *et al*, 2008; Corso, 2009; Elorriaga & Muñoz, 2013), it would appear that display behaviour is not an established prezygotic barrier to hybridisation. Given that all evidence appears to indicate that the colonising buzzards do indeed provide a viable partner base for *B. trizonatus*, hybridisation may continue across this frontier of the range of *B. trizonatus*. With austral winter sightings of Steppe-type buzzards (per obs.) in Knysna, the heart of the range of *B. trizonatus*, it appears *B. trizonatus* could face a serious threat if this colonisation and hybridisation continues to spread.

Chapter 5: Summary and implications of the findings and recommendations for future research

Summary of the findings

The evidence gathered in this study establishes that the majority of small buzzards in the Western Cape, based on their phenotypic and genetic characteristics, appear to be either *B. trizonatus* or *B. b. vulpinus*. Traditionally, only *B. trizonatus* was known to breed in South Africa, however the evidence presented here through extensive field observations (Chapter 4) and morphometric assessment (Chapter 2) suggests that *B. b. vulpinus* has colonised the south-western Cape, with many breeding pairs containing at least one buzzard appearing to be *B. b. vulpinus* (Chapter 4).

Additionally, an unidentified genetic signature (Chapter 3), together with supporting morphometric evidence (Chapter 2), suggests there is a possibility that *B. b. menetriesi* could also be present and indeed breeding in the south-west Cape. A number of birds were considered to match this taxon most closely in their morphometric characters, but displayed the genetic identity of *B. b. vulpinus,* suggesting they may have just been particularly large *B. b. vulpinus*. However, two birds appearing to match *B. b. menetriesi* in their morphology also displayed a genetic signature that appears different from both *B. b. vulpinus* and *B. trizonatus*. This provides some support for the idea that the unidentified signature revealed may be that of *B. b. menetriesi,* the only other likely candidate in this study. One of the most interesting findings came from three buzzards (CF001C, BUIT20091 and BUIT20092) that were deemed to most closely match *B. b. menetriesi* in their phenotypic characteristics but were revealed to be a firm genetic match for *B. trizonatus*. These juvenile buzzards feature uniformly rufous plumage and large morphology, removed from the morphological variation of *B. b. vulpinus* and *B. trizonatus,* being more similar to two true *B. b. menetriesi* specimens from the Kruckenhauser *et al.* (2004) data. These birds were also born to buzzard pairs in which both parents were uniform rufous, quite unlike *B. trizonatus* which is believed to be monomorphic. No evidence of hybridisation was found in the genetic make-up of these birds. Thus, there is potential to suggest, quite remarkably, that there could be a previously undescribed uniform rufous morph of *B. trizonatus*. Although the morphology of these birds and our current understanding of the plumage variation of *B. trizonatus* would seem to contradict this hypothesis, the strong genetic signature of the birds is certainly clear. Clearly the plumage variation of *B. trizonatus* requires further study.

It has long been suspected by birders in the Western Cape that hybridisation is occurring between *B. b. vulpinus* and the resident endemic *B. trizonatus*. Evidence and observations presented here suggest that these hybrid pairs do indeed occur in the south-west of the Western Cape, with 24.4% of pairs (n=11) within the study area appearing to consist of mixed pairing between *B. b. vulpinus* and *B. trizonatus* (chapter 4). These hybrid pairings appear to occur without pre- or post-zygotic barriers, which is perhaps unsurprising given the prolific and widespread hybridisation among this taxonomically-young group of raptors.

Implications of the findings in this thesis

The evidence presented within this thesis indicates that *B. b. vulpinus* is indeed a colonising taxon, appearing to be a locally common breeding resident of the south-west Cape, from the Cape Peninsula in the west to the Elgin Valley in the east; future revisions to field guides should now indicate it as such. Additionally, though there is evidence that suggests *B. b. menetriesi* may be a rare migrant and indeed breeder in South Africa, identification of this taxon based on current knowledge appears difficult at best. Until further clarity of understanding is achieved with regards to the full plumage variation and field identification of *B. b. menetriesi,* or until we can confirm that either of our two unidentified genetic signatures belong to this taxon, we will not be unable to confirm that *B. b. menetriesi* is present in the Western Cape.

Given the ongoing hybridisation between buzzards in the south-west Cape, it is perhaps concerning that *B. b. vulpinus* has recently been observed over-wintering (i.e. remaining during the Boreal summer/Austral winter) in the breeding core of *B. trizonatus*. This over-wintering may prove to be the early stage of wider colonisation by *B. b. vulpinus* in the Cape. Given the propensity for hybridisation between these taxa, the genetic integrity of *B. trizonatus* could potentially be swiftly compromised through introgression, should a population of *B. b. vulpinus* become established in this area. Given the uncommon status of *B. trizonatus* over a relatively small geographic range, this could have a profound effect on the continued survival of this taxon as a genetically and evolutionarily distinct species. Whether we should be concerned about the loss of the purity of this taxon through a natural process, though, is open to philosophical debate.

Suggestions for future research

The taxon-composition of buzzards in the south-west Cape of South Africa clearly remains complex, and only partially resolved by this research. Whilst it has been established that *B. b. vulpinus* is indeed breeding in the south-west Cape, the presence and breeding status of *B. b. menetriesi* remains suspected but unconfirmed. Several avenues of further research are recommended:

1. The possibility, and indeed status of *B. b. menetriesi* breeding in South Africa should be further investigated. This could be initiated by re-analysing buzzards WOB003 and WOB005 from this study, together with pure *B. b. menetriesi* samples from its native range, to establish whether this unidentified genetic signature is indeed that of *B. b. menetriesi*.

2. The unexpected genetic composition of buzzards CF001C, BUIT20091 and BUIT20092 should also be further investigated, together with the apparent suggestion that there could be a previously unrecognised uniformly rufous morph of *B. trizonatus*. Though seemingly unlikely, the genetic evidence revealed through this study would appear to give some credence to this theory. Given the apparent lack of evidence of hybridisation in the genetic structure of these particular individuals, and the conflicting genetic and phenotypic results, this seems an avenue worth pursuing.

3. The status and extent of *Buteo* hybridisation in the Cape should be further investigated. Whilst hybridisation currently appears to be limited to the area stretching from the Cape Peninsula to the Elgin Valley, the first signs of potential further colonisation have been observed in the breeding core of *B. trizonatus*. Whilst the rate, or indeed occurrence, of further colonisation and potential subsequent hybridisation cannot be estimated here, the situation as it develops could potentially provide an extremely interesting opportunity to document the extinction of an endemic species through introgression.

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Appendix 1: ‘Mystery Buzzard’ specimens

Buzzard 1: WOB001
World of Birds, Hout Bay, Cape Peninsula

Buzzard 2: WOB002
World of Birds, Hout Bay, Cape Peninsula

Buzzard 3: WOB003
World of Birds, Hout Bay, Cape Peninsula

Buzzard 4: WOB004
World of Birds, Hout Bay, Cape Peninsula

Buzzard 5: WOB005
World of Birds, Hout Bay, Cape Peninsula

Buzzard 6: WOB006
World of Birds, Hout Bay, Cape Peninsula

Buzzard 7: WOB007
World of Birds, Hout Bay, Cape Peninsula

Buzzard 8: WOB008
World of Birds, Hout Bay, Cape Peninsula

Buzzard 9: WOB009
World of Birds, Hout Bay, Cape Peninsula

Buzzard 10: WOB010

World of Birds, Hout Bay, Cape Peninsula

Buzzard 11: WOB011

World of Birds, Hout Bay, Cape Peninsula

Buzzard 12: WOB012

World of Birds, Hout Bay, Cape Peninsula

Buzzard 13: WOB013
World of Birds, Hout Bay, Cape Peninsula

Buzzard 14: WOB014
World of Birds, Hout Bay, Cape Peninsula

Buzzard 15: WOB015
World of Birds, Hout Bay, Cape Peninsula

Buzzard 16: WOB016
World of Birds, Hout Bay, Cape Peninsula

Buzzard 17: BUIT20091
Buitenverwachtin Farm, Cape Peninsula

Buzzard 18: BUIT20092
Buitenverwachtin Farm, Cape Peninsula

Buzzard 19: REST2009

Restanwold Farm, Elgin Valley

Buzzard 20: ZONN2008

Zonnestraal Farm, Cape Peninsula

Buzzard 21: SWART2008

Swartrivier Road, north of Elgin Valley