Avian ecology of arid habitats in Namibia

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Abstract

Examination of bird assemblages along an environmental gradient which encompasses both climate and habitat change is needed if we are to better understand the potential effects of these changes for avians and the ecological process that depend upon them. Climate change is predicted to have a significant impact on deserts and desert margins, resulting in distributional shifts of entire ecosystems and new community associations. This study explores the probable responses of avian communities to increasing desertification.

In general, species richness and numbers of birds in arid zones are low compared to more mesic areas. Different combinations of habitat types and the variety of patches in a landscape influence the diversity and community structures of avians in that landscape. The role of vegetation structure in avian habitat selection in semi-arid areas is dictated by horizontal habitat density as well as vertical structure. Although bird distribution is determined by habitat boundaries, most birds are flexible and can disperse across small habitat barriers.

The hypothesis tested, was that bird species assemblages along an aridity gradient are affected primarily by rainfall and secondarily by habitat type. Assessing the impacts of rainfall and habitat on bird variables, such as species richness, abundance, diversity, biomass, and life history traits, were the objectives of the study.

An east-west aridity gradient of 300 mm, stretching over 370 km, was chosen in central Namibia for the study area. The climate is harsh with localised rain and considerable daily fluctuations in temperature. Grasses, and trees and shrubs up to 7 m in height are the co-dominant life-forms. Surveys were conducted over three years; one winter and one summer survey in each year. Rainfall, seasons and vegetation height were recorded as environmental variables.

Three structurally different habitat types were selected for stratified sampling: open areas, rivers and thickets. Open areas were dominated by grass; river refers to ephemeral dry river lines with mature trees; and thickets comprise woody shrubs and trees. At each site, the same three habitats were used for bird sampling, resulting in 15 sample units. Sampling took place on 51 discontinuous line transects of 1km in length and without a width limit.

Univariate analyses included ANOVA and t-tests. Multivariate analyses consisted of cluster analysis, MRPP tests, indicator analysis, Shannon diversity index and NMS ordinations. NMS bi-plots were used to define avian community structures responding to aridity, habitat, migration and life history traits.

The results showed that bird species richness, abundance, and diversity remained relatively constant across the aridity gradient, until they declined significantly once a certain aridity threshold was crossed at the most arid site. There were significantly more bird species and individual birds at the wetter sites than at the drier sites. Rivers contained more birds than thickened or open habitat types, suggesting the importance of riparian habitat types for maintaining avian diversity. The three more mesic sites included higher numbers of species from the nesting and feeding guilds, regardless of habitat type, than the two more arid sites. The aridity threshold had a significant effect on bird community structures: more migrant and nomadic species, and omnivore and insectivore species persisted in very arid conditions.

From the results it was predicted that climate change will cause avian species to undergo range shifts from west to east, resulting in community composition changes and a reduction in diversity. Life history traits affect the adaptive capabilities of bird species and it is predicted that nomadism, flexibility in diet, and adaptability of nesting requirements will contribute to species persistence in the drier conditions predicted under current climate change scenarios. Dry river lines will act as refugia for avian diversity, but crucial habitat types that currently contain less diversity are also important for maintaining unique avian assemblages.

Key words

Avian, Birds, Aridity gradient, Namibia, Avian community, Vegetation structure, Desertification, Seasonal influences, Feeding guilds, Nesting guilds, Migration, Nomadism

Abbreviations

ANOVA: Analysis of variance
BIOTA: Biodiversity Monitoring Transect Analysis in Africa
GPS: Global Positioning System
NMS: Non-metric Multi-dimensional Scaling
IV: Observed Indicator Value
SD: Standard Deviation
UNCCD: United Nations Convention to Combat Desertification
UNEP: United Nations Environment Program

Sites, univariate analyses

420: Okasewa
370: Neudamm
315: Claratal
215: Weissenfels
128: Rooiklip

Sites, multivariate analyses

O 420: Okasewa
N 370: Neudamm
C 315: Claratal
W 215: Weissenfels
R 128: Rooiklip

Sample units

OO: Okasewa Open
OR: Okasewa River
OT: Okasewa Thicket
NO: Neudamm Open
NR: Neudamm River
NT: Neudamm Thicket
CO: Claratal Open
CR: Claratal River
CT: Claratal Thicket
WO: Weissenfels Open
WR: Weissenfels River
WT: Weissenfels Thicket
RO: Rooiklip Open
RR: Rooiklip River
RT: Rooiklip Thicket

1 Introduction

1.1 Introduction

The extent to which recent observed changes in natural biological systems have been caused by climate change is a contentious topic. Biologists are convinced that they are seeing biological impacts of climate change but they find it difficult to convince other policy-makers and the public to take convincing actions (Parmesan & Yohe, 2003).

The IPCC (2013) predicts a change in global mean surface air temperature of 0.3-0.7°C between 2016 and 2035, more than 1°C above the mean for 1850-1900. This translates to a global warming of 0.2°C per decade, and changes in rainfall patterns over the next 80 years (IPCC, 2007).

At the regional scale, an intensification of aridity (combined mean annual precipitation and evapotranspiration) in many arid and semi-arid areas together with a rise in the human population from 3.9 billion in 1970 to more than 7.1 billion at present (United States Census Bureau, 2014) has altered land use practices. Africa is thought to be the continent most vulnerable to climate change (IPCC, 2001). Forty percent of the sub-Saharan population of Africa (270 million people) live in arid, semi-arid and dry-humid regions of Africa, where the mean ratio of annual precipitation to evapotranspiration ranges between 0.05 and 0.65 (UNEP, 1997).

The major environmental challenges to biodiversity are human land use patterns and anthropogenic climate change as has emerged through probabilistic modelling (Parmesan & Yohe, 2003). Their meta-analysis of 893 species, functional groups and biogeographic groups across taxa, including birds, revealed that less than a third showed stable distributions in the 20th century. On the regional scale, South Africa is likely to experience substantial climate change in the next decades and the effects of this change will be dramatic, especially on biodiversity (Van Jaarsveld and Chown, 2001).

This study explores the probable responses of avian communities to increasing desertification.

1.1.1 Desertification

Desertification is a process that causes an expansion of desert into semi-arid areas with a net result of xeric areas with few plants encroaching into mesic habitats that sustain a greater diversity and density of vegetation (Warren and Agnew, 1988). The United Nations Convention to Combat Desertification (UNCCD) (2012) defines land degradation as the reduction or loss of the biological or economic productivity and complexity of land resulting from a combination of processes, including human activities. They define desertification as a subset of land degradation in dry climates (arid, semi-arid and dry sub-humid areas).

Human causes of desertification include over-grazing, over-cultivation, vegetation removal, salinisation and anthropogenic climate change. Natural causes of desertification are lack of rainfall and climate change. McClean *et al* (2005) argue that climate change will have a significant impact on desert and desert margin areas which may result in significant distributional shifts of entire ecosystems and the creation of novel community associations.

Historic extinction rates based on the fossil record are estimated to have been 0.001-0.01% of species per century, while the current observed extinction rate of birds and mammals is approximately 1% per century (Begon *et al*, 1996). McClean *et al* (2005) postulate that the anthropogenic contribution to the current climate change cycle has accelerated the change to such an extent that species do not have time to adapt with the result that there may be a mass extinction and a collapse of ecosystems.

Recent range changes by birds are not random and habitat change might have a marked impact on biodiversity and ecosystem processes. Hockey *et al* (2011) found that both land use changes and climate change simultaneously influence range change by Southern African birds and that these two drivers operate concurrently. Their results show that habitat generalists shifted their ranges to the south, corresponding with climate change drivers, and to the west, which was inconsistent with climate drivers but consistent with land use. They further conclude that migrants and nomads moved south, while the westward movers were associated with human-modified elements in the landscape. Seymour & Dean (2010) show that the loss of bird species is linked to their life history traits and that bush encroachment together with large tree removal will result in a shift to impoverished bird assemblages. Both these regional studies support the global findings of Parmesan & Yohe (2003), referred to earlier.

Drier areas may mimic what future climate change may bring to areas presently experiencing higher rainfall; bird communities in these areas may contain information on how climate change will affect birds in different habitat types (Simmons & Seymour, 2010).

1.1.2 Birds in arid and semi-arid ecosystems

Lovegrove (1993) defines a desert as a water-controlled ecosystem with infrequent, discrete and unpredictable water inputs combined with a high ratio of evaporation to precipitation. Southern Africa has four desert biomes (Lovegrove, 1993):

- Desert biome with dominant plant life-forms as annuals constituting 96% of canopy cover.
- Succulent Karoo biome with dominant plant life-form as dwarf shrubs.
- Nama Karoo biome with dominant plant life-forms as dwarf shrubs and grasses.
- Arid Savanna biome with dominant plant life-forms as grasses (more than 50% of canopy cover) and woody trees or shrubs.

Dean (2004) names the Namib as one of the eight true deserts of the world, the others being the Sahara, Australian, Arabian, Turkestan, Takla Makan, Gobi, and Atacama. Arid savannas include the Kalahari Desert (Dean, 2004) and the central parts of Namibia where this study was conducted (Lovegrove, 1993; Mendelsohn, 2002).

The semi-arid ecosystems of Southern Africa are characterised by extremes in weather, from periods of intense and prolonged drought to exceptionally high rainfall events. Both wet and dry states are patchy in time and space (Dean *et al*, 2009). Drought-induced dormancy in vegetation has an impact on birds and they cope with droughts and changes in vegetation by using behavioural and physiological tactics. Being highly dispersive organisms, birds deal with rainfall fluctuations through two main strategies, residency and nomadism. Droughts have different effects on bird populations, often stimulating movements into better-watered areas, but also, conversely and seemingly inexplicably, stimulating movements into dry areas (Dean *et al*, 2009).

Dean (2004) found that species richness and numbers of birds confined to deserts and arid zones are low compared to more mesic areas and he maintains that there is no distinctive “desert avifauna”. Only 44 species worldwide spend most of their lives in hyper-arid environments and most of them move into more vegetated areas adjacent to deserts or remain at drainage lines. Desert avifauna consists of adaptable species, rather than specialised for life in deserts (Dean, 2004).

Githaiga-Mwicigi *et al* (2002) showed that arid zone endemic birds are associated with climate extremes and seasonality and that birds species restricted and endemic to the arid Karoo biome may be more sensitive to climate rather than vegetation structure. This is particularly relevant seeing as Rutherford (1999) predicts an increase in the extent of the desert biome in South Africa (by extension include Namibia in this prediction). Restricted range birds in the arid parts of Southern Africa are distributed over areas with low human population densities and these areas are forecast to undergo rapid transformation under predicted climate change scenarios for the region (Githaiga-Mwicigi *et al*, 2002).

Most changes in bird communities in semi-arid areas in the region have been attributed to changes in land use, degradation of habitats and declining primary production (Dean *et al*, 2002). According to Joubert *et al* (2008) bush thickening is a major ecological problem in semi-arid savanna. In the semi-arid Highland savanna in central Namibia bush thickening by *Acacia mellifera* remains a problem despite interventions. It is not yet clear what resident bird species do when faced with increasing aridity (Dean *et al*, 2009): for those that move, the benefits must outweigh the costs and for species that stay, the benefits of being resident must outweigh the cost of moving.

1.1.3 Biodiversity

Biodiversity is jeopardised by desertification, land degradation and drought to the extent of an estimated 27 000 species lost each year (Wilson, 1992; UNCCD, 1994), which makes the protection of biodiversity a central tenet in conservation biology.

Turner (2004) explains the Unified Neutral Theory of Biodiversity as the maintenance of a dynamic equilibrium of species diversity between loss of species by ecological drift and the birth of new species. Maurer & McGill (2004) extend the neutral model to incorporate two biological factors:

- Introduce competitive asymmetries among species to explain how some species have an advantage in replacing individuals that die.
- Introduce environmental heterogeneity by assuming sites available to individuals differ in quality to individuals of different species.

Biodiversity can generally be considered on three levels:

- Genetic diversity: genetic variation within species. An effective population size (where loss of individuals is balanced by genetic mutation and birth) prevents genetic drift from eliminating genes and reducing the variability of the population as a whole (Wilson, 1992). In conservation biology this means that large enough populations need to be maintained because in small populations the mutation rate is not high enough to replenish the loss due to genetic drift and the species loses its ability to adapt to environmental changes.
- Species diversity: range of species. Wilson (1992) says the size of the population and the manner by which it subdivides and spreads across the terrain is more important than an effective population size alone.
- Community diversity: Begon *et al* (1996) define it as a variety of biological communities in a region and their interactions with the physical environment. The implication of community diversity for conservation biology is that long-term conservation should focus on communities and ecosystems because, according to Begon *et al* (1996) the scale of

conservation has to consider the ecological functional links that are required to keep a system going, with particular reference to the functional integrity of food webs.

Should the conservation of biodiversity then be approached on genetic, species or community level? This question can only be addressed by discussing habitat diversity. Chen *et al* (2005) discussed two approaches for characterising occupied habitats within landscapes. The first is the single species approach which focuses on a single or few species but it is a reductionist approach and is helpful only to protect environmental resources for the survival of the target species. The second is the multi-species approach which is a better indicator of community level biodiversity at regional scales because it provides information about habitat clusters, distribution of habitat loss, habitat overlaps, community structures, species interactions and their spatio-temporal scales, critical resource needs of overall diversity and ecosystem associations (Chen *et al*, 2005). By adopting the multispecies approach, as in this study, all three levels of biodiversity can be addressed.

The mechanism of protecting biodiversity ranges between two extremes: preserving systems and preserving the processes upon which biodiversity depends (Wood, 2001). The second alternative is suitable for large and relatively pristine systems while the first alternative is employed in small and modified systems to prevent species loss. Wood (2001) concludes that a mixed strategy is often the optimum solution. With endemism levels high in the arid west of Southern Africa (Hockey *et al*, 2005) it is tempting to focus on the preservation of local systems to ensure the persistence of rare bird species. However, from the discussion of arid ecosystems (section 1.1.2), it emerges that natural dynamic processes are important and interrelated and that sites cannot be isolated from other natural areas with which they interact.

Different combinations of habitat types influence the diversity and community structures that can occur in a region and a landscape where a greater variety of habitats would support greater species diversity. Habitat fragmentation results not only in a reduction in the size of populations but also the division of the population into sub-populations with a decrease in the average size of fragments (Begon *et al*, 1996).

It is apparent that both the number of species and the number of individuals of a species are relevant. Diversity indices quantify biodiversity within an area and are based on two basic measures: species richness (number of species) and evenness of abundance (number of individuals per species) along a spatial scale (McCune & Grace, 2002). Both measures are used to assess biodiversity in this study area (section 4.6.3)

Climatic factors influence species richness not only directly, but in large part indirectly, via effects on plant structure. Climate and habitat heterogeneity play a prominent role at broad spatial scales in the creation and maintenance of geographic gradients in bird species diversity (Kissling *et al*, 2008). This concurs with the view of Hockey *et al* (2005) that the diversity of bird species in different habitats in Southern Africa is strongly dependent on habitat structure and rainfall.

1.1.4 Birds as biological indicators

Bio-indicators are species or groups of organisms that provide early warnings of the nature, severity and extent of natural responses to environmental impacts and they are considered to be more useful than abiotic indicators (Read *et al*, 2000). To overcome the obstacle of limited resources, biodiversity studies use well-known bioindicator taxa that are quickly and easily studied but whose patterns are likely to be representative of many other species (Pearson & Carrol, 1998). Bio-indicators are applied as an important technique for the preliminary prioritisation of conservation efforts at a large geographical scale (hundreds or thousands of square kilometres) because patterns of biodiversity at that scale are generally the product of only a few factors (Pearson & Carroll, 1998). This study took place over an area commensurate with such a geographical scale.

Bird species assemblages are often selected for assessing how environmental changes might modify the functioning of ecosystems. Reasons that birds are good indicators include (Hausner *et al,* 2003; Read *et al,* 2000):

- Well-known ecology and behaviour
- Ecological versatility
- Stable taxonomy
- Use a large variety of habitats for foraging and nesting
- Diverse roles in food chains make them suitable for monitoring structural and functional changes in ecosystems
- Large home ranges of some species enable detection of changes on coarser scales
- Field identification by vocalisation in addition to visual identification makes data collection easy and inexpensive

1.1.5 Habitat selection

Birds are mobile horizontally (on the ground) and vertically (in the air). This mobility means a wide range of habitats are available for them to colonise. Begon *et al* (1996) define the physical and biotic properties of a habitat as all the resources needed for survival such as habitat structure, microclimate, edges, floristics, food and water availability, nesting suitability, shelter, breeding mates, and other species. Birds select their habitats according to these properties and according to their specific needs, leading to distinct bird distribution patterns. Although bird distribution is determined by habitat boundaries, most birds are flexible and can disperse across small habitat barriers (Hockey *et al*, 2005).

Wiens (1989b) proposes that individual birds use a basic decision-making process in selecting their habitats, based on an internal template that is genetically determined or learned of what constitutes a suitable habitat. Habitats that fit the bird's template provide it with cues on the physical and biotic properties of the habitat that may lead an individual to settle there. If a habitat conforms to the optimal pattern determined by the template, more complicated determinations then come into play to influence the realised habitat selection of the individual bird: population density, inter-specific interactions and time lags. The outcome is that the realised habitat selection of individuals is dynamic and the result of an ongoing process (Wiens, 1989b).

The environmental variations that determine habitat selection vary in time and space, often in different ways on different scales (Wiens, 1989b). Bird size can predict the scale at which they select a habitat: the Peregrine Falcon, Barn Owl and Osprey occur on virtually every continent (Hockey *et al*, 2005) whereas larks, for example, select smaller areas. The ability to disperse across unsuitable habitat plays a role in the distribution patterns of birds (Hockey *et al*, 2005) so although the Peregrine Falcon, Barn Owl, Osprey and larks use the same decision-making process in selecting their habitats, they have different abilities to overcome habitat barriers. Isacch *et al* (2005) assume vegetative structure and floristic composition to be the primary proximate factors that determine habitat selection, with vegetation acting as an ultimate factor for critical variables such as food, nesting sites and cover from predators whereas MacArthur & MacArthur (1961) showed high avian diversity to be more strongly associated with highly structured patterns of habitats rather than with floral composition or prey diversity. Furthermore, each species requires a patch of vegetation with a particular profile for its selected habitat, and the variety of patches of vegetation within a habitat determines the variety of bird species breeding there (MacArthur *et al*, 1962). Species with similar ecological functions are often found in the same habitat because they need similar resources, while species with different ecological functions occupy different habitats (Begon *et al,* 1996), resulting in definite species assemblages co-occupying a specific habitat.

The role of vegetation structure in avian habitat selection in a semi-arid area, the southern Kalahari, was explored by Seymour & Dean (2011) and they found that the relationship was not simply dictated by horizontal habitat density but also by vertical structure, with scattered trees acting as important keystone structures that moderate the effects of bush thickening on bird diversity. The presence of canopies extending above the thicker lower layers enabled bird species for which type and structure of ground cover is unimportant to persist in these habitats (Seymour & Dean, 2011).

1.1.6 Community ecology

A community can be described as an assemblage of species populations that occur together in space and time (Begon *et al*, 1996) or as the co-occurring of individuals of several species, where the individuals of the species interact with one another thereby creating a certain community structure in an ecosystem(Wiens, 1989a). Community ecology attempts to identify patterns that characterise natural assemblages of species, understand what caused these patterns, and determine how common they are. Composition, distribution, abundance, morphology, and behaviour of the species in a community all determine community patterns in space and time; the most basic pattern being the number of species it contains (Wiens, 1989a). Measuring the character of a community would incorporate species richness, commonness and rarity (Begon *et al*, 1996), in other words, the diversity of a community.

Communities and ecosystems cannot be studied separately but should rather be seen as complementary means of understanding community structure and functioning (Begon *et al*, 1996). Bird communities can be characterised by the habitat types they select (Wiens, 1998a) and vegetation structure and floristic composition strongly influence the structures of bird communities (Powell & Steidl, 2000). In section 1.1.5. it was mentioned that definite species assemblages co-occupy a specific habitat; it follows that habitat selection affects the community structure of an area.

1.2 Motivation

The chosen study area has a steep aridity gradient, marked seasonal rainfall differences and variable habitat including thickened bush, riparian and open areas which make it perfect for exploring community patterns in an arid environment with the aim of predicting large-scale reaction to climate change and developing strategies to deal with increasing aridity in Southern Africa.

1.3 Objectives and hypothesis

1.3.1 Research question

How do bird assemblages change along the aridity gradient and between habitat types?

1.3.2 Hypothesis

Along an aridity gradient, bird species assemblages are affected primarily by rainfall and secondarily by habitat type.

1.3.3 Objectives:

- Assess the impact of rainfall on bird variables.
- Assess the impact of habitat on bird variables.

Bird variables include species richness, abundance, diversity index, biomass, and life history traits such as nesting, feeding and movements.

1.4 Research framework

Planning

Introduction (chapter 1)
Motivation for the study (section 1.2)
Literature review (chapter 2)
Develop hypothesis (section **Error! Reference source not found.**)
Develop objectives (section **Error! Reference source not found.**)
Information about the study area (section 3.2)

Data collection

Surveys (chapter 3)

Data analysis

Statistical analysis and graphic representation of results (chapter 4)

Data interpretation

Discussion of results (chapter 4)
Formulation of conclusions (chapter 4)

2 Literature review

Species richness of plants and animals is influenced by eight major factors (Currie, 1991):

- Climate: benign conditions permit more species
- Climatic variability: stability permits specialisation
- Habitat heterogeneity: complex habitats provide more niches
- History: time permits colonisation and the evolution of new species
- Energy: richness is limited by the partitioning of energy among species
- Competition: reduced niche breadth and elimination of species
- Predation: retards competitive exclusion
- Disturbance: moderate disturbance retards competitive exclusion

Species variation in a given area correlates with geographical scales: large-scale patterns are primarily determined by climate while at smaller scales factors tend to act locally, such as biotic interactions (Bellocq and Gomez-Insausti, 2005; Currie, 1991). In the arid savanna and desert of the study area, bird communities are affected by factors acting on both large and smaller, local scales, therefore conservation managers should take scale into account in their efforts.

The major gradients of bird species variation are determined by climatic variables such as season temperature, seasonality of rainfall and water balance (Fairbanks, 2001). The relationships between bird species assemblages and environmental variables are affected over time and space by vegetation, habitat types, disturbance, land use, weather, topography, water, food, nesting sites, competition, predation, and presence of other species (Begon *et al,* 1996; Dean, 2000; Fairbanks, 2001; Rotenberry, 1978; Wiens, 1989a; Wiens, 1989b). Dean (1999) is of the opinion that arid savanna habitats provide a focal point for animal activity because they supply nest sites, shade and scarce food resources.

2.1 Factors affecting avian diversity and communities in arid ecosystems

2.1.1 Water

In deserts, the ratio of water gain to moisture loss through evaporation is negative (Lovegrove, 1993), consequently there is no or temporally limited drinking water available to birds. Physiological characteristic that allow birds to survive these conditions include a high body temperature (40°C), the ability to drink saline water if need be or to metabolise water from their food, and efficient water conservation through adaptive behaviour (Maclean, 1996; MacMillen & Snelling,1966). Species vary in their needs for water with granivores needing to drink daily and many insectivores acquiring water from their food, making them less dependent on open water (Hockey *et al,* 2005; MacMillen, 1990).

Arid environments experience severe fluctuations: long periods of low productivity, interrupted by sporadic rainfall which stimulates reproduction and movement. Birds are among the most dramatic indicators of these fluctuations (Dean *et al*, 2009). Commercial farming in Namibia resulted in the provision of permanent water sources in an otherwise dry region and this, according to Read (2000), can mask or overshadow the negative impacts of human activities on the arid landscape.

2.1.2 Temperature

Deserts are harsh environments characterised by intense solar radiation, temperature extremes, low primary productivity, and scarcity of drinking water (McKechnie & Wolf, 2010; Tieleman & Williams, 1999). Behavioural adaptations to deal with high temperatures include wing-drooping, gular fluttering, raising feathers to allow evaporation from skin, trailing legs behind body during flights, shading chicks, pointing the beak in the direction of prevailing breeze, roosting in shade, and limiting activity in the heat of the day (Lovegrove, 1993).

An example of arid-zone birds that exhibit striking adaptations to desert life is the sandgrouse, a group of birds that occur widely in the study area. The Namaqua Sandgrouse can fly up to 60 km a day to the nearest water source to fulfill its need to drink fresh water regularly. In addition, it has a unique solution to the water needs of its young: the adult male’s abdominal feathers are highly water absorbent; at the water source, he soaks his ventral feathers and then carries the water to the nest (Hockey *et al,* 2005; Lovegrove, 1993).

Apart from behavioural adaptations, birds, like other endotherms, also have physiological traits that make thermoregulation more efficient. These include increasing evaporative water loss or undertaking facultative hyperthermia, which brings about a conflict between evaporating water to maintain body temperature below lethal limits and the need to conserve water and avoid dehydration (Cunningham *et al,* 2013; Du Plessis *et al,* 2012; McKechnie & Wolf, 2010; Smit *et al,* 2013).

Bird body size also plays a role in thermoregulation: smaller birds undergo extreme evaporative water loss to maintain their core temperatures while larger bodied birds in the same conditions do not lose water but suffer from hyperthermia more quickly (Cunningham *et al,* 2013; McKechnie & Wolf, 2010; Tieleman & Williams, 1999; Wolf & Walsberg, 1996).

The thermal landscape is species-specific and the benefits of behavioural adjustments differ between species (Cunningham *et al,* 2012; Martin *et al,* 2012), often in keeping with life history traits. Arid zone specialists such as the Southern Pied Babbler have higher temperature thresholds than habitat generalists, e.g. Common Fiscal (Cunningham *et al,* 2013; Du Plessis *et al,* 2012). Smit *et al* (2013) showed that there is flexibility in the thermal physiology of birds. They found a relatively large variation in body temperature, both within and between conspecific populations of an arid-zone passerine, suggesting that the bird responds differently to weather conditions in two locations over its range, and that it also responds to seasonal changes in weather conditions.

There is a trade-off between thermoregulation and foraging. Limited resources often force desert birds to forage during hot weather (Tieleman & Williams, 2002). As the temperature increases, birds forage the same amount so foraging effort is unaffected by daily maximum temperature. However, foraging efficiency as reflected in a drop in body mass on hotter days is decreased significantly if the birds are panting and wingspreading. Thermoregulation at high air temperatures also affects reproductive performance through its impact on body condition and reduced provisioning rates to nests (Cunningham *et al,* 2013; Du Plessis *et al,* 2012).

2.1.3 Food

Various behavioural strategies are employed by different birds to satisfy their different food preferences (Begon *et al*, 1996). The availability of food is an important determinant of population size, diversity, and community patterns (Steyn, 1996; Wiens, 1989a; Wiens, 1989b), especially so in arid zones. Nevertheless, suitable food being present and abundant does not mean it is available to birds. Coleman (2008) defines availability of food as a function of food abundance and its actual accessibility to the consumer. Accessibility is affected by several factors (Cueto *et al*, 2013):

- The vulnerability of immobile prey.
- Foliage structure modifying the chances of capturing prey by arthropod-feeding birds.
- Substrate complexity making seeds less accessible to ground-foraging birds.
- Seed detection, which is determined by microhabitat structure.
- Predator-prey encounter rates being reduced by microhabitat complexity.
- Seed burial affecting the foraging efficiency of granivores.

Not only food availability, but also the suitability of feeding and perching sites is important (Wiens, 1989b). An example of this is the Marico Flycatcher. It uses the perch-and-pounce hunting technique, perching on the outermost branches of trees and shrubs for long periods interrupted by short forays to the ground or, less often, aerial sallies, where it catches its prey and then returning to its perch (Hockey *et al*, 2005). In this study area the Marico Flycatcher engaged in foraging behaviour mainly in and near river lines, infrequently in thickets and then only where trees and large shrubs are present, and not at all in open areas (personal observation). The complex relationship between food availability, foraging behaviour and habitat structure (Thiele *et al*, 2008) is illustrated by the Southern Pied Babbler, endemic to the savannas of Southern Africa and a specialist of semi-arid to arid environments (Hockey *et al*, 2005). The Southern Pied Babbler uses large thorn trees to nest and perch but needs low vegetation cover on the ground where it forages on insects. Predator avoidance is particularly important at foraging sites for a group-living bird that forages on the ground, where it uses shrubs and trees as hiding places (Thiele *et al*, 2008). Thiele *et al* (2008) showed that shrub encroachment affects the Southern Pied Babbler positively whereas woodcutting has negative effects, illustrating that vertical habitat heterogeneity plays a determining role in its feeding habits.

Bellocq & Gomez-Insausti (2005) explored the climatically based energy productivity hypothesis, which postulates that the supply of energy limits the number of species co-existing in an area and that animal richness is limited by the availability of food. The productivity hypothesis accounted for geographical variations in the number of birds from the tropics to temperate zones (Bellocq & Gomez-Insausti, 2005), concurring with the view of Currie (1991) that the energy hypothesis depends on scale.

2.1.4 Breeding requirements

Birds use an assortment of materials to construct their nests and utilise a wide variety of substrates, such as trees, shrubs, grass, reeds, cliffs, sand banks, the ground and anthropogenic structures. In addition, many birds are specific in their nesting requirements (Hockey *et al*, 2005).

Many desert birds rely on short-lived resources and are adapted to nest and raise chicks quickly and then move on together with the young when resources run out (Dean, 2004). The single most important factor regulating the timing of breeding is food supply (Steyn, 1996; Lovegrove, 1993). Vegetation has a direct link with breeding necessities because it affects the distribution of birds by providing shelter, food and potential nest-sites (Seoane *et al*, 2004).

Some arid area species cope with the marginal environment by breeding at any time of year and raising several consequtive broods. Clutch sizes vary and can decrease or increase depending on the food supply which in turn is determined by the amount of rain that has fallen (Lovegrove, 1993). Wet years often stimulate higher densities of nests, larger clutch sizes, unseasonal breeding, and higher breeding success (Dean *et al,* 2009). As a rule insectivores breed sooner than granivores (Steyn, 1996).

Rainfall above a certain threshold triggers breeding in resident arid area species and an influx of nomadic species that breed and then move on (Dean *et al,* 2009). Breeding response to rainfall is dramatic; birds may start nesting within a week and often stop as suddenly as they began. (Steyn, 1996; Lovegrove, 1993)

2.1.5 Migration and movements

Flight enables birds to include larger areas in their home ranges (Simmons & Seymour, 2010) and in arid areas mobility is a key to their survival (Dean, 2004). Two basic ways that birds survive in the desert are:

- Resident and sedentary birds use behavioural or physiological tactics to withstand extreme fluctuations in temperature and availability of food, water and plant cover.
- Migrants move opportunistically or seasonally where resources are available (Dean, 2004).

Dean (2004) categorises the movements of desert birds into either regular and seasonal, or irregular and aseasonal in response to rainfall. The first type of movement refers to migration and the second to nomadism. In addition, the amount of rainfall has consequences on the proportion of species that are resident, migratory or nomadic. Non-breeding visitors may be functionally resident, nomadic or locally nomadic during their stay and intra-continental migrants move into arid areas to breed. Resident species are not always sedentary and some are locally nomadic in response to rainfall and other environmental factors (Dean, 2004).

Species that are specialists rely on restricted resources or are resident in areas with specific resource conditions (Begon *et al,* 1996; Wiens, 1989b). The proportion of granivores and insectivores in nomadic birds is relatively high but the proportions of frugivores and nectarivores are significantly lower than expected compared to sedentary species. The proportion of species feeding on vertebrates does not differ between nomads and sedentary species (Dean, 2004).

Nomadism is an evolutionary stable strategy for individual species only when extremes in environmental conditions are frequent and unpredictable enough to maintain movements to and from resource patches. There has been selection for nomadism in species that are able to use patchy environments because fewer species are able to cope with resources that are patchy in time and space and not move between them (Dean, 1997).

2.1.6 Habitat

Pavey & Nano (2009) found that arid bird assemblage patterns are not primarily driven by resource availability and disturbance but more by the interaction between bird foraging behaviour and breeding requirements, and vegetation assemblages. Heterogeneity of vegetation structure seems to be a primary driver for bird species diversity (Child *et al,* 2009; Dean, 1999; Diaz, 2006; Hudson & Bouwman, 2007; McArthur, 1964), although Kaboli *et al*

(2006) found that the richness, abundance and composition of avifauna in Iran were better correlated with topography, specifically complexity of the substrate, than with vegetation. In complex environments the suitability of a habitat is determined not by a single vegetation attribute but by an interaction of several factors that all make significant changes in the acceptability of the habitat to bird species (MacArthur, 1964).

Grassland and open ground with sparse vegetation cover is needed by ground foragers and ground nesters, e.g. Larks and Sandgrouse (Hockey *et al*, 2005). Bush thickening due to overgrazing results in a decline in this habitiat whereas bush clearing often removes not only the homogeneous thickets of stunted acacias but also larger trees. Large trees supply nutrients for micro-habitat formation as well as shade for resting during the heat of the day, raptors and vultures perch on trees, frugivores favour mature trees over saplings or dead trees and many species need large trees for their nests, e.g. raptors, Sociable Weaver, Southern Pied Babbler, Crimson-breasted Shrike and White-browed Sparrow-Weaver (Dean, 1999; Steyn, 1996). Bird species richness is significantly higher in mixed forests than in single-species plantations (Diaz, 2006). In the arid zones of Southern Africa, a variety of patches of vegetation is needed to maintain avian diversity (Child *et al,* 2009; MacArthur, 1964).

One of the most significant impacts of land use practises on avian biodiversity is the changes it wroughts on landscape structure. Variations in vegetation structure because of land-use types correlate significantly with bird species diversity (Hudson & Bouwman, 2007). Raptors and scavengers display consistent losses, while nutrient dispersers and grazers tend to increase in agriculturally dominated landscapes (Child *et al*, 2009). Avian richness and diversity are reduced on communal rangelands, with a loss in insectivore abundance, an increase in granivore abundance, and, on both communal and commercial rangelands, an absence of some large bird species such as bustards (Joubert & Ryan, 1999). Simmons & Seymour (2010) relate the effect of bush thickening on bird assemblages to the density of horizontal habitat and the heterogeneity of vertical habitat. They found no difference in species density (number of species per area) between encroached and non-encroached habitats, but there was greater species richness (number of species per number of birds surveyed) in less encroached areas (Simmons & Seymour, 2010).

Human-transformed habitats can be beneficial to some bird species by creating new food sources and opening foraging habitats. Rodriguez-Estrella (2007) showed no differences in bird species richness between natural sites and those transformed by agriculture or urbanisation, although they did find an association with human-transformed habitats that can be either positive or negative. Their study of arid desert scrub considered only presence-absence data and abundance surveys could give other insights (Rodriguez-Estrella, 2007). The overall richness of avifauna in Southern Africa's arid zones may have increased since European colonisation in the 19th century, but the evolutionary framework has changed in that it now selects for species more tolerant of humans and species able to use new niches more effectively (Dean, 2000).

It is not only land use that affects habitat and consequently bird assemblages, but also climate change. Gardner *et al* (2009) used bird body size as an indicator because it directly affects energy and water requirements for thermoregulation, energy, mass acquisition, utilisation rates and life-history traits (Gardner *et al*, 2011). There was a significant decrease in body size as well as a shift in latitudinal cline, demonstrating a generalised response to major environmental change over the last 100 years (Gardner *et al*, 2009; Gardner *et al*, 2011).

2.1.7 Rivers

River lines, although a subcategory of habitat, are discussed separately here in view of its increasingly important role in maintaining biodiversity in arid zones (Knopf *et al*, 1988; Palmer & Bennett, 2006; Simmons & Seymour, 2010). Southern Africa is characterised by rivers which have low levels of runoff compared to precipitation (Allsopp *et al*, 2007) and the majority of these are ephemeral rivers, which seldom flow and have highly variable runoff (Davies *et al*, as quoted in Allsopp *et al*, 2007). According to Brand *et al* (2008), riparian systems in the arid and semiarid southwestern United States contain some of the highest avian density and species richness totals in North America corresponding with Gentry *et al* (2006), who indicated that riparian corridors are especially important habitats for breeding birds. Seymour & Simmons (2008) suggest that riparian fringes serve as corridors and refugia in arid environments and Naiman *et al* (1993) state that riparian corridors could ameliorate ecological issues related to land use and environmental quality. Environmental factors that increase species richness in riparian habitats include increased vertical structural complexity, moisture, and disturbance levels (Brand *et al*, 2008).

2.2 Management

The level at which conservation decisions are made has a profound impact on the efficacy of management practises for the maintenance of biodiversity. Maintaining the character and integrity of bird assemblages requires planning from regional and continental perspectives. Conservation actions must consider how local activities affect potential dispersal opportunities (Knopf & Samson, 1994). Local conservation decisions should be made within a multi-scale framework that acknowledges landscape and regional goals based on historical heterogeneity (Brawn *et al*, 2001). In selecting nature reserves, the major gradients of biotic and environmental variation should be identified as well as the environmental variables that correlate most closely with the distribution and abundance patterns of species (Fairbanks *et al*, 2001). Short-term goals include identifying critical conservation areas for the major taxa and this can then be included in a comprehensive regional conservation plan that integrates formal reserves and priority areas in the human-managed matrix (Rodrigues *et al*, 2000).

In Africa, people co-exist within and adjacent to ecologically important areas, therefore the human milieu has to be considered when making short- and long-term conservation decisions, both at local and at regional level. Establishing a reserve network is not adequate when the goal is to identify conservation areas on a biologically sound basis (Fairbanks *et al*, 2001). Broad levels of biodiversity have to be integrated to maintain systems; therefore, areas that can contribute to the longer-term retention of avian diversity outside formally protected areas need to be demarcated and incorporated in the conservation network (Fairbanks *et al*, 2001). In Namibia, large conservation areas are interspersed with low-density human-transformed landscapes, used mainly for communal and commercial farming as well as mining purposes. Conservation buffers can ameliorate the effects of widely-dispersed conservation zones by making available suitable habitat for the enhancement of bird community diversity (Henningsen & Best, 2005). These buffers have been shown to benefit generalists, provide breeding habitat for vulnerable species, and make habitat available for grassland, forest edge and woodland birds (Henningsen & Best, 2005). Vegetation structure and diversity, geographic location, spatial distribution and the size of a conservation area play an important role in shaping local communities (Selmi & Boulinier, 2003), suggesting that these factors have to be taken into account when establishing links between formal conservation areas across the human landscape.

What does this mean for land managers in Namibia? A key finding of the BIOTA study was that land and conservation managers in arid Namibia should reduce the extent of bush thickets, retain taller trees when thinning bush-encroached areas, and conserve dry river lines (Simmons & Seymour, 2010). Fleishman *et al* (2003) suggest that eradication strategies should avoid clear-cutting extensive stands of trees to provide refuge for species that require structural complexity.

3 Methods

3.1 The BIOTA project

Biodiversity Monitoring Transect Analysis in Africa (BIOTA) was a continent-wide research project that addressed the global change in biodiversity against the background of the perceived decline in biodiversity and its impact on human societies (Jürgens *et al*, 2010). BIOTA Southern Africa was an interdisciplinary and applied research project focusing on South Africa and Namibia.

The avian diversity section of BIOTA Southern Africa was designed by Dr. R.E. Simmons of the University of Cape Town and Dr. C.L. Seymour of the South African National Biodiversity Institute and field work was conducted by Dr Simmons. This study was based entirely on the data obtained from his field research in which the author participated as a field assistant. Field research took place along transects and consisted of six surveys over three years. The data for this thesis was used with permission.

Figure 1 Map of the BIOTA Southern Africa observatories and cross-country transects (BIOTA http://www.biota-africa.org/)

Comparing Figure 1 and Figure 3 shows that the current five study sites were located along one of the BIOTA cross-country transects: site Okasewa was a few kilometres west of BIOTA observatory Sandveld, Claratal observatory was site Claratal in this study, and site Rooiklip was approximately 20 km west of the BIOTA observatory Rooisand.

3.2 Research area

The study took place along an aridity gradient in central Namibia (Figure 2). Central Namibia is in the Arid Savanna biome of Southern African deserts (Lovegrove, 1993). Most of the biome consists of level plains, broken by die Khomas Hochland mountain range west and south-west of Windhoek. The climate is harsh with localised rain in the form of short thunderstorms and considerable daily fluctuations in temperature: -10°C at night to 30°C during the day in winter, and 5°C at night to 45°C during the day in summer. Grasses and trees and shrubs ranging from 3 – 7 m in height are the co-dominant life-forms. This region has the highest overall animal richness of all the Southern African desert biomes (Lovegrove, 1993).

According to Mendelsohn's (2002) classification of Namibia's biomes and vegetation types, the area is in the tree-and-shrub savanna biome of Namibia and it spans four vegetation types (from east to west): Central Kalahari, Highland Shrubland, Western Highlands and Western-Central Escarpment/ Inselbergs.

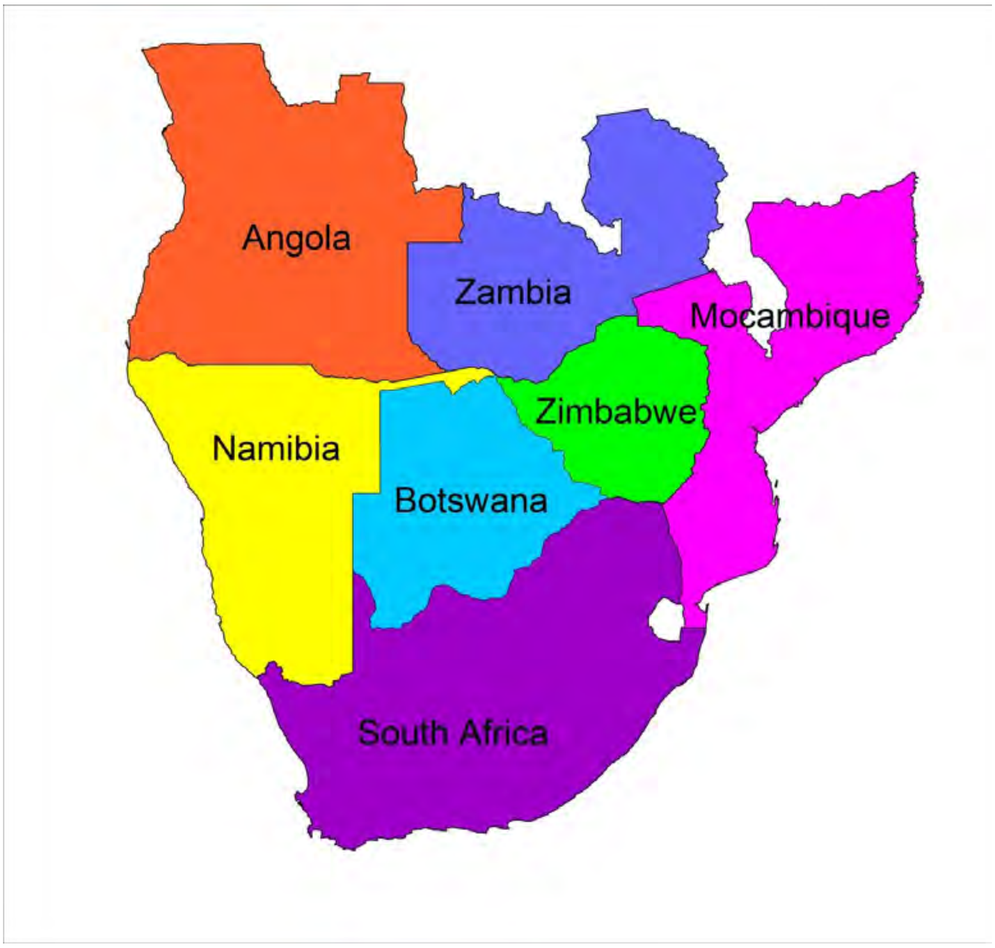

Figure 2 Map of Southern Africa

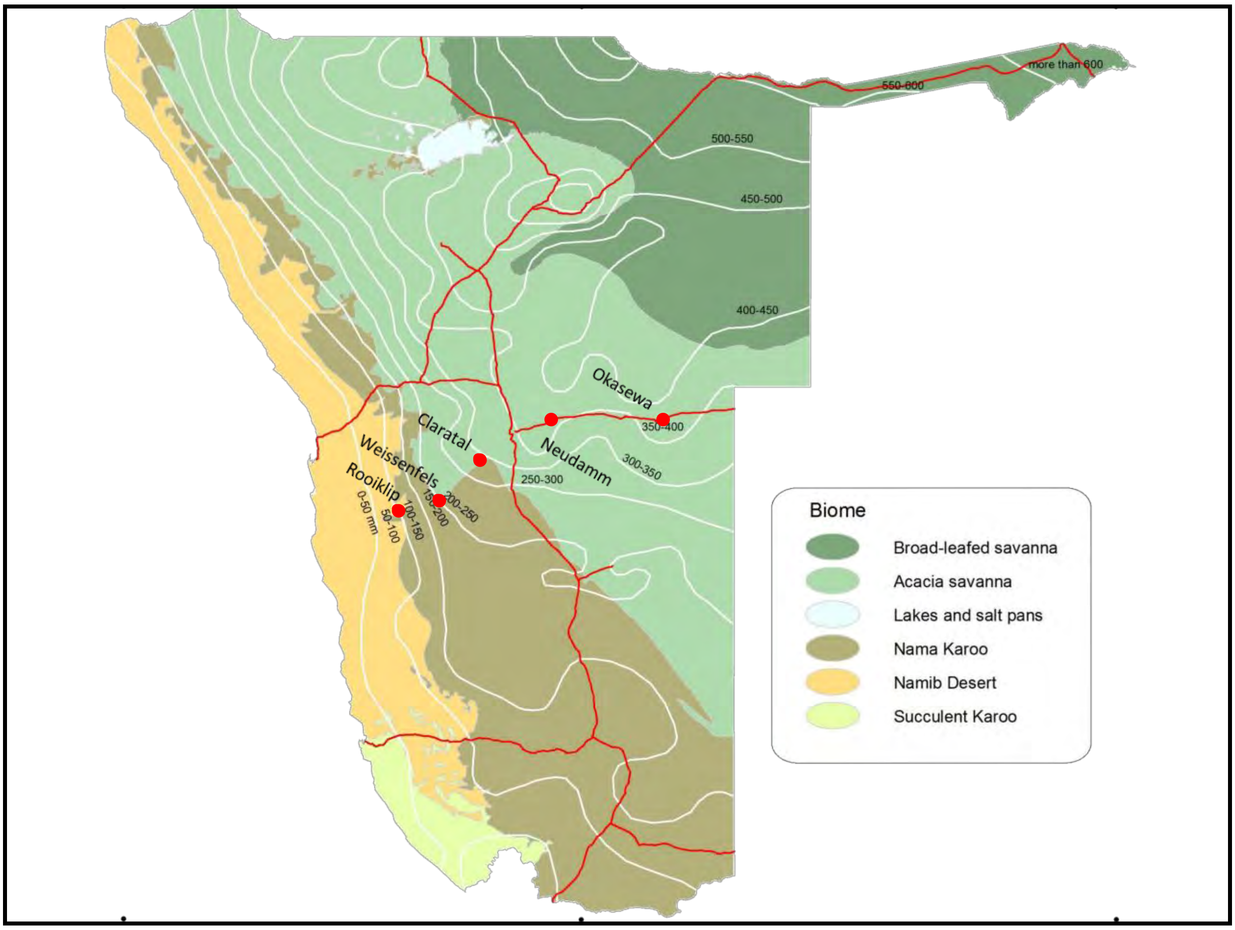

Figure 3 Map of Namibia with rainfall isohyets and biomes, showing the five study sites (Map courtesy of Dr. R.E. Simmons)

Five study sites were chosen differing in aridity from east (approx 420 mm/year) to west (approx 120 mm/year), a decrease in mean annual precipitation of approximately 300 mm over the relatively short distance of 370 km. Each site is located on a farm, named (east to west) Okasewa, Neudamm, Claratal, Weissenfels and Rooiklip. The sites were chosen to represent increasing levels of aridity representing possible predicted changes in years to come in Namibia and other arid savannas in which the climate is expected to become more arid (Simmons, pers. comm). Three structurally different habitat types were selected: Open areas, dry river lines, and bush-encroached thickets. At each site, sampling was done in the same three habitat types.

Average maximum temperatures: Gobabis (Okasewa) 32–34 °C, Windhoek (Neudamm, Claratal and Weissenfels) 30–32 °C, Rooiklip 32-34 °C. Average minimum temperatures: Gobabis (Okasewa) 2–4°C, Windhoek (Neudamm, Claratal and Weissenfels) 4-6°C, Rooiklip 6-8°C. Median annual rainfall: Gobabis (Okasewa) 350-400 mm, Windhoek (Neudamm and Claratal) 300-350 mm, Weissenfels 200-250 mm, Rooiklip 100-150mm. Variation in rainfall, percentage coefficient of variation: Gobabis and Windhoek (Okasewa and Neudamm) 30-40%, Claratal 40-50%, Weissenfels 60-70% and Rooiklip 80-90% (Mendelsohn, 2002).

The area from the Botswana border, around Windhoek and throughout the Khomas Hochland to the west of Windhoek is used for commercial cattle farming. Okasewa, Neudamm, Claratal and Weissenfels fall in this area. The farms are fenced and divided into fenced camps for grazing rotation. Water is provided mainly by windmills into cement reservoirs. Supplementary feed is provided in the dry months. Rooiklip is at the bottom of the western-central escarpment where livestock is mainly goats and sheep with some cattle. The farms are also fenced and divided into camps, much larger than on the more easterly farms, and water points are further apart.

3.2.1 Rooiklip

Small-scale goat and sheep farming takes place and livestock is sold out of hand. No grazing management is applied. The farm is situated at the western foot of the Gamsberg pass, at the bottom of the western-central escarpment. The topography is broken, with steep hills and steep, rocky cliffs along river banks (fig. 4 and fig. 5).

Figure 4 Rooiklip river, showing steep rocky cliffs. At bottom left is a vertical measuring stick of 1.2 m long

Figure 5 River bed at Rooiklip in summer, the opposite side of the river from that shown in the previous photo. Vegetation consists mainly of *Boscia spp*, *Ziziphus mucronata* and *Acacia reficiens*

3.2.2 Weissenfels

Activities include cattle farming and horse training for jumping and endurance riding. No grazing management is applied. Weissenfels is on the western edge of the central highlands, at the top of the western-central escarpment. The topography is broken, with rocky hills and deep gullies (fig. 6).

Figure 6 River bed at Weissenfels in summer, showing mature *Acacia karroo*

3.2.3 Claratal

Activities include commercial cattle farming and horse training for jumping and endurance riding. Some bush clearing is done. On the central highlands of Namibia, the topography is flat with rocky gullies and low hills (fig. 7).

Figure 7 River bed at Claratal in summer showing mature *Acacia karroo* and low hills in background

3.2.4 Neudamm

The Faculty of Agriculture and Natural Resources of the University of Namibia is based on 10 187 ha comprising the Neudamm Campus and Farm. Student training and diversified commercial farming take place: cattle, goats, sheep, pigs and chickens. Topography is broken, rocky and hilly (fig. 8).

Figure 8 River bed at Neudamm in summer

3.2.5 Okasewa

Topography is flat, undulating with no outcrops or hills (fig. 9). There is extensive bush clearing to provide grazing for cattle.

Figure 9 Riverine vegetation at Okasewa in summer, showing a mature *Acacia erioloba* surrounded by the dominant tree species, *Acacia karroo*

3.3 Sampling design

3.3.1 Bird surveys

Transects

Although the quadrat method produces unbiased information, it is labour intensive (Engeman & Sugihara, 1998). Line transects are less time-consuming and more cost-effective and therefore more efficient for a large-scale study such as this. A disadvantage of the transect method is that the intrusion of an observer may cause mobile organisms to move before being detected (Smith, 1979). This problem was in a large measure overcome by using auditory cues in addition to visual identification. Another factor that minimised bias was good visibility due to the sparseness of vegetation, which enabled detection and identification of birds from a distance.

Line transects of approximately 1 km long were carried out through each habitat at each site to survey bird assemblages. A total of 51 transects were surveyed:

- Rooiklip (R 128): 4 open, 3 River, 3 Thicket
- Weissenfels (W 215): 4 open, 3 River, 3 Thicket
- Claratal (C 315): 4 open, 4 River, 3 Thicket
- Neudamm (N 370): 3 open, 3 River, 3 Thicket
- Okasewa (O 420): 3 open, 4 River, 4 Thicket

Data from these 51 transects were used for analysis.

The start and end point of each transect was recorded on GPS as well as intermediate points where the geography of the area necessitated a turn. Transect width was not limited and birds were recorded at any distance perpendicular to the centre of the transect.

Table 1 List of transects and their GPS coordinates. Transects are identified by the first letter of the site name, followed by the first letter of the habitat type, and then the transect number.

Site	Habitat	Transect	Start coordinates	End coordinates
Rooiklip	Open	RO1	S23 24.696 E16 03.309	S23 25.256 E16 03.215
Rooiklip	Open	RO2	S23 24.683 E16 03.321	S23 24.796 E16 02.963
Rooiklip	Open	RO3	S23 24.858 E16 02.928	S23 25.001 E16 02.979
Rooiklip	Open	RO4	S23 24.880 E16 04.688	S23 24.459 E16 05.068
Rooiklip	River	RR1	S23 24.611 E16 05.101	S23 25.024 E16 04.483
Rooiklip	River	RR2	S23 24.551 E16 05.132	S23 23.785 E16 05.154
Rooiklip	River	RR3	S23°24.835 E16°04.912	S23°24.930 E16°05.490
Rooiklip	Thicket	RT1	S23 23.813 E16 05.267	S23 24.347 E16 05.284
Rooiklip	Thicket	RT2	S23°22.663 E16°05.336	S23° 22.779 E16°05.206
Rooiklip	Thicket	RT3	S23°21.450 E16°06.366	S23 21.480 E16 06.451
Weissenfels	Open	WO1	S23 17.769 E16 27.316	S23 17.786 E16 26.940
Weissenfels	Open	WO2	S23 18.305 E16 27.313	S23 18.857 E16 27.483
Weissenfels	Open	WO3	S23 17.703 E16 25.317	S23 17.381 E16 24.843
Weissenfels	Open	WO4	S23 16.741 E16 26.273	S23 16.372 E16 25.892
Weissenfels	River	WR1	S23 18.378 E16 27.107	S23 17.959 E16 27.410
Weissenfels	River	WR2	S23 19.040 E16 26.963	S23 19.408 E16 26.880
Weissenfels	River	WR3	S23 18.785 E16 27.375	S23 19.076 E16 26.987
Weissenfels	Thicket	WT1	S23 17.604 E16 26.501	S23 17.876 E16 26.942
Weissenfels	Thicket	WT2	S23 17.033 E16 26.256	S23 17.411 E16 25.894
Weissenfels	Thicket	WT3	S23 17.470 E16 25.659	S23 17.027 E16 26.249
Claratal	Open	CO1	S22 48.492 E16 51.451	S22 48.263 E16 50.924
Claratal	Open	CO2	S22 48.764 E16 51.526	S22 49.256 E16 52.032
Claratal	Open	CO3	S22 51.581 E16 47.397	S22 51.416 E16 47.504
Claratal	Open	CO4	S22 51.581 E16 47.397	S22 51.507 E16 47.834
Claratal	River	CR1	S22 50.968 E16 48.897	S22 51.460 E16 49.139
Claratal	River	CR2	S22 51.416 E16 47.504	S22 51.463 E16 47.829
Claratal	River	CR3	S22 49.113 E16 52.107	S22 48.936 E16 51.599
Claratal	River	CR4	S22 48.207 E16 50.973	S22 47.806 E16 50.826
Claratal	Thicket	CT1	S22 51.256 E16 48.277	S22 51.125 E16 48.749
Claratal	Thicket	CT2	S22 51.343 E16 48.247	S22 51.746 E16 47.980
Claratal	Thicket	CT3	S22 51.749 E16 47.753	S22 52.153 E16 47.462

Site	Habitat	Transect	Start coordinates	End coordinates
Neudamm	Open	NO1	S22 29.950 E17 18.210	S22 29.809 E17 18.863
Neudamm	Open	NO2	S22 30.267 E17 19.582	S22 30.490 E17 19.913
Neudamm	Open	NO3	S22 30.589 E17 19.927	S22 30.318 E17 19.368
Neudamm	River	NR1	S22°27.685 E17°21.791	S22°27.224 E17°21.487
Neudamm	River	NR2	S22°27.905 E17°21.746	S22°27.975 E17°22.248
Neudamm	River	NR3	S22°29.547 E17°18.491	S22 29.793 E17 19.010
Neudamm	Thicket	NT1	S22°28.626 E17°22.013	S22°28.762 E17°21.471
Neudamm	Thicket	NT2	S22°28.779 E17°21.488	S22°28.603 E17°22.030
Neudamm	Thicket	NT3	S22°27.767 E17°21.781	S22°28.060 E17°21.354
Okasewa	Open	OO1	S22 21.812 E18 19.335	S22 21.531 E18 18.514
Okasewa	Open	OO2	S22 23.383 E18 19.611	S22 23.208 E18 19.951
Okasewa	Open	OO3	S22 23.323 E18 19.616	S22 23.337 E18 19.778
Okasewa	River	OR1	S22 24.765 E18 19.689	S22 24.439 E18 20.213
Okasewa	River	OR2	S22 24.765, E18 19.689	S22 24.461, E18 20.899
Okasewa	River	OR3	S22 24.439, E18 20.213	S22 24.461, E18 20.899
Okasewa	River	OR4	S22 24.461, E18 20.899	S22 24.477, E18 21.379
Okasewa	Thicket	OT1	S22 21.882 E18 19.315	S22 21.804 E18 18.732
Okasewa	Thicket	OT2	S22 21.540 E18 18.465	S22 21.775 E18 18.780
Okasewa	Thicket	OT3	S22 23.214 E18 19.966	S22 23.889 E18 20.295
Okasewa	Thicket	OT4	S22 24.315 E18 20.165	S22 24.246 E18 19.543

During the February 2009 survey, Okasewa river transects OR1 and OR3 were walked continuously as one transect. This single survey is recorded as transect OR2.

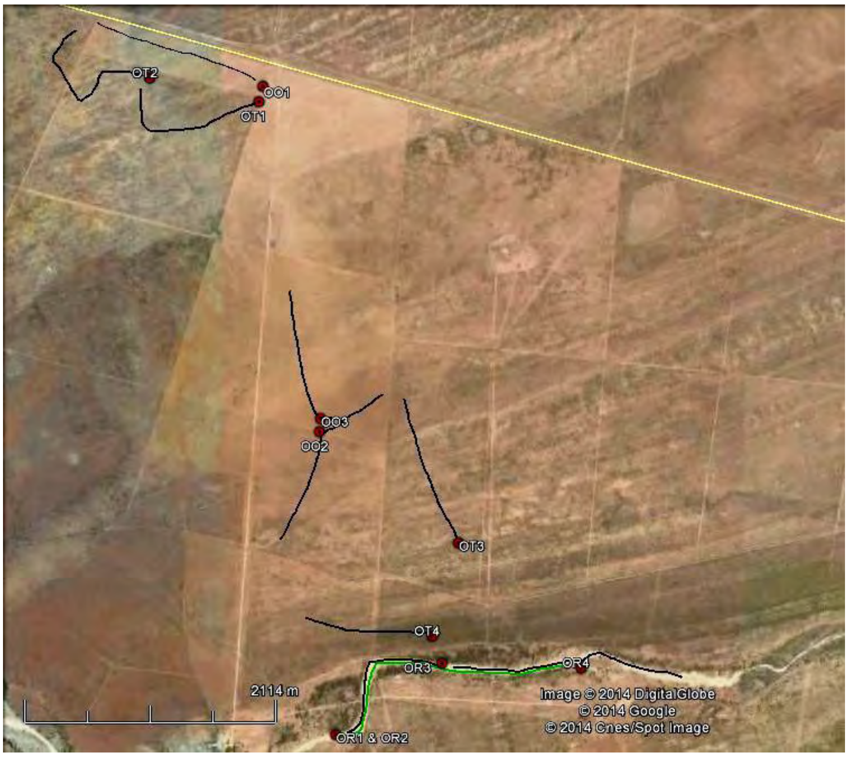

Figure 10 The layout of transects at Okasewa

Figure 11 The layout of transects at Neudamm

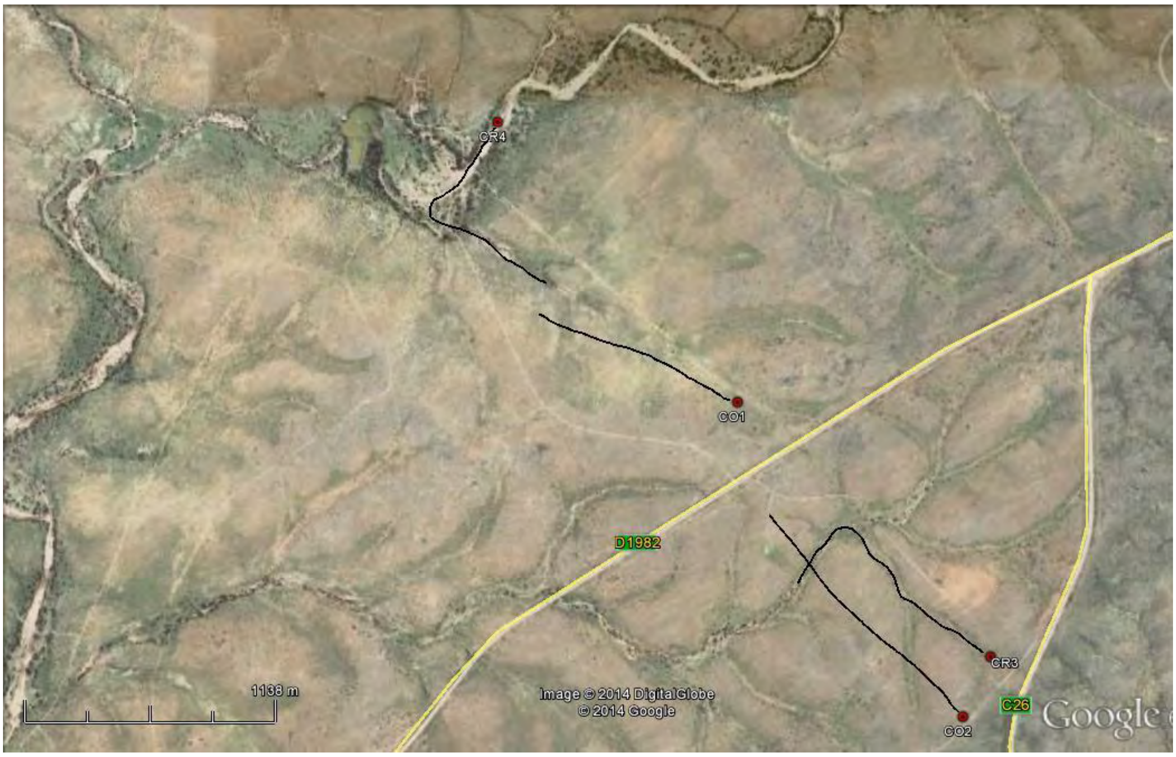

Figure 12 The layout of the four north-eastern transects at Claratal

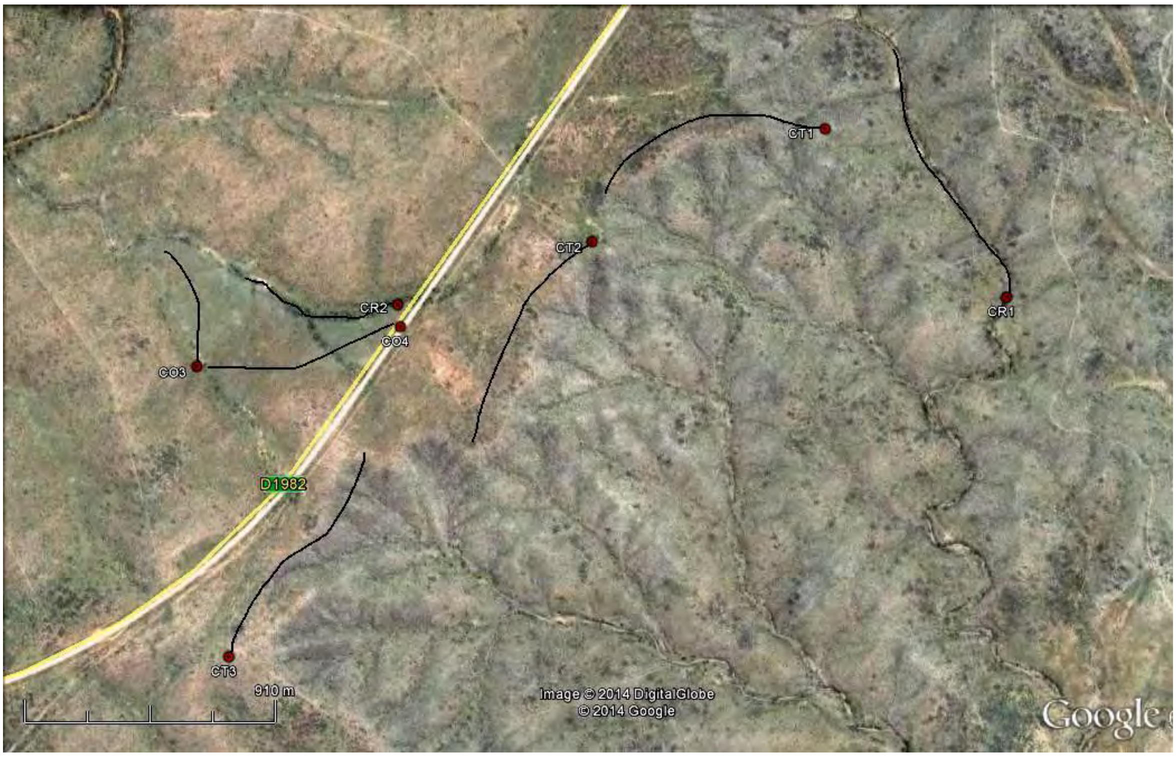

Figure 13 The layout of the seven south-western transects at Claratal

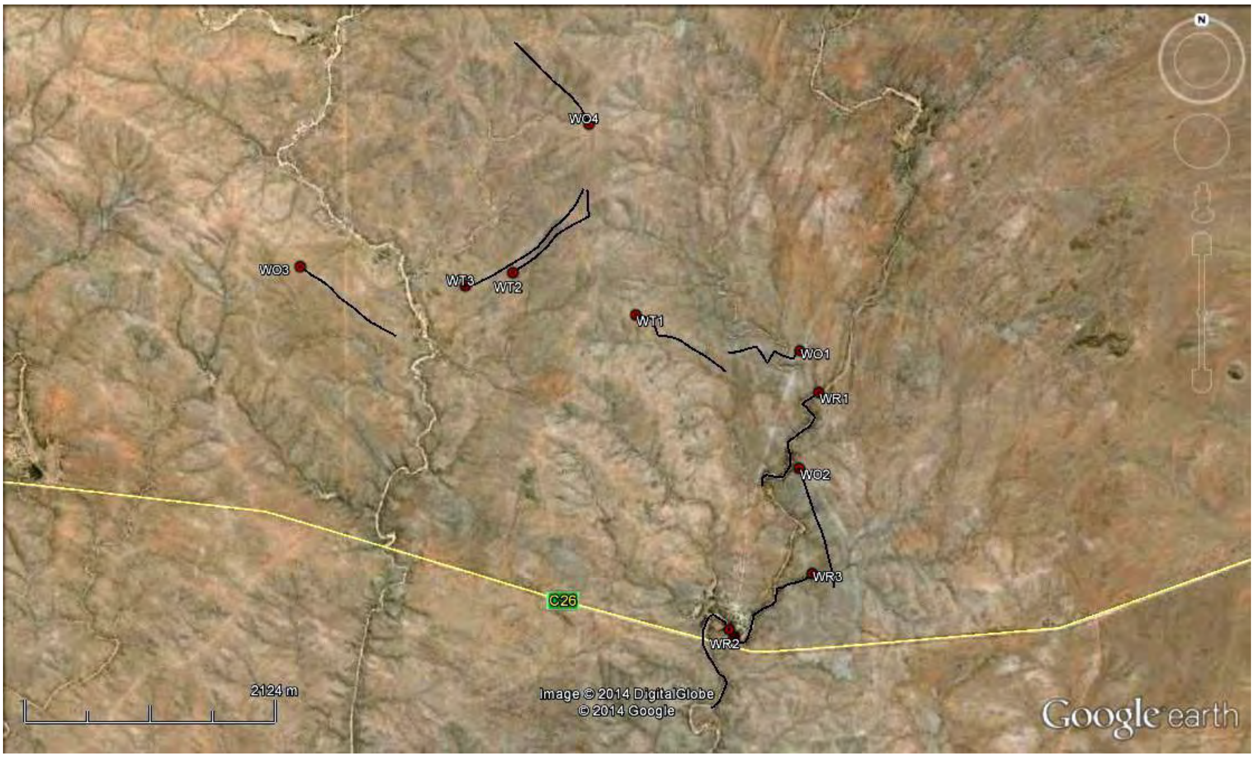

Figure 14 The layout of transects at Weissenfels

Figure 15 The layout of the two northern transects at Rooiklip

Figure 16 The layout of the eight central transects at Rooiklip

Sampling

Sampling was carried out over three years in the dry winter as well as the wet summer season, resulting in six separate surveys: August of 2007, 2008 and 2009, and February/March of 2008, 2009 and 2010. The wet summer season (February/March) in this area coincided with the breeding season of birds.

Dr Simmons designed the sampling, chose the sites, habitats and transects and he was the lead researcher at each of the six surveys. He employed field assistants to ensure that each survey could be completed within 2-3 days at each site within a two week period by dividing transects between himself and the assistant. The assistants were experienced in bird surveying and there was a different assistant for each survey, except February and August 2009 when the author of this dissertation was the assistant.

Surveys were conducted in the morning from approximately 07:30 to 11:00, the time in this area when birds are most active and thus most visible. Transects were walked without time limit and both visual and auditory cues were used to identify birds. For each observation, information was recorded on voice recorder or tape recorder and in the afternoon, the information was transferred to Excel spread sheets. The following information was recorded: bird species, number of individuals, distance (m) of bird/s from observer, distance (m) of bird/s perpendicular from centre of transect.

The following materials were used for bird surveys:

Binoculars

GPS

Digital voice recorder

Tape recorder

Field guides to bird identification

Laptop computer

3.3.2 Vegetation survey

One vegetation survey was carried out in August 2009 using the nearest individual distance measure.

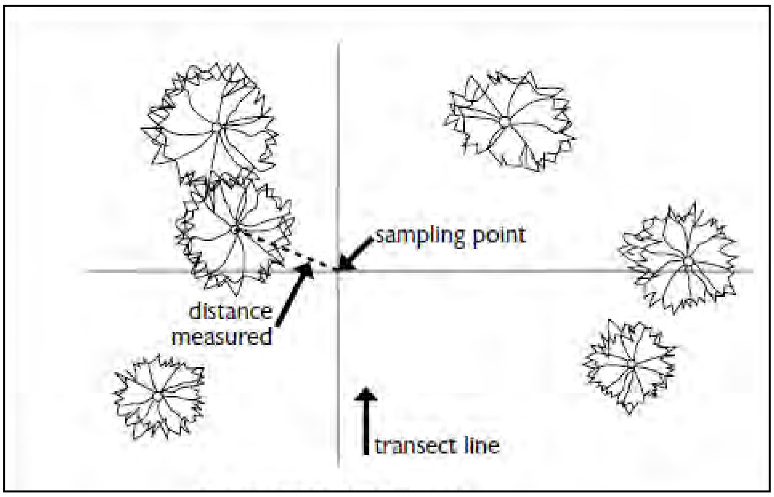

Figure 17 Nearest individual distance measure used for vegetation survey (Elzinga, 1998)

Each transect had 50 sampling points, spaced 20 m apart along the centre of the transect, comprising 2750 sampling points. All transects were the same length, so the surveys can be assumed to represent equal-effort sampling, and therefore comparable. At each sampling point, the vegetation height was recorded as well as the distance of the plant from sampling point.

Plant height was measured from ground to the uppermost part of the plant at rest (not stretched out). Heights of tall trees and shrubs were estimated: the measuring stick was placed at the base of the plant to provide scale and the observer moved back to approximately 20 – 50 m from the base of the plant to reduce parallax and from there the height was estimated. Distance was measured at the main stem for woody plants and at the centre of a grass clump. Distance from sampling point can be used to calculate density but it was not done in this study because of two weaknesses of the method. Firstly, it did not take canopy cover into account and birds utilise horizontal as well as vertical layers of vegetation. Secondly, no distinction was made between grass, forbs, shrubs and trees. This shortcoming means that a given distance to a mature tree and the same distance to a grass or forb with this method would result in the same density, which would not give an accurate indication of the vegetation density as utilised by birds. Consequently, only vegetation height was used in this study.

The following materials were used for vegetation surveys:
GPS
Measuring stick
Field lists

Each transect was 1 km long and the same transects were used for bird and vegetation surveys. Bird surveys did not have static sampling points, but the same distance was walked for approximately the same duration on each bird survey. Vegetation surveys had 50 sampling points, spaced 20 m apart along the centre of the transect, comprising 2750 sampling points. Surveys were therefore assumed to be equal-effort, and therefore considered as comparable between sites and habitats.

3.4 Environmental factors

3.4.1 Rainfall

Average annual rainfall for each site was calculated based on data obtained from the farm owners. At Weissenfels the current owner did not record rainfall and the average of 215 mm/year was based on records from 1963-2001 by the previous owner. Rooiklip records were available from 2000-2010, Claratal 1928-2010, Neudamm 1999-2010 and Okasewa 1952-2010. Mean annual rainfall for the sites:

- Rooiklip: 128 mm
- Weissenfels: 215 mm
- Claratal: 315 mm
- Neudamm: 370 mm
- Okasewa: 420 mm

3.4.2 Habitat types

Three structurally different habitat types (based on dominant vegetation cover) were visually selected for stratified sampling: Open areas, dry river lines, and bush-encroached thickets. At each site, the same three habitat types were chosen in which to sample birds. The vegetation cover in thickets (T) comprises woody shrubs and trees, mainly *Acacia mellifera* and *Catophractes alexandri* on the three eastern sites, and *Acacia reficiens* on the two western sites. Open areas (O) are dominated by grass with scattered trees, shrubs and forbs. River (R) refers to ephemeral dry river lines that comprise mature *Acacia karroo*, *Acacia erioloba*, *Ziziphus mucronata* and *Boscia albitrunca* trees.

The heights of individual plants were simplified into eight categories:

Category (cm)	Plant ht (cm)
10	0 – 10
20	11 – 20
50	21 – 50
100	51 – 100
200	101 – 200
500	201 – 500
800	501 – 800
1600	801 – 1600

The sum of (# individual plants at each sample unit x categorised height) = total height at each sample unit. Total height divided by total number of plants = mean height of vegetation at each sample unit.

3.5 Data analysis

McCune & Grace (2002) explain that deleting rare variables is a useful way of reducing bulk and noise in a data set without losing much information. They suggest deleting species that occur in fewer than 5% of the sample units. In arid areas birds are distributed patchily and the larger species like raptors and bustards occur singly and across large ranges. Following the premise of McCune & Grace (2002) in this study would lose crucial ecological information because species that play important ecological roles would be eliminated. Instead, an ecological approach was followed when deciding which variables to delete, dealt with fully in Section 4.5, as well as in Table 5.

Sampling was stratified by site according to rainfall and further by habitat type, similar to the stratified sampling done by Higgins (1999). Three structurally different, easily identifiable habitat types were identified. Therefore, sampling units were not defined by transects but by combining site and habitat types: five sites and three habitat types on each site, for a total of fifteen sampling units.

The habitat types were named as follows:
O: Open
R: River
T: thicket

For univariate analyses, the five sites were named according to the mean annual rainfall (mm) on each farm:
420: Okasewa
370: Neudamm
315: Claratal
215: Weissenfels
128: Rooiklip

For multivariate analyses, the five sites were named as follows:
O 420: Okasewa
N 370: Neudamm
C 315: Claratal
W 215: Weissenfels
R 128: Rooiklip

The fifteen sampling units are designated by the first letter of the farm, followed by the abbreviation for the habitat:
CO: Claratal Open
CR: Claratal River
CT: Claratal Thicket
NO: Neudamm Open
NR: Neudamm River
NT: Neudamm Thicket
OO: Okasewa Open
OR: Okasewa River
OT: Okasewa Thicket
RO: Rooiklip Open
RR: Rooiklip River
RT: Rooiklip Thicket
WO: Weissenfels Open
WR: Weissenfels River
WT: Weissenfels Thicket

3.5.1 Microsoft Excel

Pivot tables were used extensively to sort and organise raw data and to compile tables. All tables in this study were created using Microsoft Excel. Information for Prism and PC-ORD was imported from Microsoft Excel spread sheets.

3.5.2 Graphpad Prism 4

Analysis of variance (ANOVA) was performed to assess the impact of environmental variables on bird species richness, abundance, biomass, and diversity. Environmental variables that were investigated include rainfall, habitat, season (winter and summer) and vegetation height.

ANOVA is helpful even if data do not follow the exact Gaussian curve, especially for large samples. One-way ANOVA was used to compare the means of three or more groups when the data of each of these groups is in one category (Motulsky, 2003). Probability (p-value) and the fraction of overall variance (r^2) were the metrics used to assess the effect of environmental variables on bird communities. A $p < 0.05$ indicates that there is a less than 5% probability that the differences can be attributed to random sampling. A large r^2 value means that a large fraction of the variation can be explained by the variable being assessed.

Two-way ANOVA was used to establish how two factors (e.g. rainfall and habitat) affected a response by determining how the results were affected by each of the two factors, how the results were affected by interaction between the two factors, and whether the residual variation is unrelated to differences between rows and columns. The null hypothesis for the two-way ANOVA is that there would be no interaction between the columns and rows (Motulsky, 2003). The p-value and % of total variation were used to assess how environmental factors affect bird communities.

The Bonferroni post-test (a modification of t-tests) compares variables and in this study all pairs of variables (rainfall and/or habitat types) were compared in both one-way and two-way ANOVA. The Neuman-Keuls post-test compares the means of all pairs of variables. It was used in section 4.5.3. where the Bonferroni post-test was considered too conservative to show real differences.

Paired, two-way, t-tests were conducted to measure the percentage difference between summer and winter for both species richness and abundance. P-value and r^2 were the metrics used to assess the effect of season on bird communities.

3.5.3 PC-ORD 6.0

Species-accumulation curve

A species-accumulation curve was constructed to determine if enough transects were surveyed.

Cluster analysis

Classification is a common goal in ecology and cluster analysis assigns sample units to discrete groups, based on their similarities, as opposed to ordination that orders sampled units along a continuum (Peck, 2010), which makes cluster analysis a useful tool in management. Two-way cluster analyses were done using the Sorenson (Bray-Curtis) distance measure and a flexible beta of -0.25 for two data sets: sites (sample units) were grouped by habitat type and transects were grouped by site. The results are displayed in cluster dendrograms that show the hierarchy of clusters (McCune & Mefford, 1999).

MRPP (Multi-response Permutation Procedures)

MRPP evaluates hypotheses for sample units that can be assigned to discrete groups (Peck, 2010). The null hypothesis is that there is no difference between two or more groups (McCune & Grace, 2002). MRPP provides a p-value for statistical significance and an A-value which is a measure of homogeneity within groups. For $A = 1$, all items within groups are identical and for $A = 0$, heterogeneity within groups equals expectation by chance. Two MRPP analyses were done: one with groups defined by habitat and the other defined by site.

NMS (Non-metric Multidimensional Scaling)

The advantages of NMS as ordination method include that it avoids the assumption of linear relationships among variables, uses rank distances, allows the use of any distance measure and minimises the error produced by zero that is common in community data (McCune & Mefford, 1999). It is also suitable for data that is heterogeneous and discontinuous, traits that characterise this study. Distance measures used were Relative Sorenson or Sorenson (Bray-Curtis), depending on the suitability for the specific data.

Two or more dimensions can be derived from NMS and the number of dimensions is determined by plotting final stress against the number of dimensions (McCune & Mefford, 1999). The best solution is the one with the lowest final stress from a real run and PC-ORD selects the highest dimensionality that meets this criterion (McCune & Mefford, 1999). Where three dimensions were obtained, only two were selected for representation on the NMS graphs in Chapter 4. The following information is provided at each NMS graph:

- Number of dimensions (derived and represented)
- Final stress
- Percentage coefficients of determination for the correlations between ordination distances in the original n-dimensional space (r^2). The two dimensions with the highest r^2 were chosen for the graphs.

Final stress can be interpreted as follows: 0 - 5 excellent, 5 - 10 good, 10 – 20 general picture good but not in detail, > 20 not good (McCune & Grace, 2002). Stress can be considerably higher if the distances among objects in a group of ties are not equal (McCune & Mefford, 1999).

Bi-plots represent bird variables and environmental factors on one graph. Biplots show the ordination of 188 species and 15 sample units (5 sites x 3 habitats) with environmental factors on the second matrix.

Indicator species analysis

Indicator species analysis describes the value of different species for indicating environmental conditions and it is based on both abundance and frequency (McCune & Grace, 2002). Two non-hierarchical indicator species analyses were performed to describe associations of species with the habitats and with the sites. Observed Indicator Values (IV's) were obtained by combining the relative abundances and relative frequencies of the birds observed. The Monte Carlo test of significance used 4999 randomisation runs to produce an observed IV, mean, standard deviation and P-value. Combined IV and p-values from the Monte Carlo test were evaluated to determine indicator species: IV > 30 and $p \leq 0.1$.

Outlier analysis

Guild ordinations that did not find a useful NMS were subjected to outlier analysis to check for weakly structured data and all these analyses showed no outliers.

Row and column summary

Guild ordinations that did not find a useful NMS and showed no outliers, were subjected to row and column summary to find out whether some variables carried drastically greater weight than the other variables. Where data had to be manipulated by removing variables (species) before NMS ordination, it is indicated at the relevant ordination graph.

4 Results

4.1 Vegetation height

The mean height (cm) of the vegetation at each sample unit was used to analyse trends across the aridity gradient and habitat types (fig. 18).

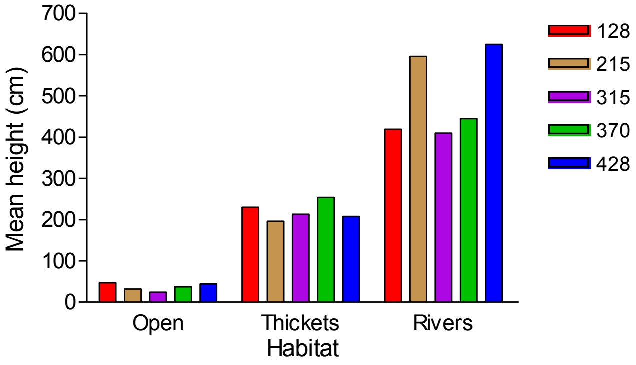

Figure 18 Mean height of vegetation at the different habitat types. The five sites are represented by different colours, as indicated in the legend.

A highly significant difference was found (2-way ANOVA, $p < 0.0001$) in vegetation height of the different habitat types within sites. No significant difference was found (2-way ANOVA, $p = 0.61$) in vegetation height of the same habitat types. Habitat types accounted for 92.4% of total variation and sites 2%. Bonferroni post-test shows $p > 0.05$ for all pairings of habitat and site.

4.2 Observer bias

Five different field assistants were used for the six surveys, in addition to Dr. Simmons, who was present at each survey. Different levels of experience and local knowledge could affect observations and/or identification, and result in observer bias.

Table 2 Testing for observer bias. Each survey is indicated by the month and year in which it took place. Observers are referred to by numbers. The author is indicated as *Observer 4*

	Aug 2007	Feb 2008	Aug 2008	Feb 2009	Aug 2009	March 2010
	Observer 1	Observer 2	Observer 3	Observer 4	Observer 4	Observer 5
Species Richness	86	135	122	149	113	137
Abundance	1755	2375	7802	5175	4161	4917

There was no significant difference ($p > 0.1$) between the six surveys conducted by five different observers, therefore there was no observer bias in the study (1-way repeated measures ANOVA with Bonferroni's post-test, $p = 0.493$, $r^2 = 0.5042$) (table 2).

4.3 Species-accumulation curves

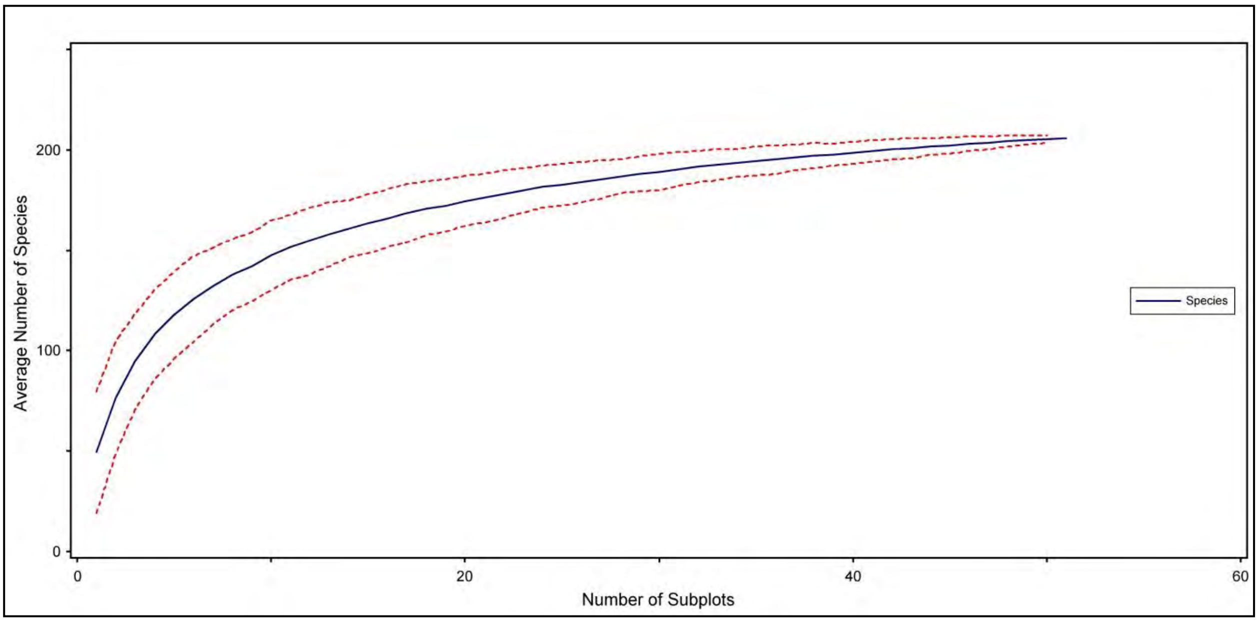

Figure 19 Species-accumulation curve of total number of bird species observed on 51 transects (subplots). Dotted lines are confidence bands, indicating +/- two standard deviations from the line. (McCune & Mefford, 2011)

No significant increase in number of species after 40 transects (subplots) (fig. 19), therefore enough transects were surveyed.

4.4 Identifying groups

Cluster analyses and MRPP (Multi-response Permutation Procedure) were used to identify groups (habitats and sites) within the study area.

4.4.1 Cluster analysis of transects

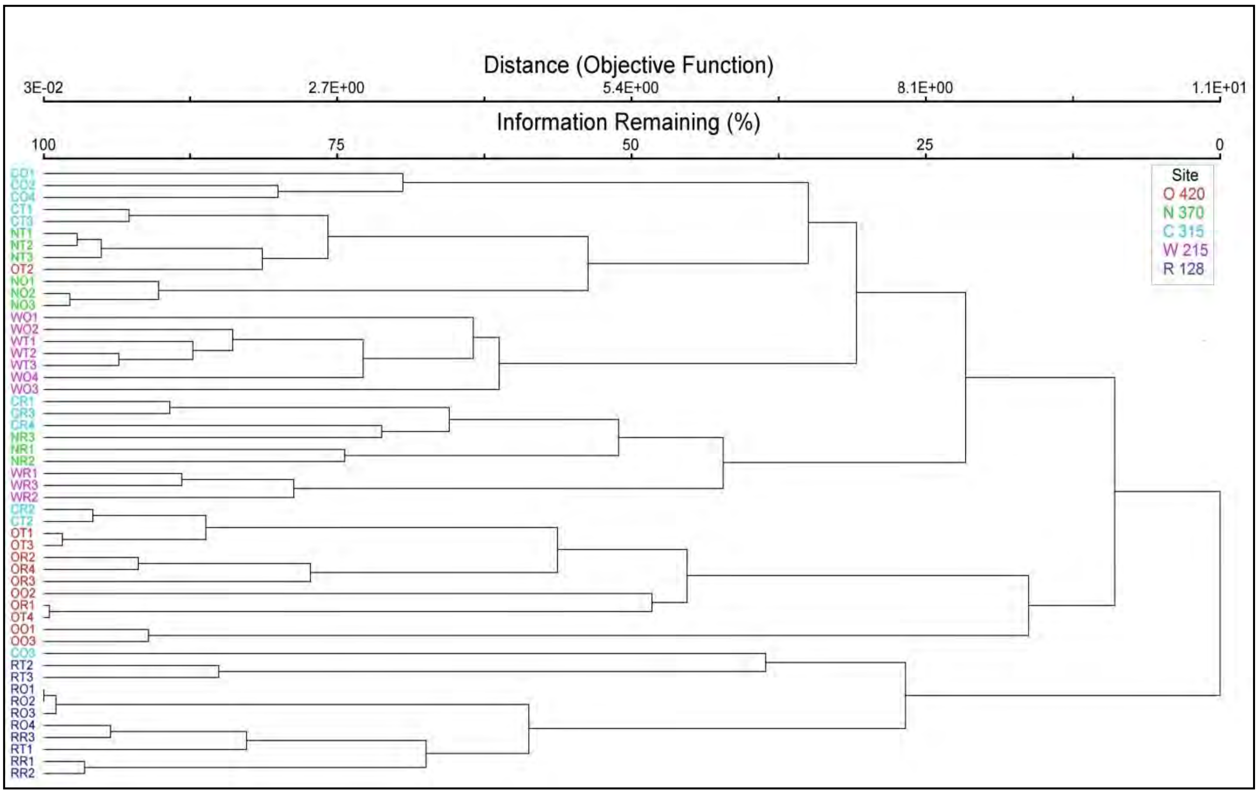

Figure 20 Cluster dendrogram of 51 transects and avian composition, grouped by site

Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket. Sites are named according to mean annual rainfall: O: 420 mm, N: 370 mm, C: 315 mm, W: 215 mm, R: 128 mm.

A cluster analysis of avian composition was done to investigate whether the *a priori* clustering of transects into sample units (habitat per site) was reasonable. Figure 20 is a cluster dendrogram of 51 transects, grouped by site.

All transects at the most arid site, R 128, were grouped at 25%, indicating more similarities between the avian composition of the three habitats at that site than there were intra-habitat similiarities across the aridity gradient at the other three sites. The most mesic site, O 420, also showed a strong similarity between the three habitats, except OT2, which was more similar with the thickets at the next mesic site, N 370, than with the other thicket transects at O 420. Rivers at the three middle sites had an avian composition more similar than with other habitats at the same three sites, with the river transects of the three middle sites grouped at 40%. C 315, in the middle of the aridity gradient had the most disparate avian composition grouping: three open and two thicket transects were grouped at 35%; CO3 grouped close to the R 128 thicket transects at 25%; and CR2 and CT2 were grouped with O 420 thickets and rivers at 62%.

4.4.2 Cluster analysis of sample units

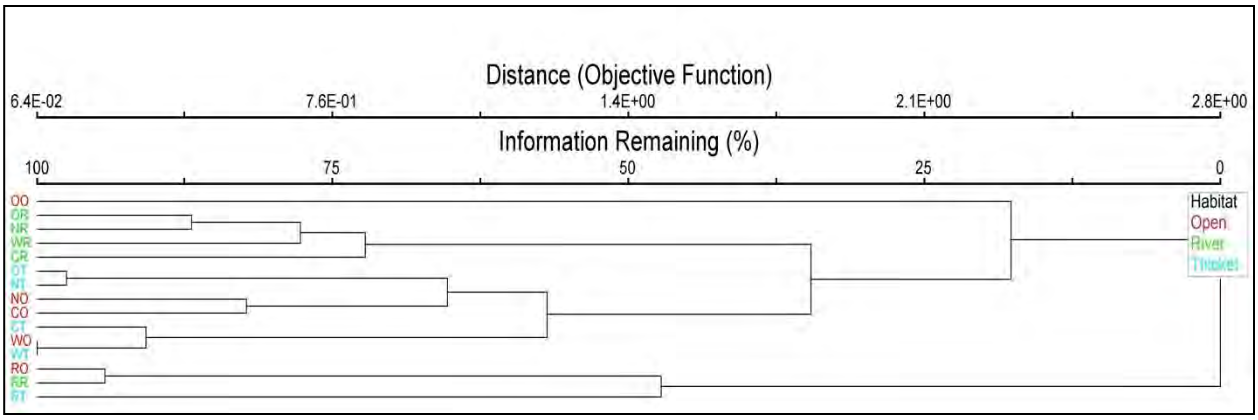

Figure 21 Cluster dendrogram of sample units and avian composition, grouped by habitat

Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

Cluster analysis was used to investigate avian composition, habitat and site associations. Figure 21 is a cluster dendrogram of the 15 sample units, grouped by habitat.

The most arid site, R 128 (RO, RR, and RT), was easily classifiable as a site, because the three habitat types clustered close together, indicating similarities in avian composition of the three habitats. This confirms the trend from Figure 20. There was a strong similarity in avian composition between riverine habitats regardless of aridity, with OR, NR, WR and CR clustering at 70%. Thicket and open habitats of the four more mesic sites were clustered at 56%, indicating similarities in avian composition with one another and with aridity, except for OO, open, at the most mesic site, which showed a grouping at 15%.

4.4.3 MRPP

Two MRPP (Multi-Response Permutation Procedure) analyses were done to investigate within-group homogeneity: one for habitat type and one for site. Distance measure for both was Sorenson (Bray-Curtis).

Habitat

Groups were defined by habitat and group size was 5. $p = 0.003$, $A = 0.077$

Site

Groups were defined by site and group size was 3. $p = 0.008$, $A = 0.098$

The low A value (smaller than 0.3) suggests more heterogeneity within groups than expected by chance. However, in community ecology, an A value as low as 0.01 may be statistically significant if the sample size is large (N=200). Then the ecological significance, not only the statistical, should be considered (McCune & Grace, 2002). Since the sample size of this study was large (N=206) and there was a small p-value for both MRPP analyses ($p < 0.05$), there was sufficient homogeneity within habitats and within sites to classify them as separate groups.

The combined results from the cluster analyses and MRPP suggest that the *a priori* grouping of transects into sample units (site-habitat type) was justified.

4.5 Bird species richness, abundance and diversity: all observed bird species included.

Over the three years of sampling, 24 596 individuals were observed, representing 206 bird species. Outliers in a data set can obscure the information carried by the bulk of the data and rare species can introduce noise into a data set (McCune & Grace, 1999). These problems are most commonly caused by a few very large or a few very small values. The analyses in this section were done to investigate whether there were species that contributed little to the overall ecological information on the biodiversity of the study area.

The decision as to which species should be removed was taken on biological grounds rather than statistical, by analysing species richness, abundance and diversity across the aridity gradient and in the different habitats, then excluding each species or group of species that could possibly affect information and then running the same analyses again. Finally, the results from the two sets of analyses (‘all observed species included’ versus ‘non-contributive species removed’) were compared.

In this section, the results of the first set of analyses (all observed species included) are given and from section 4.6 onward all analyses were done with non-contributive species excluded. All the species observed in six surveys during three years of sampling are listed in Table 3.

Table 3 Presence/absence of all bird species observed at the five sites

Sites are arranged left to right, from arid (west) to mesic (east). The mean annual rainfall (mm) recorded on the farm designates the site name. Indicated are common name, scientific name, abbreviated name, and presence/absence at each of the five sites. Sites are arranged in the table according to mean annual rainfall from arid (west) to mesic (east). 1 indicates presence, 0 indicates absence.

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Abdim's Stork	*Ciconia abdimii*	AbSt	0	0	0	0	1
Acacia Pied Barbet	*Tricholaema leucomelas*	AcPiBa	1	1	1	1	1
African Black Swift	*Apus barbatus*	AfBlSw	1	0	1	1	0
African Fish-Eagle	*Haliaeetus vocifer*	AfFi	0	1	0	1	0
African Golden Oriole	*Oriolus auratus*	AfGoOr	0	1	0	1	1
African Grey Hornbill	*Tockus nasutus*	AfGrHo	1	1	0	1	0

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
African Harrier-Hawk	*Polyboroides typus*	AfHa	0	0	0	0	1
African Hawk-Eagle	*Aquila spilogaster*	AfHaE	0	1	1	1	1
African Hoopoe	*Upupa africana*	AfHo	1	1	1	1	1
African Palm-Swift	*Cypsiurus parvus*	AfPa	0	1	1	1	1
African Pipit	*Anthus cinnamomeus*	AfPi	0	1	1	1	1
African Quailfinch	*Ortygospiza articollis*	AfQu	0	0	0	1	1
African Red-eyed Bulbul	*Pycnontus nigricans*	AfReBu	1	1	1	1	1
Alpine Swift	*Tachymarptis melba*	AlSw	0	1	1	1	0
Amur Falcon	*Falco amurensis*	AmFa	0	0	1	1	0
Ant-eating Chat	*Myrmecocichla formicivora*	AnCh	0	0	1	1	1
Ashy Tit	*Parus cinerascens*	AsTi	1	1	1	1	1
Augur Buzzard	*Buteo augur*	AuBu	1	0	0	1	0
Banded Martin	*Riparia cincta*	BaMa	0	0	0	0	1
Barn Owl	*Tyto alba*	BaOw	1	0	0	0	0
Barn Swallow	*Hirundo rustica*	BaSw	0	1	1	1	1
Barred Wren-Warbler	*Calamonastes fasciolatus*	BaWr	0	1	1	1	1
Bearded Woodpecker	*Dendropicos namaquus*	BeWo	0	1	1	1	1
Black Cuckoo	*Cuculus clamosus*	BlCu	0	1	1	1	1
Black-chested Prinia	*Prinia flavicans*	BlPri	1	1	1	1	1
Black-chested Snake-Eagle	*Circaetus pectoralis*	BlSn	1	1	1	1	1
Black-faced Waxbill	*Estrilda erythronotos*	BlWa	1	1	1	1	1
Black-headed Heron	*Ardea melanocephala*	BlHe	0	0	0	1	0
Black-shouldered Kite	*Elanus caeruleus*	BlKi	0	0	1	1	1
Blacksmith Lapwing	*Vanellus armatus*	BlLa	0	0	0	1	1
Black-throated Canary	*Serinus atrogularis*	BlCa	1	1	1	1	0
Black-winged Pratincole	*Glareola nordmanni*	BlPr	0	0	0	0	1
Bradfield's Swift	*Apus bradfieldi*	BrSw	1	1	1	1	0
Bronze-winged Courser	*Rhinoptilus chalcopterus*	BrCo	0	0	1	0	0
Brown Snake-Eagle	*Circaetus cinereus*	BrSn	0	0	0	1	1
Brown-crowned Tchagra	*Tchagra australis*	BrTc	1	1	1	1	1
Brown-throated Martin	*Riparia paludicola*	BrMa	0	0	0	1	0
Brubru	*Nilaus afer*	Br	0	1	0	1	1
Buffy Pipit	*Anthus vaalensis*	BuPi	0	0	1	0	1
Burchell's Sandgrouse	*Pterocles burchelli*	BuSa	0	0	0	0	1
Burchell's Starling	*Lamprotornis australis*	BuSt	0	0	0	1	1
Burnt-necked Eremomela	*Eremomela usticollis*	BuEr	0	1	1	1	1
Cape Bunting	*Emberiza capensis*	CaBu	1	0	0	0	0
Cape Clapper Lark	*Mirafra apiata*	CaClLa	0	0	0	1	1
Cape Crow	*Corvus capensis*	CaCr	0	0	0	0	1
Cape Glossy Starling	*Lamprotornis nitens*	CaGlSt	1	1	1	1	1
Cape Penduline-Tit	*Anthoscopus minutus*	CaPe	1	1	1	1	1
Cape Sparrow	*Passer melanurus*	CaSp	1	1	1	1	0
Cape Turtle-Dove	*Streptopelia capicola*	CaTu	1	1	1	1	1

Common name	Scientific name	Abbreviated name	128	215	315	370	420
Cape Wagtail	*Motacilla capensis*	CaWa	0	0	1	1	0
Capped Wheatear	*Oenanthe pileata*	CaWh	0	0	1	1	1
Cardinal Woodpecker	*Dendropicos fuscescens*	CaWo	1	1	1	1	1
Chat Flycatcher	*Bradornis infuscatus*	ChFl	1	1	1	1	1
Chestnut Weaver	*Ploceus rubiginosus*	ChWe	1	1	1	0	1
Chestnut-backed Sparrowlark	*Eremopterix leucotis*	ChSp	0	0	1	0	1
Chestnut-vented Tit-Babbler	*Parisoma subcaeruleum*	ChTi	1	1	1	1	1
Cinnamon-breasted Bunting	*Emberiza tahapisi*	CiBu	1	1	0	1	0
Common Fiscal	*Lanius collaris*	CoFi	1	1	1	1	1
Common Greenshank	*Tringa nebularia*	CoGr	0	0	0	0	1
Common House-Martin	*Delichon urbicum*	CoHo	1	1	0	1	0
Common Quail	*Coturnix coturnix*	CoQu	1	1	1	1	1
Common Scimitarbill	*Rhinopomastus cyanomelas*	CoSc	1	1	1	1	1
Common Swift	*Apus apus*	CoSw	1	1	1	1	1
Common Waxbill	*Estrilda astrild*	CoWa	0	0	1	0	0
Common Whitethroat	*Sylvia communis*	CoWh	0	1	0	0	0
Crested Francolin	*Peliperdix sephaena*	CrFr	0	0	0	0	1
Crimson-breasted Shrike	*Laniarius atrococcineus*	CrSh	0	1	1	1	1
Crowned Lapwing	*Vanellus coronatus*	CrLa	0	0	1	1	1
Damara Hornbill	*Tockus damarensis*	DaHo	0	0	0	1	0
Desert Cisticola	*Cisticola aridulus*	DeCi	1	1	1	1	1
Diderick Cuckoo	*Chrysococcyx caprius*	DiCu	1	1	1	1	1
Double-banded Courser	*Rhinoptilus africanus*	DoCo	0	0	1	0	0
Double-banded Sandgrouse	*Pterocles bicinctus*	DoSa	1	0	0	0	1
Dusky Sunbird	*Cinnyris fusca*	DuSu	1	1	1	1	1
Eastern Clapper Lark	*Mirafra fasciolata*	EaClLa	0	0	0	1	1
Egyptian Goose	*Alopochen aegyptiacus*	EgGo	0	1	1	1	1
Eurasian Golden Oriole	*Oriolus oriolus*	EuGoOr	0	1	0	0	1
European Bee-eater	*Merops apiaster*	EuBe	0	0	0	1	1
Familiar Chat	*Cercomela familiaris*	FaCh	1	1	1	1	0
Fawn-coloured Lark	*Mirafra africanoides*	FaLa	1	1	1	1	1
Fork-tailed Drongo	*Discrurus adsimilis*	FoDr	0	1	1	1	1
Freckled Nightjar	*Camprimulgus tristigma*	FrNi	1	0	0	1	0
Gabar Goshawk	*Melierax gabar*	GaGo	0	1	1	1	1
Golden-breasted Bunting	*Emberiza flaviventris*	GoBu	0	1	1	1	1
Golden-tailed Woodpecker	*Campethera abingoni*	GoWo	0	1	0	0	1
Great Sparrow	*Passer motitensis*	GrSp	1	1	1	1	1
Great Spotted Cuckoo	*Clamator glandarius*	GrSpCu	0	0	0	1	1
Great White Pelican	*Pelecanus onocrotalus*	GrWhPe	0	0	1	1	0
Greater Honeyguide	*Indicator indicator*	GrHo	0	0	0	1	0
Greater Kestrel	*Falco rupicoloides*	GrKe	0	0	0	0	1
Greater Striped Swallow	*Hirundo cucullata*	GrStSw	0	1	1	1	1
Green Wood-Hoopoe	*Phoeniculus purpureus*	GrWo	0	1	0	0	1

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Green-winged Pytilia	*Pytilia melba*	GrPy	0	1	1	1	1
Grey Go-away-bird	*Corythaixoides concolor*	GrGo	1	1	1	1	1
Grey-backed Camaroptera	*Camaroptera brevicaudata*	GrCa	0	0	0	1	1
Grey-backed Cisticola	*Cisticola subruficapilla*	GrCi	0	1	0	0	0
Grey-backed Sparrowlark	*Eremopterix verticalis*	GrSpL	1	1	1	1	1
Grey-headed Kingfisher	*Halcyon leucocephala*	GrKi	0	0	0	1	1
Groundscraper Thrush	*Psophocichla litsitsirupa*	GrTh	0	1	1	1	1
Hamerkop	*Scopus umbretta*	Ha	0	0	0	1	0
Harlequin Quail	*Coturnix delegorguei*	HaQu	0	0	0	0	1
Helmeted Guineafowl	*Numdia meleagris*	HeGu	0	1	1	1	1
House Sparrow	*Passer domesticus*	HoSp	0	1	0	0	1
Icterine Warbler	*Hippolais icterina*	IcWa	1	1	1	1	1
Jacobin Cuckoo	*Clamator jacobinus*	JaCu	0	1	0	0	1
Kalahari Scrub-Robin	*Cercotrichas paena*	KalSR	1	1	1	1	1
Karoo Long-billed Lark	*Certhilauda subcoronata*	KaLoLa	1	1	1	1	0
Karoo Scrub-Robin	*Cercotrichas coryphoeus*	KarSR	0	1	1	0	1
Klaas's Cuckoo	*Chrysococcyx klaas*	KlCu	1	0	1	1	0
Kori Bustard	*Ardeotis kori*	KoBu	0	1	1	1	1
Kurrichane Buttonquail	*Turnix sylvaticus*	KuBu	0	0	0	1	0
Lappet-faced Vulture	*Aegypius tracheliotus*	LaVu	0	1	1	1	1
Lark-like Bunting	*Emberiza impetuani*	LaBu	1	1	1	1	1
Laughing Dove	*Streptopelia senegalensis*	LaDo	1	1	1	1	1
Lesser Grey Shrike	*Lanius minor*	LeGrSh	1	1	1	1	1
Lesser Kestrel	*Falco naumanni*	LeKe	0	0	1	0	1
Lesser Masked-Weaver	*Ploceus intermedius*	LeMa	0	0	1	1	1
Lilac-breasted Roller	*Coracias caudatus*	LiRo	1	0	1	1	1
Little Grebe	*Tachybaptus ruficollis*	LiGr	0	0	0	1	0
Little Swift	*Apus affinis*	LiSw	1	1	1	1	1
Long-billed Crombec	*Sylvietta rufescens*	LoCr	1	1	1	1	1
Long-billed Pipit	*Anthus similis*	LoPi	1	1	1	0	1
Long-tailed Paradise-Whydah	*Vidua paradisaea*	LoPa	0	0	0	1	1
Ludwig's Bustard	*Neotis ludwigii*	LuBu	0	0	1	0	0
Marico Flycatcher	*Bradornis mariquensis*	MaFl	1	1	1	1	1
Marico Sunbird	*Cinnyris mariquensis*	MaSu	0	0	0	1	1
Monotonous Lark	*Mirafra passerina*	MoLa	0	1	1	1	0
Monteiro's Hornbill	*Tockus monteiri*	MoHo	1	0	0	1	0
Mountain Wheatear	*Oenanthe monticola*	MoWh	1	0	0	0	0
Namaqua Dove	*Oena capensis*	NaDo	1	1	1	1	1
Namaqua Sandgrouse	*Pterocles namaqua*	NaSa	1	1	1	1	1
Northern Black Korhaan	*Eupodotis afraoides*	NoBlKo	0	1	1	1	1
Orange River Francolin	*Scleroptila levaillantoides*	OrRiFr	0	0	0	1	1
Pale-winged Starling	*Onychognathus nabouroup*	PaSt	1	1	1	1	0
Pearl-breasted Swallow	*Hirundo dimidiata*	PeSw	0	1	1	1	1

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Pearl-spotted Owlet	*Glaucidium perlatum*	PeOw	0	1	0	1	1
Plain-backed Pipit	*Anthus leucophrys*	PlPi	0	1	0	0	0
Pririt Batis	*Batis pritit*	PrBa	1	1	1	1	1
Purple Roller	*Coracias naevia*	PuRo	1	0	1	1	1
Rattling Cisticola	*Cisticola chiniana*	RaCi	1	1	1	1	1
Red-backed Shrike	*Lanius collurio*	ReSh	1	1	1	1	1
Red-billed Buffalo-Weaver	*Bubalornis niger*	ReBu	0	1	1	1	1
Red-billed Hornbill	*Tockus erythorhynchus*	ReHo	0	0	0	0	1
Red-billed Quelea	*Quelea quelea*	ReQu	0	0	1	1	1
Red-billed Spurfowl	*Pternistes adspersus*	ReSp	1	1	1	1	1
Red-billed Teal	*Anas erythrorhyncha*	ReTe	0	0	0	0	1
Red-breasted Swallow	*Hirundo semirufa*	ReSw	0	0	0	1	1
Red-crested Korhaan	*Eupodotis ruficrista*	ReKo	1	1	1	1	1
Red-faced Mousebird	*Urocolius indicus*	ReMo	1	1	1	1	0
Red-footed Falcon	*Falco vespertinus*	ReFa	0	1	1	0	1
Red-headed Finch	*Amadina erythrocephala*	ReFi	1	0	1	1	1
Rock Kestrel	*Falco [tinnunculus] rupicolis*	RoKe	1	1	1	1	1
Rock Martin	*Hirundo fuligula*	RoMa	1	1	1	1	1
Rockrunner	*Achaetops pycnopygius*	Ro	0	0	1	1	0
Rosy-faced Lovebird	*Agapornis roseicollis*	RoLo	1	1	1	0	0
Rufous-eared Warbler	*Malcorus pectoralis*	RuWa	0	1	1	1	1
Rufous-naped Lark	*Mirafra africana*	RuLa	1	0	1	1	1
Ruppell's Korhaan	*Eupodotis rueppellii*	RuKo	1	0	0	0	0
Sabota Lark	*Calendulauda sabota*	SaLa	1	1	1	1	1
Scaly-feathered Finch	*Sporopipes squamifrons*	ScFi	1	1	1	1	1
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	ScSu	0	1	0	1	0
Sclater's Lark	*Spizocorys sclateri*	ScLa	0	0	0	0	1
Secretarybird	*Sagittarius serpentarius*	Se	0	0	0	1	1
Shaft-tailed Whydah	*Vidua regia*	ShWh	0	1	1	1	1
Shikra	*Accipiter badius*	Sh	0	0	0	1	0
Short-toed Rock-Thrush	*Monticola brevipes*	ShRo	1	1	1	1	1
Sociable Weaver	*Philetarius socius*	SoWe	0	1	1	0	1
South African Cliff-Swallow	*Hirundo spilodera*	SoAfCl	0	0	0	0	1
South African Shelduck	*Tadorna cana*	SoAfSh	0	1	1	1	0
Southern Grey-headed Sparrow	*Passer diffusus*	SoGrSp	1	1	1	1	1
Southern Masked-Weaver	*Ploceus velatus*	SoMa	1	1	1	1	1
Southern Pale Chanting Goshawk	*Melierax canorus*	SoPaCh	1	1	1	1	1
Southern Pied Babbler	*Turdoides bicolor*	SoPiBa	0	1	1	1	1
Southern Red Bishop	*Euplectes orix*	SoReBi	0	0	0	1	0
Southern White-crowned Shrike	*Eurocephalus anguitimens*	SoWhSh	0	0	0	0	1
Southern Yellow-billed Hornbill	*Tockus leucomelas*	SoYeHo	0	0	0	1	1
Speckled Pigeon	*Columba guinea*	SpPi	1	1	0	0	0
Spike-heeled Lark	*Chersomanes albofasciata*	SpLa	0	1	1	1	1

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Spotted Eagle-Owl	*Bubo africanus*	SpEa	1	0	0	0	0
Spotted Flycatcher	*Muscicapa striata*	SpFl	1	1	1	1	1
Stark's Lark	*Spizocorys starki*	StLa	0	0	1	0	1
Steppe Buzzard	*Buteo vulpinus*	StBu	0	1	1	0	1
Steppe Eagle	*Aquila nipalensis*	StEa	1	0	0	0	0
Swallow-tailed Bee-eater	*Merops hirundineus*	SwBe	1	1	1	1	1
Tawny Eagle	*Aquila rapax*	TaEa	0	1	1	0	1
Temminck's Courser	*Cursorius temminckii*	TeCo	0	0	1	0	0
Three-banded Plover	*Charadrius tricollaris*	ThPl	0	1	0	0	0
Tractrac Chat	*Cercomela tractrac*	TrCh	1	0	0	0	0
Violet-backed Starling	*Cinnyricinclus leucogaster*	ViSt	1	0	0	0	0
Violet-eared Waxbill	*Granatina granatina*	ViWa	1	1	1	1	1
Wattled Starling	*Creatophora cinerea*	WaSt	1	1	1	1	1
White Stork	*Ciconia ciconia*	WhSt	0	0	0	0	1
White-backed Mousebird	*Colius colius*	WhMo	0	1	1	1	0
White-backed Vulture	*Gyps africanus*	WhVu	0	1	1	1	1
White-browed Sparrow-Weaver	*Plocepasser mahali*	WhSpW	1	1	1	1	1
White-rumped Swift	*Apus caffer*	WhSw	0	0	1	1	1
White-tailed Shrike	*Lanioturdus torquatus*	WhSh	1	1	1	1	1
White-throated Canary	*Serinus albogularis*	WhCa	1	1	1	1	1
White-throated Swallow	*Hirundo albigularis*	WhSw	0	0	0	1	0
Willow Warbler	*Phylloscopus trochilus*	WiWa	0	1	1	1	1
Wood Sandpiper	*Tringa glareola*	WoSa	0	1	0	0	0
Yellow Canary	*Serinus flaviventris*	YeCa	1	1	1	1	1
Yellow-bellied Eremomela	*Eremomela icteropygialis*	YeEr	1	1	1	1	1
Yellow-billed Kite	*Milvus parasitus*	YeKi	0	0	1	1	1
Yellow-crowned Bishop	*Euplectes afer*	YeBi	0	0	0	0	1
Zitting Cisticola	*Cisticola juncidis*	ZiCi	0	1	1	1	1
Totals			**89**	**124**	**132**	**152**	**151**

For the purposes of this study, abundance refers to aggregate values of observations. It is defined here as the total number of individual birds per species observed. The abundances (total number of observations) of all species observed are given in Table 4.

Table 4 Abundances of all bird species observed at the five sites

Sites are arranged left to right, from arid (west) to mesic (east). The mean annual rainfall (mm) recorded on the farm designates the site name. Common name, scientific name, the five sites, and totals are given. Values are total number of birds per species observed.

Common name	**Scientific name**	**128**	**215**	**315**	**370**	**420**	**Totals**
Abdim's Stork	Ciconia abdimii	0	0	0	0	290	290
Acacia Pied Barbet	Tricholaema leucomelas	83	5	20	8	11	127
African Black Swift	Apus barbatus	239	0	3	21	0	263

Common name	Scientific name	128	215	315	370	420	Totals
African Fish-Eagle	Haliaeetus vocifer	0	1	0	1	0	2
African Golden Oriole	Oriolus auratus	0	2	0	1	1	4
African Grey Hornbill	Tockus nasutus	2	2	0	1	0	5
African Harrier-Hawk	Polyboroides typus	0	0	0	0	1	1
African Hawk-Eagle	Aquila spilogaster	0	1	2	2	3	8
African Hoopoe	Upupa africana	2	4	7	14	3	30
African Palm-Swift	Cypsiurus parvus	0	4	15	36	18	73
African Pipit	Anthus cinnamomeus	0	4	23	13	34	74
African Quailfinch	Ortygospiza articollis	0	0	0	16	18	34
African Red-eyed Bulbul	Pycnontus nigricans	31	100	15	3	9	158
Alpine Swift	Tachymarptis melba	0	2	3	2	0	7
Amur Falcon	Falco amurensis	0	0	1	18	0	19
Ant-eating Chat	Myrmecocichla formicivora	0	0	111	71	23	205
Ashy Tit	Parus cinerascens	2	15	34	32	15	98
Augur Buzzard	Buteo augur	1	0	0	1	0	2
Banded Martin	Riparia cincta	0	0	0	0	2	2
Barn Owl	Tyto alba	1	0	0	0	0	1
Barn Swallow	Hirundo rustica	0	57	21	40	43	161
Barred Wren-Warbler	Calamonastes fasciolatus	0	15	15	37	28	95
Bearded Woodpecker	Dendropicos namaquus	0	1	1	3	4	9
Black Cuckoo	Cuculus clamosus	0	7	3	12	4	26
Black-chested Prinia	Prinia flavicans	106	54	128	211	156	655
Black-chested Snake-Eagle	Circaetus pectoralis	4	4	3	1	1	13
Black-faced Waxbill	Estrilda erythronotos	2	46	21	48	76	193
Black-headed Heron	Ardea melanocephala	0	0	0	1	0	1
Black-shouldered Kite	Elanus caeruleus	0	0	5	8	16	29
Blacksmith Lapwing	Vanellus armatus	0	0	0	5	3	8
Black-throated Canary	Serinus atrogularis	13	50	20	103	0	186
Black-winged Pratincole	Glareola nordmanni	0	0	0	0	68	68
Bradfield's Swift	Apus bradfieldi	5	2	140	9	0	156
Bronze-winged Courser	Rhinoptilus chalcopterus	0	0	1	0	0	1
Brown Snake-Eagle	Circaetus cinereus	0	0	0	1	2	3
Brown-crowned Tchagra	Tchagra australis	4	8	17	16	24	69
Brown-throated Martin	Riparia paludicola	0	0	0	1	0	1
Brubru	Nilaus afer	0	8	0	8	4	20
Buffy Pipit	Anthus vaalensis	0	0	1	0	6	7
Burchell's Sandgrouse	Pterocles burchelli	0	0	0	0	38	38
Burchell's Starling	Lamprotornis australis	0	0	0	4	2	6
Burnt-necked Eremomela	Eremomela usticollis	0	1	7	1	3	12
Cape Bunting	Emberiza capensis	2	0	0	0	0	2
Cape Clapper Lark	Mirafra apiata	0	0	0	2	16	18
Cape Crow	Corvus capensis	0	0	0	0	4	4
Cape Glossy Starling	Lamprotornis nitens	16	90	119	80	78	383

Common name	**Scientific name**	**128**	**215**	**315**	**370**	**420**	**Totals**
Cape Penduline-Tit	Anthoscopus minutus	5	28	39	72	25	169
Cape Sparrow	Passer melanurus	1	5	3	3	0	12
Cape Turtle-Dove	Streptopelia capicola	68	91	177	134	249	719
Cape Wagtail	Motacilla capensis	0	0	3	1	0	4
Capped Wheatear	Oenanthe pileata	0	0	25	40	1	66
Cardinal Woodpecker	Dendropicos fuscescens	4	1	1	6	6	18
Chat Flycatcher	Bradornis infuscatus	3	5	4	5	17	34
Chestnut Weaver	Ploceus rubiginosus	94	18	21	0	20	153
Chestnut-backed Sparrowlark	Eremopterix leucotis	0	0	1	0	2	3
Chestnut-vented Tit-Babbler	Parisoma subcaeruleum	37	68	72	61	76	314
Cinnamon-breasted Bunting	Emberiza tahapisi	4	70	0	47	0	121
Common Fiscal	Lanius collaris	7	6	2	15	18	48
Common Greenshank	Tringa nebularia	0	0	0	0	2	2
Common House-Martin	Delichon urbicum	32	1	0	2	0	35
Common Quail	Coturnix coturnix	2	3	1	6	8	20
Common Scimitarbill	Rhinopomastus cyanomelas	1	8	17	14	20	60
Common Swift	Apus apus	14	35	134	2	17	202
Common Waxbill	Estrilda astrild	0	0	2	0	0	2
Common Whitethroat	Sylvia communis	0	2	0	0	0	2
Crested Francolin	Peliperdix sephaena	0	0	0	0	1	1
Crimson-breasted Shrike	Laniarius atrococcineus	0	48	80	45	92	265
Crowned Lapwing	Vanellus coronatus	0	0	60	8	55	123
Damara Hornbill	Tockus damarensis	0	0	0	1	0	1
Desert Cisticola	Cisticola aridulus	1	36	9	44	83	173
Diderick Cuckoo	Chrysococcyx caprius	28	4	18	4	8	62
Double-banded Courser	Rhinoptilus africanus	0	0	5	0	0	5
Double-banded Sandgrouse	Pterocles bicinctus	3	0	0	0	19	22
Dusky Sunbird	Cinnyris fusca	302	49	17	9	6	383
Eastern Clapper Lark	Mirafra fasciolata	0	0	0	5	61	66
Egyptian Goose	Alopochen aegyptiacus	0	1	3	4	3	11
Eurasian Golden Oriole	Oriolus oriolus	0	1	0	0	2	3
European Bee-eater	Merops apiaster	0	0	0	7	16	23
Familiar Chat	Cercomela familiaris	68	14	3	3	0	88
Fawn-coloured Lark	Mirafra africanoides	5	24	13	7	11	60
Fork-tailed Drongo	Discrurus adsimilis	0	31	15	37	41	124
Freckled Nightjar	Camprimulgus tristigma	1	0	0	1	0	2
Gabar Goshawk	Melierax gabar	0	5	5	3	3	16
Golden-breasted Bunting	Emberiza flaviventris	0	10	7	26	4	47
Golden-tailed Woodpecker	Campethera abingoni	0	2	0	0	3	5
Great Sparrow	Passer motitensis	96	70	113	103	43	425
Great Spotted Cuckoo	Clamator glandarius	0	0	0	5	1	6
Great White Pelican	Pelecanus onocrotalus	0	0	11	7	0	18
Greater Honeyguide	Indicator indicator	0	0	0	1	0	1

Common name	**Scientific name**	**128**	**215**	**315**	**370**	**420**	**Totals**
Greater Kestrel	Falco rupicoloides	0	0	0	0	7	7
Greater Striped Swallow	Hirundo cucullata	0	26	7	1	4	38
Green Wood-Hoopoe	Phoeniculus purpureus	0	2	0	0	5	7
Green-winged Pytilia	Pytilia melba	0	9	12	6	45	72
Grey Go-away-bird	Corythaixoides concolor	2	63	8	6	24	103
Grey-backed Camaroptera	Camaroptera brevicaudata	0	0	0	1	10	11
Grey-backed Cisticola	Cisticola subruficapilla	0	2	0	0	0	2
Grey-backed Sparrowlark	Eremopterix verticalis	18	7	40	1	630	696
Grey-headed Kingfisher	Halcyon leucocephala	0	0	0	1	4	5
Groundscraper Thrush	Psophocichla litsitsirupa	0	12	5	2	5	24
Hamerkop	Scopus umbretta	0	0	0	1	0	1
Harlequin Quail	Coturnix delegorguei	0	0	0	0	1	1
Helmeted Guineafowl	Numdia meleagris	0	2	27	68	31	128
House Sparrow	Passer domesticus	0	11	0	0	2	13
Icterine Warbler	Hippolais icterina	2	3	6	5	28	44
Jacobin Cuckoo	Clamator jacobinus	0	1	0	0	1	2
Kalahari Scrub-Robin	Cercotrichas paena	6	88	104	45	87	330
Karoo Long-billed Lark	Certhilauda subcoronata	46	6	1	1	0	54
Karoo Scrub-Robin	Cercotrichas coryphoeus	0	5	3	0	1	9
Klaas's Cuckoo	Chrysococcyx klaas	11	0	1	1	0	13
Kori Bustard	Ardeotis kori	0	3	4	1	1	9
Kurrichane Buttonquail	Turnix sylvaticus	0	0	0	3	0	3
Lappet-faced Vulture	Aegypius tracheliotus	0	1	26	15	1	43
Lark-like Bunting	Emberiza impetuani	256	130	97	27	523	1033
Laughing Dove	Streptopelia senegalensis	77	66	27	29	168	367
Lesser Grey Shrike	Lanius minor	31	23	42	18	11	125
Lesser Kestrel	Falco naumanni	0	0	2	0	7	9
Lesser Masked-Weaver	Ploceus intermedius	0	0	3	1	3	7
Lilac-breasted Roller	Coracias caudatus	1	0	3	3	5	12
Little Grebe	Tachybaptus ruficollis	0	0	0	4	0	4
Little Swift	Apus affinis	4	68	111	10	22	215
Long-billed Crombec	Sylvietta rufescens	3	2	4	4	4	17
Long-billed Pipit	Anthus similis	2	8	1	0	1	12
Long-tailed Paradise-Whydah	Vidua paradisaea	0	0	0	1	18	19
Ludwig's Bustard	Neotis ludwigii	0	0	8	0	0	8
Marico Flycatcher	Bradornis mariquensis	3	29	77	53	34	196
Marico Sunbird	Cinnyris mariquensis	0	0	0	1	1	2
Monotonous Lark	Mirafra passerina	0	15	3	4	0	22
Monteiro's Hornbill	Tockus monteiri	12	0	0	22	0	34
Mountain Wheatear	Oenanthe monticola	55	0	0	0	0	55
Namaqua Dove	Oena capensis	19	40	38	34	84	215
Namaqua Sandgrouse	Pterocles namaqua	877	110	58	46	115	1206
Northern Black Korhaan	Eupodotis afraoides	0	16	36	36	39	127

Common name	**Scientific name**	**128**	**215**	**315**	**370**	**420**	**Totals**
Orange River Francolin	Scleroptila levaillantoides	0	0	0	8	6	14
Pale-winged Starling	Onychognathus nabouroup	45	22	4	4	0	75
Pearl-breasted Swallow	Hirundo dimidiata	0	3	1	24	7	35
Pearl-spotted Owlet	Glaucidium perlatum	0	1	0	2	8	11
Plain-backed Pipit	Anthus leucophrys	0	1	0	0	0	1
Pririt Batis	Batis pritit	22	27	32	19	23	123
Purple Roller	Coracias naevia	13	0	1	1	2	17
Rattling Cisticola	Cisticola chiniana	1	7	25	81	43	157
Red-backed Shrike	Lanius collurio	3	7	3	1	36	50
Red-billed Buffalo-Weaver	Bubalornis niger	0	2	4	2	7	15
Red-billed Hornbill	Tockus erythorhynchus	0	0	0	0	1	1
Red-billed Quelea	Quelea quelea	0	0	311	37	4413	4761
Red-billed Spurfowl	Pternistes adspersus	1	46	24	7	44	122
Red-billed Teal	Anas erythrorhyncha	0	0	0	0	82	82
Red-breasted Swallow	Hirundo semirufa	0	0	0	1	4	5
Red-crested Korhaan	Eupodotis ruficrista	1	55	39	36	28	159
Red-faced Mousebird	Urocolius indicus	2	2	3	1	0	8
Red-footed Falcon	Falco vespertinus	0	10	1	0	2	13
Red-headed Finch	Amadina erythrocephala	30	0	54	78	34	196
Rock Kestrel	Falco [tinnunculus] rupicolis	13	2	5	1	3	24
Rock Martin	Hirundo fuligula	148	104	29	56	11	348
Rockrunner	Achaetops pycnopygius	0	0	1	5	0	6
Rosy-faced Lovebird	Agapornis roseicollis	70	52	48	0	0	170
Rufous-eared Warbler	Malcorus pectoralis	0	17	3	8	8	36
Rufous-naped Lark	Mirafra africana	1	0	23	70	16	110
Ruppell's Korhaan	Eupodotis rueppellii	17	0	0	0	0	17
Sabota Lark	Calendulauda sabota	200	105	111	87	59	562
Scaly-feathered Finch	Sporopipes squamifrons	6	86	245	495	401	1233
Scarlet-chested Sunbird	Chalcomitra senegalensis	0	6	0	1	0	7
Sclater's Lark	Spizocorys sclateri	0	0	0	0	21	21
Secretarybird	Sagittarius serpentarius	0	0	0	1	1	2
Shaft-tailed Whydah	Vidua regia	0	9	11	22	35	77
Shikra	Accipiter badius	0	0	0	1	0	1
Short-toed Rock-Thrush	Monticola brevipes	15	10	9	5	1	40
Sociable Weaver	Philetarius socius	0	5	577	0	2	584
South African Cliff-Swallow	Hirundo spilodera	0	0	0	0	10	10
South African Shelduck	Tadorna cana	0	2	1	1	0	4
Southern Grey-headed Sparrow	Passer diffusus	5	77	118	29	63	292
Southern Masked-Weaver	Ploceus velatus	12	38	208	86	91	435
Southern Pale Chanting Goshawk	Melierax canorus	3	6	12	18	12	51
Southern Pied Babbler	Turdoides bicolor	0	24	26	7	34	91
Southern Red Bishop	Euplectes orix	0	0	0	2	0	2
Southern White-crowned Shrike	Eurocephalus anguitimens	0	0	0	0	3	3

Common name	**Scientific name**	**128**	**215**	**315**	**370**	**420**	**Totals**
Southern Yellow-billed Hornbill	Tockus leucomelas	0	0	0	5	25	30
Speckled Pigeon	Columba guinea	13	2	0	0	0	15
Spike-heeled Lark	Chersomanes albofasciata	0	13	72	20	15	120
Spotted Eagle-Owl	Bubo africanus	2	0	0	0	0	2
Spotted Flycatcher	Muscicapa striata	33	8	1	13	8	63
Stark's Lark	Spizocorys starki	0	0	2	0	1	3
Steppe Buzzard	Buteo vulpinus	0	1	1	0	4	6
Steppe Eagle	Aquila nipalensis	2	0	0	0	0	2
Swallow-tailed Bee-eater	Merops hirundineus	2	19	36	25	36	118
Tawny Eagle	Aquila rapax	0	2	1	0	1	4
Temminck's Courser	Cursorius temminckii	0	0	3	0	0	3
Three-banded Plover	Charadrius tricollaris	0	1	0	0	0	1
Tractrac Chat	Cercomela tractrac	1	0	0	0	0	1
Violet-backed Starling	Cinnyricinclus leucogaster	8	0	0	0	0	8
Violet-eared Waxbill	Granatina granatina	11	41	26	101	23	202
Wattled Starling	Creatophora cinerea	11	75	103	28	14	231
White Stork	Ciconia ciconia	0	0	0	0	1	1
White-backed Mousebird	Colius colius	0	1	2	6	0	9
White-backed Vulture	Gyps africanus	0	9	35	68	12	124
White-browed Sparrow-Weaver	Plocepasser mahali	1	8	107	177	189	482
White-rumped Swift	Apus caffer	0	0	5	6	3	14
White-tailed Shrike	Lanioturdus torquatus	4	9	6	4	1	24
White-throated Canary	Serinus albogularis	77	7	2	2	7	95
White-throated Swallow	Hirundo albigularis	0	0	0	3	0	3
Willow Warbler	Phylloscopus trochilus	0	3	5	1	3	12
Wood Sandpiper	Tringa glareola	0	1	0	0	0	1
Yellow Canary	Serinus flaviventris	1	7	18	5	16	47
Yellow-bellied Eremomela	Eremomela icteropygialis	11	13	23	16	18	81
Yellow-billed Kite	Milvus parasitus	0	0	3	2	2	7
Yellow-crowned Bishop	Euplectes afer	0	0	0	0	13	13
Zitting Cisticola	Cisticola juncidis	0	12	20	18	72	122
Totals		**3,499**	**2,825**	**4,751**	**3,707**	**9,814**	**24,596**

4.5.1 Species richness across the aridity gradient: all observed bird species

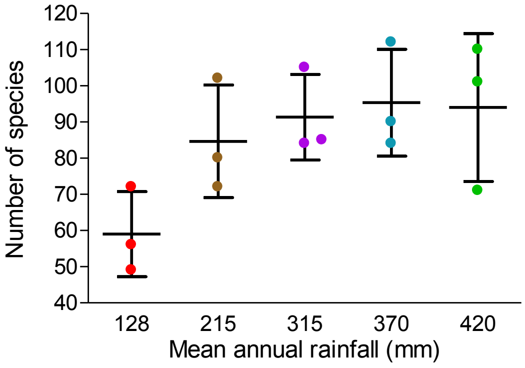

Figure 22 Species richness of all observed bird species across the aridity gradient. Points are number of species per habitat type. Means of habitat types and SD (lines) are shown.

Aggregated values, combined from all observations over three years, were used to create the graph in Figure 22. The total number of species observed at each sample unit was plotted against site to investigate trends across the aridity gradient.

4.5.2 Species richness by habitat types: all observed bird species

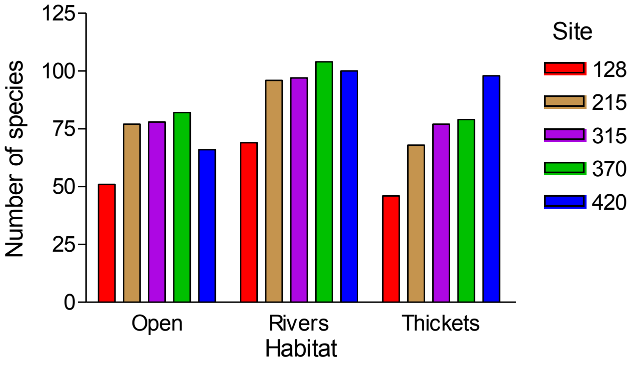

Figure 23 Species richness by habitat type for all observed species. The five sites are indicated by colour.

Aggregated values, combined from all observations over three years, were used to create the bar graph in figure 23. The total number of species observed at each sample unit was plotted against habitat type to investigate trends in the habitats.

Figure 22 and Figure 23 were obtained from the same data. The two graphs illustrate the effect of two different factors on the distribution of species; rainfall and habitat type. There was in increase in mean species richness with increasing rainfall (Figure 22). Within each habitat type, there was an increase in species richness with increasing rainfall, except for a decrease in Open at 420 and a slight decrease in Rivers at 420 Figure 23)

Trends across the aridity gradient (Figure 22) suggest that species richness remained constant except for the most arid site, 128, where species numbers were reduced. Means and SD's for the sites were: 128 (mean = 59, SD = 12), 215 (mean = 85, SD = 16), 315 (mean = 92, SD = 12), 370 (mean = 95, SD = 15) and 420 (mean = 94, SD = 20). Species richness at 128 (Figure 22) were compared with species richness at the other sites (Repeated measures 1-way ANOVA, Bonferroni post-test): $p < 0.05$ when comparing 128 with 215 and 315, and $p < 0.01$ when comparing 128 with 370 and 420.

The role of habitat type was significant at 420 (Figure 23), where open habitats had fewer species than the other sites except 128. Comparing the habitat types at 420, a significant difference was shown between rivers and open (Repeated measures 1-way ANOVA, Bonferroni post-test $p < 0.05$). All other pairings of habitat type and site showed no significant difference (2-way ANOVA, Bonferroni post-test $p > 0.05$) (Figure 23). A 2-way ANOVA for Figure 23 found significant differences in species numbers across the aridity gradient with rainfall explaining 54% and habitat type 35% of the variance ($p = 0.0032$ for rainfall, and $p = 0.0029$ for habitat).

4.5.3 Abundance across the aridity gradient: all observed bird species

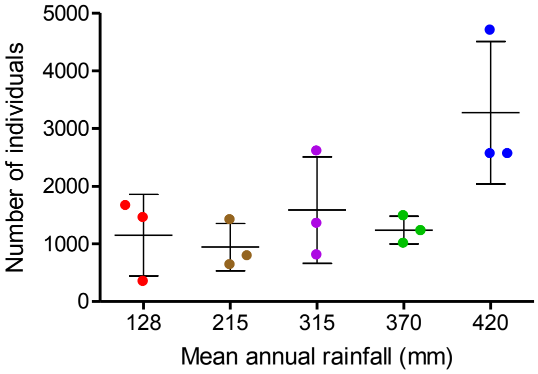

Figure 24 Abundance of all observed species across the aridity gradient. Points are number of individuals per habitat type. Means and SD (lines) are shown.

For the purposes of this study, abundance is defined as the total number of individuals observed. Abundances per habitat type from all observations over the three years were used to create a scatterplot of the means (Figure 24) to investigate trends across the aridity gradient.

There was a statistically significant difference (1-way ANOVA, $p < 0.05$) in the number of observations across the aridity gradient (Figure 24), when comparing 128 (mean = 1166, SD = 717) with 215 (mean = 942, SD = 411), 315 (mean = 1584, SD = 922), 370 (mean = 1236, SD = 240) and 420 (mean = 3271, SD = 1236). Neuman-Keuls post-test showed significant differences between 420 and the other four sites (1-way ANOVA, $p < 0.05$).

4.5.4 Diversity: all observed bird species across the aridity gradient and habitat type

Aggregated values, combined from all observations over three years, were used to do a row-column summary on PC-ORD 6.0. The main matrix consisted of species (columns) and sample units (rows). Values for the matrix were the total number of individuals of each species observed at each sample unit. Results of the row-column summary of 15 sample units and 206 species gave the Shannon diversity index (H) values for each site. These values were used to create Figure 25. Diversity at each sample unit was plotted against site to investigate trends across the aridity gradient.

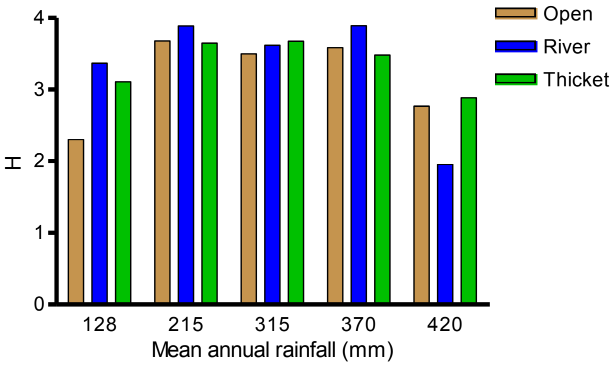

Figure 25 Diversity (Shannon Diversity Index, H) of all observed species across the aridity gradient

There was a significant difference (2-way ANOVA, $p < 0.05$) in diversity across the aridity gradient (rainfall explained 73% of variance) (Figure 25). No significant difference was found in diversity across the different habitat types (2-way ANOVA, $p = 0.68$, habitat type explained 3% of variance). There was a significant difference (Bonferroni post-test $p < 0.05$) when comparing river habitat of 420 with the river habitat of 215, 315 and 370. Together with comparisons of species richness (Figure 23 and **Error! Reference source not found.**) and abundance (Figure 24 and Figure 29), diversity measures assisted in establishing whether outliers should be excluded from analyses.

4.5.5 Non-contributive bird species

Species and groups of species considered for exclusion on the grounds of not contributing towards interpretation were:

- All species occurring in fewer than 5% of the transects
- All species with fewer than 5 records
- Species, for various other reasons, not contributing towards interpretation

The species in the first two bullet points were not excluded because they represent birds that were considered to play important roles in the functioning of ecosystems even though they occur in low numbers throughout their range. They are mainly raptors, as well as breeding migrants (e.g. cuckoos) that utilise resources and contribute to the avian diversity of the area.

The 18 species that were considered non-contributive are given in Table 5. Listed in the table are the common names and the reasons why each species or group of species were excluded.

Table 5 Species excluded from analyses and motivations for their exclusion

Common name	Motivation for exclusion
Abdim's Stork	290 individuals observed at one observation only, site 420. Non-breeding migrant, moves in response to local conditions.
African Black Swift	Swifts. Migrants, never on ground and they don't use resources on site.
African Palm-Swift	
Alpine Swift	
Bradfield's Swift	
Common Swift	
Little Swift	
White-rumped Swift	
Common Greenshank	Water and wading species that rely on bodies of water for completion of their life cycle. Present only when standing water available in pans & depressions and these appear sporadically and are short-lived. Numbers of migrants in the desert are low and probably insignificant for ecosystem functioning although some species, including waders, move through the desert on their way to better watered habitats (Dean, 2004).
Egyptian Goose	
Little Grebe	
Red-billed Teal	
South African Shelduck	
Wood Sandpiper	
Namaqua Sandgrouse	A true desert species that occurs in all four desert biomes of Southern Africa (Lovegrove, 1993). Although it uses resources on the ground, in wilderness conditions it flies up to 60 km daily for water. All five sites are working farms providing man-made water resources closer than would be available in the wild. Most observations were of birds in the air. At site 128 it constitutes 25% of the site total abundance (4% at 215, and 1 % at 315, 370 and 420 each).
Red-billed Quelea	Migrant, its presence occasional and independent of local conditions. Excluded mainly because of the high number of individuals observed in a single survey: 4413 at site 420, constituting 45% of the total number of individuals at 420.
Great White Pelican	Observed flying over transects, flying birds contribute little to ecological information.
White Stork	Only one individual observed. Non-breeding migrant, moves in response to local conditions.

Trends in bird diversity with all observed species included (Figure 25) were compared with trends in bird diversity (Figure 32) after removing 18 non-contributive species (Table 5). Comparing Figure 25 and Figure 32, 2-way ANOVA analysis showed the following results:
For Figure 25, rainfall explained 73% and habitat type 3% of variance. For Figure 32, rainfall explained 42% of variance and habitat type 31%. For Figure 25, $p < 0.05$, and for Figure 32, $p < 0.1$. The 2-way ANOVA, Bonferroni post-test for Figure 25 showed $p < 0.05$ when comparing river of 420 with the rivers of 215, 315 and 370. For Figure 32, the Bonferroni post-test showed $p > 0.05$ for all pairings.

Subsequent analyses used data from the remaining 188 species.

4.6 Analyses after removing non-contributive bird species

4.6.1 Species richness

The 188 bird species used for analyses are listed in Table 6.

Table 6 Bird species presence/absence at the five sites after exclusion of non-contributive species

Sites are arranged left to right, from arid (west) to mesic (east). The mean annual rainfall (mm) recorded on the farm designates the site name. Common name, scientific name, abbreviated name, and presence/absence at each of the five sites are given. 1 indicates presence, 0 indicates absence.

Common name	Scientific name	Abbreviated name	128	215	315	370	420
Acacia Pied Barbet	*Tricholaema leucomelas*	AcPiBa	1	1	1	1	1
African Fish-Eagle	*Haliaeetus vocifer*	AfFi	0	1	0	1	0
African Golden Oriole	*Oriolus auratus*	AfGoOr	0	1	0	1	1
African Grey Hornbill	*Tockus nasutus*	AfGrHo	1	1	0	1	0
African Harrier-Hawk	*Polyboroides typus*	AfHa	0	0	0	0	1
African Hawk-Eagle	*Aquila spilogaster*	AfHaE	0	1	1	1	1
African Hoopoe	*Upupa africana*	AfHo	1	1	1	1	1
African Pipit	*Anthus cinnamomeus*	AfPi	0	1	1	1	1
African Quailfinch	*Ortygospiza articollis*	AfQu	0	0	0	1	1
African Red-eyed Bulbul	*Pycnontus nigricans*	AfReBu	1	1	1	1	1
Amur Falcon	*Falco amurensis*	AmFa	0	0	1	1	0
Ant-eating Chat	*Myrmecocichla formicivora*	AnCh	0	0	1	1	1
Ashy Tit	*Parus cinerascens*	AsTi	1	1	1	1	1
Augur Buzzard	*Buteo augur*	AuBu	1	0	0	1	0
Banded Martin	*Riparia cincta*	BaMa	0	0	0	0	1
Barn Owl	*Tyto alba*	BaOw	1	0	0	0	0
Barn Swallow	*Hirundo rustica*	BaSw	0	1	1	1	1
Barred Wren-Warbler	*Calamonastes fasciolatus*	BaWr	0	1	1	1	1
Bearded Woodpecker	*Dendropicos namaquus*	BeWo	0	1	1	1	1
Black Cuckoo	*Cuculus clamosus*	BlCu	0	1	1	1	1

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Black-chested Prinia	*Prinia flavicans*	BlPri	1	1	1	1	1
Black-chested Snake-Eagle	*Circaetus pectoralis*	BlSn	1	1	1	1	1
Black-faced Waxbill	*Estrilda erythronotos*	BlWa	1	1	1	1	1
Black-headed Heron	*Ardea melanocephala*	BlHe	0	0	0	1	0
Black-shouldered Kite	*Elanus caeruleus*	BlKi	0	0	1	1	1
Blacksmith Lapwing	*Vanellus armatus*	BlLa	0	0	0	1	1
Black-throated Canary	*Serinus atrogularis*	BlCa	1	1	1	1	0
Black-winged Pratincole	*Glareola nordmanni*	BlPr	0	0	0	0	1
Bronze-winged Courser	*Rhinoptilus chalcopterus*	BrCo	0	0	1	0	0
Brown Snake-Eagle	*Circaetus cinereus*	BrSn	0	0	0	1	1
Brown-crowned Tchagra	*Tchagra australis*	BrTc	1	1	1	1	1
Brown-throated Martin	*Riparia paludicola*	BrMa	0	0	0	1	0
Brubru	*Nilaus afer*	Br	0	1	0	1	1
Buffy Pipit	*Anthus vaalensis*	BuPi	0	0	1	0	1
Burchell's Sandgrouse	*Pterocles burchelli*	BuSa	0	0	0	0	1
Burchell's Starling	*Lamprotornis australis*	BuSt	0	0	0	1	1
Burnt-necked Eremomela	*Eremomela usticollis*	BuEr	0	1	1	1	1
Cape Bunting	*Emberiza capensis*	CaBu	1	0	0	0	0
Cape Clapper Lark	*Mirafra apiata*	CaClLa	0	0	0	1	1
Cape Crow	*Corvus capensis*	CaCr	0	0	0	0	1
Cape Glossy Starling	*Lamprotornis nitens*	CaGlSt	1	1	1	1	1
Cape Penduline-Tit	*Anthoscopus minutus*	CaPe	1	1	1	1	1
Cape Sparrow	*Passer melanurus*	CaSp	1	1	1	1	0
Cape Turtle-Dove	*Streptopelia capicola*	CaTu	1	1	1	1	1
Cape Wagtail	*Motacilla capensis*	CaWa	0	0	1	1	0
Capped Wheatear	*Oenanthe pileata*	CaWh	0	0	1	1	1
Cardinal Woodpecker	*Dendropicos fuscescens*	CaWo	1	1	1	1	1
Chat Flycatcher	*Bradornis infuscatus*	ChFl	1	1	1	1	1
Chestnut Weaver	*Ploceus rubiginosus*	ChWe	1	1	1	0	1
Chestnut-backed Sparrowlark	*Eremopterix leucotis*	ChSp	0	0	1	0	1
Chestnut-vented Tit-Babbler	*Parisoma subcaeruleum*	ChTi	1	1	1	1	1
Cinnamon-breasted Bunting	*Emberiza tahapisi*	CiBu	1	1	0	1	0
Common Fiscal	*Lanius collaris*	CoFi	1	1	1	1	1
Common House-Martin	*Delichon urbicum*	CoHo	1	1	0	1	0
Common Quail	*Coturnix coturnix*	CoQu	1	1	1	1	1
Common Scimitarbill	*Rhinopomastus cyanomelas*	CoSc	1	1	1	1	1
Common Waxbill	*Estrilda astrild*	CoWa	0	0	1	0	0
Common Whitethroat	*Sylvia communis*	CoWh	0	1	0	0	0
Crested Francolin	*Peliperdix sephaena*	CrFr	0	0	0	0	1
Crimson-breasted Shrike	*Laniarius atrococcineus*	CrSh	0	1	1	1	1
Crowned Lapwing	*Vanellus coronatus*	CrLa	0	0	1	1	1
Damara Hornbill	*Tockus damarensis*	DaHo	0	0	0	1	0
Desert Cisticola	*Cisticola aridulus*	DeCi	1	1	1	1	1
Diderick Cuckoo	*Chrysococcyx caprius*	DiCu	1	1	1	1	1
Double-banded Courser	*Rhinoptilus africanus*	DoCo	0	0	1	0	0

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Double-banded Sandgrouse	*Pterocles bicinctus*	DoSa	1	0	0	0	1
Dusky Sunbird	*Cinnyris fusca*	DuSu	1	1	1	1	1
Eastern Clapper Lark	*Mirafra fasciolata*	EaClLa	0	0	0	1	1
Eurasian Golden Oriole	*Oriolus oriolus*	EuGoOr	0	1	0	0	1
European Bee-eater	*Merops apiaster*	EuBe	0	0	0	1	1
Familiar Chat	*Cercomela familiaris*	FaCh	1	1	1	1	0
Fawn-coloured Lark	*Mirafra africanoides*	FaLa	1	1	1	1	1
Fork-tailed Drongo	*Discrurus adsimilis*	FoDr	0	1	1	1	1
Freckled Nightjar	*Camprimulgus tristigma*	FrNi	1	0	0	1	0
Gabar Goshawk	*Melierax gabar*	GaGo	0	1	1	1	1
Golden-breasted Bunting	*Emberiza flaviventris*	GoBu	0	1	1	1	1
Golden-tailed Woodpecker	*Campethera abingoni*	GoWo	0	1	0	0	1
Great Sparrow	*Passer motitensis*	GrSp	1	1	1	1	1
Great Spotted Cuckoo	*Clamator glandarius*	GrSpCu	0	0	0	1	1
Greater Honeyguide	*Indicator indicator*	GrHo	0	0	0	1	0
Greater Kestrel	*Falco rupicoloides*	GrKe	0	0	0	0	1
Greater Striped Swallow	*Hirundo cucullata*	GrStSw	0	1	1	1	1
Green Wood-Hoopoe	*Phoeniculus purpureus*	GrWo	0	1	0	0	1
Green-winged Pytilia	*Pytilia melba*	GrPy	0	1	1	1	1
Grey Go-away-bird	*Corythaixoides concolor*	GrGo	1	1	1	1	1
Grey-backed Camaroptera	*Camaroptera brevicaudata*	GrCa	0	0	0	1	1
Grey-backed Cisticola	*Cisticola subruficapilla*	GrCi	0	1	0	0	0
Grey-backed Sparrowlark	*Eremopterix verticalis*	GrSpL	1	1	1	1	1
Grey-headed Kingfisher	*Halcyon leucocephala*	GrKi	0	0	0	1	1
Groundscraper Thrush	*Psophocichla litsitsirupa*	GrTh	0	1	1	1	1
Hamerkop	*Scopus umbretta*	Ha	0	0	0	1	0
Harlequin Quail	*Coturnix delegorguei*	HaQu	0	0	0	0	1
Helmeted Guineafowl	*Numdia meleagris*	HeGu	0	1	1	1	1
House Sparrow	*Passer domesticus*	HoSp	0	1	0	0	1
Icterine Warbler	*Hippolais icterina*	IcWa	1	1	1	1	1
Jacobin Cuckoo	*Clamator jacobinus*	JaCu	0	1	0	0	1
Kalahari Scrub-Robin	*Cercotrichas paena*	KaISR	1	1	1	1	1
Karoo Long-billed Lark	*Certhilauda subcoronata*	KaLoLa	1	1	1	1	0
Karoo Scrub-Robin	*Cercotrichas coryphoeus*	KarSR	0	1	1	0	1
Klaas's Cuckoo	*Chrysococcyx klaas*	KlCu	1	0	1	1	0
Kori Bustard	*Ardeotis kori*	KoBu	0	1	1	1	1
Kurrichane Buttonquail	*Turnix sylvaticus*	KuBu	0	0	0	1	0
Lappet-faced Vulture	*Aegypius tracheliotus*	LaVu	0	1	1	1	1
Lark-like Bunting	*Emberiza impetuani*	LaBu	1	1	1	1	1
Laughing Dove	*Streptopelia senegalensis*	LaDo	1	1	1	1	1
Lesser Grey Shrike	*Lanius minor*	LeGrSh	1	1	1	1	1
Lesser Kestrel	*Falco naumanni*	LeKe	0	0	1	0	1
Lesser Masked-Weaver	*Ploceus intermedius*	LeMa	0	0	1	1	1
Lilac-breasted Roller	*Coracias caudatus*	LiRo	1	0	1	1	1
Long-billed Crombec	*Sylvietta rufescens*	LoCr	1	1	1	1	1

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Long-billed Pipit	*Anthus similis*	LoPi	1	1	1	0	1
Long-tailed Paradise-Whydah	*Vidua paradisaea*	LoPa	0	0	0	1	1
Ludwig's Bustard	*Neotis ludwigii*	LuBu	0	0	1	0	0
Marico Flycatcher	*Bradornis mariquensis*	MaFl	1	1	1	1	1
Marico Sunbird	*Cinnyris mariquensis*	MaSu	0	0	0	1	1
Monotonous Lark	*Mirafra passerina*	MoLa	0	1	1	1	0
Monteiro's Hornbill	*Tockus monteiri*	MoHo	1	0	0	1	0
Mountain Wheatear	*Oenanthe monticola*	MoWh	1	0	0	0	0
Namaqua Dove	*Oena capensis*	NaDo	1	1	1	1	1
Northern Black Korhaan	*Eupodotis afraoides*	NoBlKo	0	1	1	1	1
Orange River Francolin	*Scleroptila levaillantoides*	OrRiFr	0	0	0	1	1
Pale-winged Starling	*Onychognathus nabouroup*	PaSt	1	1	1	1	0
Pearl-breasted Swallow	*Hirundo dimidiata*	PeSw	0	1	1	1	1
Pearl-spotted Owlet	*Glaucidium perlatum*	PeOw	0	1	0	1	1
Plain-backed Pipit	*Anthus leucophrys*	PlPi	0	1	0	0	0
Pririt Batis	*Batis pritit*	PrBa	1	1	1	1	1
Purple Roller	*Coracias naevia*	PuRo	1	0	1	1	1
Rattling Cisticola	*Cisticola chiniana*	RaCi	1	1	1	1	1
Red-backed Shrike	*Lanius collurio*	ReSh	1	1	1	1	1
Red-billed Buffalo-Weaver	*Bubalornis niger*	ReBu	0	1	1	1	1
Red-billed Hornbill	*Tockus erythorhynchus*	ReHo	0	0	0	0	1
Red-billed Spurfowl	*Pternistes adspersus*	ReSp	1	1	1	1	1
Red-breasted Swallow	*Hirundo semirufa*	ReSw	0	0	0	1	1
Red-crested Korhaan	*Eupodotis ruficrista*	ReKo	1	1	1	1	1
Red-faced Mousebird	*Urocolius indicus*	ReMo	1	1	1	1	0
Red-footed Falcon	*Falco vespertinus*	ReFa	0	1	1	0	1
Red-headed Finch	*Amadina erythrocephala*	ReFi	1	0	1	1	1
Rock Kestrel	*Falco [tinnunculus] rupicolis*	RoKe	1	1	1	1	1
Rock Martin	*Hirundo fuligula*	RoMa	1	1	1	1	1
Rockrunner	*Achaetops pycnopygius*	Ro	0	0	1	1	0
Rosy-faced Lovebird	*Agapornis roseicollis*	RoLo	1	1	1	0	0
Rufous-eared Warbler	*Malcorus pectoralis*	RuWa	0	1	1	1	1
Rufous-naped Lark	*Mirafra africana*	RuLa	1	0	1	1	1
Ruppell's Korhaan	*Eupodotis rueppellii*	RuKo	1	0	0	0	0
Sabota Lark	*Calendulauda sabota*	SaLa	1	1	1	1	1
Scaly-feathered Finch	*Sporopipes squamifrons*	ScFi	1	1	1	1	1
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	ScSu	0	1	0	1	0
Sclater's Lark	*Spizocorys sclateri*	ScLa	0	0	0	0	1
Secretarybird	*Sagittarius serpentarius*	Se	0	0	0	1	1
Shaft-tailed Whydah	*Vidua regia*	ShWh	0	1	1	1	1
Shikra	*Accipiter badius*	Sh	0	0	0	1	0
Short-toed Rock-Thrush	*Monticola brevipes*	ShRo	1	1	1	1	1
Sociable Weaver	*Philetarius socius*	SoWe	0	1	1	0	1
South African Cliff-Swallow	*Hirundo spilodera*	SoAfCl	0	0	0	0	1
Southern Grey-headed Sparrow	*Passer diffusus*	SoGrSp	1	1	1	1	1

Common name	**Scientific name**	**Abbreviated name**	**128**	**215**	**315**	**370**	**420**
Southern Masked-Weaver	*Ploceus velatus*	SoMa	1	1	1	1	1
Southern Pale Chanting Goshawk	*Melierax canorus*	SoPaCh	1	1	1	1	1
Southern Pied Babbler	*Turdoides bicolor*	SoPiBa	0	1	1	1	1
Southern Red Bishop	*Euplectes orix*	SoReBi	0	0	0	1	0
Southern White-crowned Shrike	*Eurocephalus anguitimens*	SoWhSh	0	0	0	0	1
Southern Yellow-billed Hornbill	*Tockus leucomelas*	SoYeHo	0	0	0	1	1
Speckled Pigeon	*Columba guinea*	SpPi	1	1	0	0	0
Spike-heeled Lark	*Chersomanes albofasciata*	SpLa	0	1	1	1	1
Spotted Eagle-Owl	*Bubo africanus*	SpEa	1	0	0	0	0
Spotted Flycatcher	*Muscicapa striata*	SpFl	1	1	1	1	1
Stark's Lark	*Spizocorys starki*	StLa	0	0	1	0	1
Steppe Buzzard	*Buteo vulpinus*	StBu	0	1	1	0	1
Steppe Eagle	*Aquila nipalensis*	StEa	1	0	0	0	0
Swallow-tailed Bee-eater	*Merops hirundineus*	SwBe	1	1	1	1	1
Tawny Eagle	*Aquila rapax*	TaEa	0	1	1	0	1
Temminck's Courser	*Cursorius temminckii*	TeCo	0	0	1	0	0
Three-banded Plover	*Charadrius tricollaris*	ThPl	0	1	0	0	0
Tractrac Chat	*Cercomela tractrac*	TrCh	1	0	0	0	0
Violet-backed Starling	*Cinnyricinclus leucogaster*	ViSt	1	0	0	0	0
Violet-eared Waxbill	*Granatina granatina*	ViWa	1	1	1	1	1
Wattled Starling	*Creatophora cinerea*	WaSt	1	1	1	1	1
White-backed Mousebird	*Colius colius*	WhMo	0	1	1	1	0
White-backed Vulture	*Gyps africanus*	WhVu	0	1	1	1	1
White-browed Sparrow-Weaver	*Plocepasser mahali*	WhSpW	1	1	1	1	1
White-tailed Shrike	*Lanioturdus torquatus*	WhSh	1	1	1	1	1
White-throated Canary	*Serinus albogularis*	WhCa	1	1	1	1	1
White-throated Swallow	*Hirundo albigularis*	WhSw	0	0	0	1	0
Willow Warbler	*Phylloscopus trochilus*	WiWa	0	1	1	1	1
Yellow Canary	*Serinus flaviventris*	YeCa	1	1	1	1	1
Yellow-bellied Eremomela	*Eremomela icteropygialis*	YeEr	1	1	1	1	1
Yellow-billed Kite	*Milvus parasitus*	YeKi	0	0	1	1	1
Yellow-crowned Bishop	*Euplectes afer*	YeBi	0	0	0	0	1
Zitting Cisticola	*Cisticola juncidis*	ZiCi	0	1	1	1	1
Totals			**84**	**115**	**120**	**139**	**140**

Species richness by site: after exclusion of species

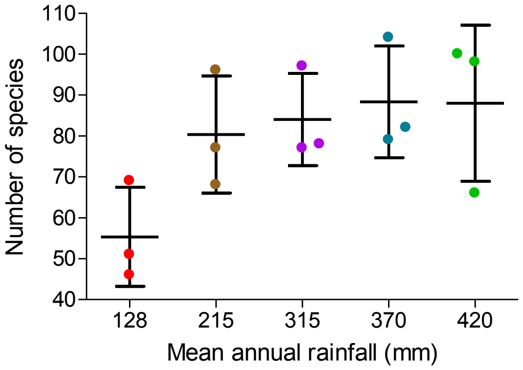

Figure 26 Species richness by site. Points are species richness per habitat type. Mean of each site and SD (lines) are shown.

Aggregated values, combined from all observations over three years (Table 6), were used to create the scatterplot in **Error! Reference source not found.**.

The number of species observed at each sample unit was plotted against site to investigate trends across the aridity gradient. Just like Figure 22, there was an increase in species richness with an increase in rainfall. A significant difference in species richness was found (1-way ANOVA, $p < 0.05$) when comparing 128 with 315, 370 and 420 (Bonferroni post-test, $p < 0.05$)

Species richness by habitat type: after exclusion of species

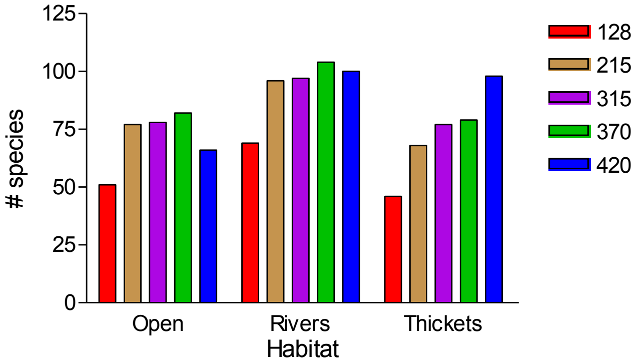

Figure 27 Species richness by habitat type.

Aggregated values, combined from all observations over three years (Table 6), were used to create the bar graph in **Error! Reference source not found.**. The total number of species observed at each sample unit was plotted against habitat type to investigate trends in the habitat types.

The trends were similar to those seen in Figure 23. Rainfall played a greater role than habitat type in explaining differences in species richness (**Error! Reference source not found.**) (2-way ANOVA, % of total variation rainfall = 52%, $p < 0.01$; habitat type = 35%, $p < 0.01$). There was a very significant difference (2-way ANOVA, Bonferroni's post-test, $p < 0.01$) when comparing species richness in open vs rivers; and a significant difference (2-way ANOVA, Bonferroni's post-test, $p < 0.05$) when comparing species richness in open vs thickets.

Although there was an increase in species numbers from arid to mesic, **Error! Reference source not found.** shows an unexpected low species richness in Open at 420, the most mesic site. Similarly, Figure 32 shows an unexpected low diversity in Open at 420, the most mesic site. Table 7 lists the species that were absent from 420 Open, but present in Open at two or more of the other sites.

Table 7 Species absent from 420 open but present in open at two or more other sites.

Common name, abbreviated name and sites are given as well as presence/absence at River and Thicket of 420. 1 indicates presence, 0 indicates absence, and asterisks indicate species whose preferred habitat is usually more structurally varied than a grass-dominated habitat.

		Open					**River**	**Thicket**
Common name	**Abbr**	**128**	**215**	**315**	**370**	**420**	**420**	**420**
Acacia Pied Barbet*	AcPiBa	1	1	1	0	0	1	1
African Hoopoe*	AfHo	0	1	1	1	0	1	1
African Red-eyed Bulbul*	AfReBu	1	1	0	0	0	1	1
Ashy Tit*	AsTi	1	1	1	1	0	1	1
Augur Buzzard	AuBu	1	0	0	1	0	0	0
Black Cuckoo*	BlCu	0	1	0	1	0	1	0
Black-chested Snake-Eagle	BlSn	1	1	0	0	0	1	0
Black-faced Waxbill	BlWa	0	1	0	1	0	1	1
Black-throated Canary	BlCa	1	1	1	1	0	0	0
Brown-crowned Tchagra*	BrTc	0	1	1	1	0	1	1
Brubru*	Br	0	1	0	1	0	1	1
Cape Penduline-Tit*	CaPe	1	1	1	1	0	1	1
Capped Wheatear*	CaWh	0	0	1	1	0	0	1
Cardinal Woodpecker	CaWo	1	0	0	1	0	1	1
Chestnut-vented Tit-Babbler	ChTi	0	1	1	1	0	1	1
Cinnamon-breasted Bunting	CiBu	1	1	0	1	0	0	0
Common Scimitarbill*	CoSc	0	1	1	0	0	1	1
Crimson-breasted Shrike*	CrSh	0	1	1	1	0	1	1
Dusky Sunbird	DuSu	1	1	1	1	0	0	1
Familiar Chat	FaCh	1	1	1	0	0	0	0
Golden-breasted Bunting	GoBu	0	1	1	0	0	1	1
Great Sparrow*	GrSp	1	1	1	1	0	1	1
Greater Striped Swallow*	GrStSw	0	1	1	0	0	1	0
Karoo Long-billed Lark	KaLoLa	1	1	0	1	0	0	0
Karoo Scrub-Robin	KarSR	0	0	0	0	0	1	0

		Open					**River**	**Thicket**
Common name	**Abbr**	**128**	**215**	**315**	**370**	**420**	**420**	**420**
Klaas's Cuckoo	KlCu	1	0	0	0	0	0	0
Kurrichane Buttonquail	KuBu	0	0	0	0	0	0	0
Laughing Dove	LaDo	1	0	1	1	0	1	1
Lesser Grey Shrike*	LeGrSh	1	1	1	1	0	1	1
Marico Flycatcher	MaFl	0	1	1	1	0	1	1
Monotonous Lark*	MoLa	0	1	1	0	0	0	0
Pale-winged Starling	PaSt	1	1	1	1	0	0	0
Pririt Batis*	PrBa	1	1	1	1	0	1	1
Red-footed Falcon	ReFa	0	1	1	0	0	1	1
Rosy-faced Lovebird	RoLo	1	1	1	0	0	0	0
Rufous-eared Warbler*	RuWa	0	1	1	1	0	0	1
Short-toed Rock-Thrush*	ShRo	1	1	1	1	0	1	0
Sociable Weaver*	SoWe	0	1	1	0	0	0	1
Southern Masked-Weaver*	SoMa	1	1	1	0	0	1	1
Violet-eared Waxbill*	ViWa	0	1	0	1	0	1	1
Wattled Starling*	WaSt	0	1	1	1	0	1	0
White-backed Vulture	WhVu	0	1	1	1	0	1	1
White-tailed Shrike*	WhSh	0	1	1	1	0	1	0
White-throated Canary*	WhCa	1	1	0	0	0	0	1

4.6.2 Abundance

For the purposes of this study, abundance is defined as the total of the number of individuals observed per species. Appendix A contains a table with abundance values for the 188 species used in analyses at each sample unit.

Abundance across the aridity gradient: after exclusion of species

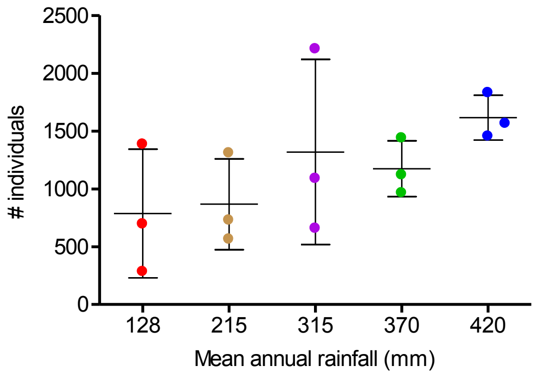

Figure 28 Abundance (number of observations) by site. Points are for habitat types. Means and SD (lines) are shown.

Abundance values, combined from all observations over three years (Table 6), were used to create Figure 28. The number of individuals of each species observed at each sample unit was plotted against site to investigate trends across the aridity gradient.

No significant difference was noted in abundance across the aridity gradient (Figure 28; 1-way ANOVA, p = 0.3) when comparing 128 (mean = 787, SD = 556), 215 (mean = 867, SD = 392), 315 (mean = 1319, SD = 802), 370 (mean = 1174, SD = 242) and 420 (mean = 1616, SD = 193). Bonferroni post-test (1-way ANOVA) indicated no significant difference in any pairing (p > 0.05 for all pairings of sites).

Abundance by habitat: after exclusion of species

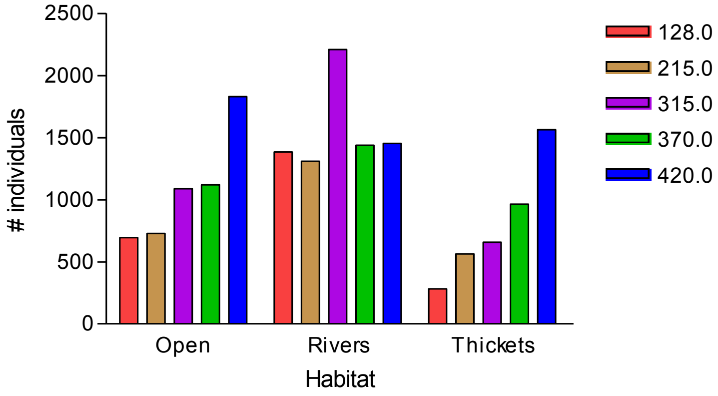

Figure 29 Abundance (number of observations) by habitat.

Aggregated values, combined from the observations over three years (Table 6), were used to create Figure 29. The number of individuals of each species observed at each sample unit was plotted against habitat to investigate trends in the habitats. Site (aridity gradient) is indicated by series.

Habitat and rainfall (Figure 29) had equal effects on the differences in abundance across the aridity gradient (2-way ANOVA, habitat = 38% and rainfall = 36% of total variation). There was a significant difference in abundance as explained by habitat (2-way ANOVA, p < 0.05) but no significant difference in abundance as explained by rainfall (2-way ANOVA, p > 0.01). When comparing the habitat types, no significant difference was found in any pairing (2-way ANOVA, Bonferroni post-test p > 0.05).

4.6.3 Diversity

Diversity indices combine species richness and evenness of abundance. Aggregated data, combined from all observations over three years (Appendix A), were used to do a row-column summary on PC-ORD 6.0. Results of the row-column summary gave the Shannon diversity index (H) values for five sites and 15 sample units. These Shannon diversity index values were used for univariate analyses of diversity.

Diversity per site and per habitat type: after exclusion of species

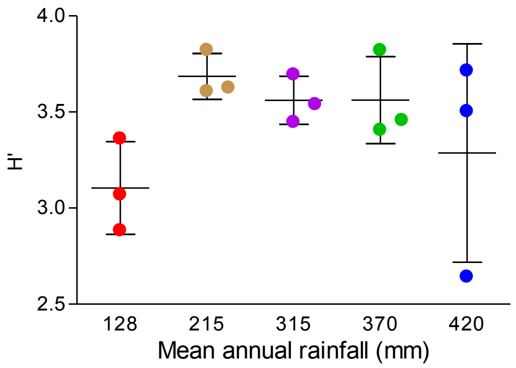

Figure 30 Diversity across the aridity gradient with Shannon diversity index values (H). Dots represent habitat types. The means and SD (lines) of the three habitat types are shown.

Diversity (H) at each sample unit (Table 6) was plotted against site to investigate trends across the aridity gradient (Figure 30).

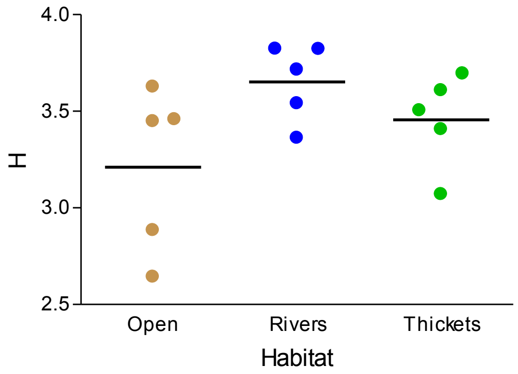

Figure 31 Diversity by habitat type with Shannon diversity index values (H). Dots represent sites. Mean of each habitat type and range of the five sites are shown.

Diversity (H) at each sample unit (Table 6) was plotted against habitat type to investigate trends in the habitats (Figure 31).

The scatterplots in Figure 30 and Figure 31 were drawn using the same data. A significant difference was noted in diversity when comparing the three habitats (2-way ANOVA, $p < 0.05$), with habitat explaining 31% of variance. Rainfall explained 42% of the variance, but there was no significant difference in diversity across the aridity gradient (2-way ANOVA, $p = 0.08$). No significant difference was found (Figure 30 and Figure 31) in any pairing of the habitat types combined with sites (2-way ANOVA, Bonferroni post-test $p > 0.05$).

Using the same data as for the scatterplots in Figure 30 and Figure 31, a bar graph was drawn (Figure 32) to illustrate the combined effects of rainfall and habitat on bird diversity (H).

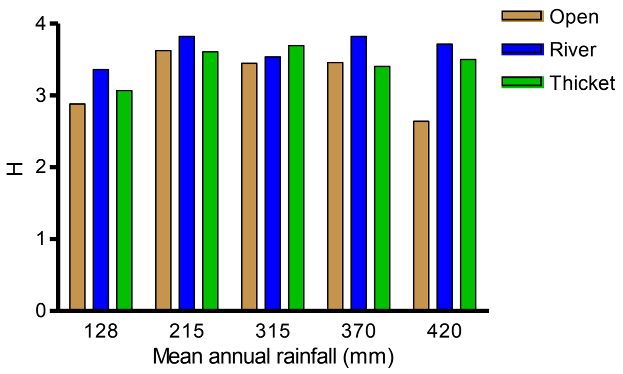

Figure 32 Shannon diversity index (H) across the aridity gradient and habitats.

4.6.4 Avian biomass

The total avian biomass at each sample unit was calculated by multiplying the means of the male & female mass (Hockey *et al*, 2005) (Table 10) with the number of individuals observed at each sample unit (Appendix A) . The results were used to investigate differences in avian biomass between habitats and across the aridity gradient.

Mean avian biomass

Transect data was used to get replicates for calculating mean biomass and SD. Figure 33 and Figure 34 were created from the same data.

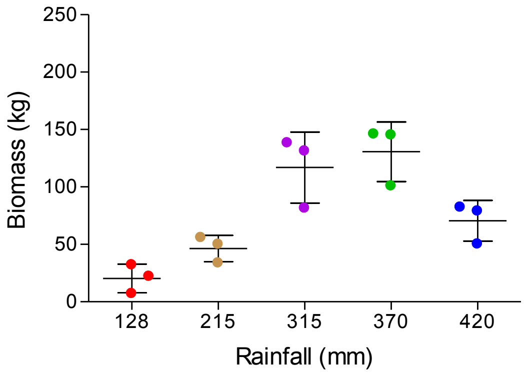

Figure 33 Mean avian biomass by site. Dots indicate habitat types. Mean and SD (lines) are shown.

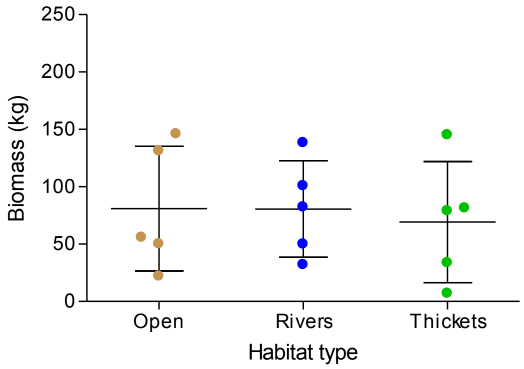

Figure 34 Mean avian biomass by habitat type. Dots indicate sites. Mean and SD (lines) are shown.

A significant difference in mean avian biomass was indicated for rainfall (2-way ANOVA, $p < 0.05$, 22% of total variance) (Figure 33 and Figure 34). Non-significant sources of variation were interaction (2-way ANOVA, $p > 0.1$, explaining 3% of variance) and habitat (2-way ANOVA, $p > 0.1$, explaining 0.4% of variance). There was a highly significant difference (1-way ANOVA, Bonferroni post-test $p < 0.01$) in mean avian biomass when comparing 128 (mean = 20, SD = 13) vs 315 (mean = 117, SD = 31) and vs 370 (mean = 131, SD = 26); and a significant difference (1-way ANOVA, Bonferroni post-test, $p < 0.05$) when comparing 215 (mean = 46, SD = 12) vs 370 (mean = 131, SD = 26).

Total avian biomass across the aridity gradient

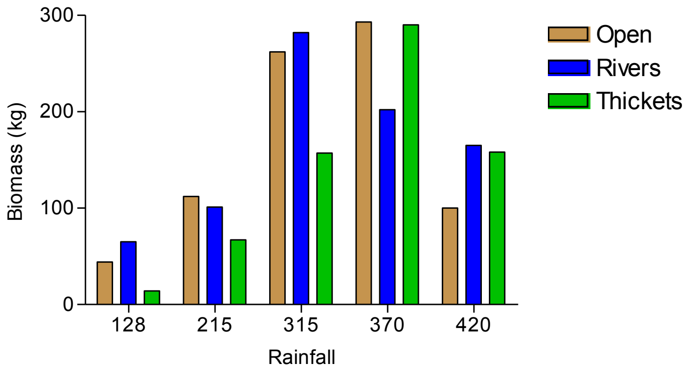

Figure 35 Total avian biomass across the aridity gradient and habitats

The total avian biomass (kg) at each sample unit was used to create the bar graph in Figure 35.

A very significant difference was found in total avian biomass across the aridity gradient (2-way ANOVA, rainfall $p < 0.01$, explained 84% of variation; habitat $p > 0.5$, explained 2% of variation). There was a very significant difference (1-way ANOVA, Bonferroni post-test $p < 0.01$) in total avian biomass when comparing 128 (mean = 41, SD = 26) vs 315 (mean = 234, SD = 67) and vs 370 (mean = 262, SD = 52); and a significant difference (Bonferroni post-test, $p < 0.05$) when comparing 215 (mean = 93, SD = 24) vs 370 (mean = 262, SD = 52).

4.6.5 Seasonal variation

Summer coincides with the wet season and winter with the dry season in the study area.

Summer and winter species richness

Table 8 lists the number of bird species observed during each season.

Table 8 Seasonal species richness

The site, habitat, total number of species observed over three years of sampling, number of species observed during three summers of sampling, number of species observed during three winters of sampling, and percentage difference between summer and winter species richness are given.

Site	Habitat type	Summer # species	Winter # species	% difference Summer-winter
128	**Open**	38	34	10.5%
	River	53	44	17%
	Thicket	43	9	79.1%
215	**Open**	57	46	19.3%
	River	77	64	16.9%
	Thicket	52	40	23.1%
315	**Open**	60	45	25%
	River	80	74	7.5%
	Thicket	57	51	10.5%
370	**Open**	67	53	20.9%
	River	85	64	24.7%
	Thicket	59	52	11.9%
420	**Open**	49	39	20.4%
	River	88	59	33%
	Thicket	79	62	21.5%

A paired t-test was carried out with the number of species observed in summer and winter at the sample units (Table 8). A highly significant difference was found (paired t-test, $p < 0.0001$, mean of differences = 14, one-tailed $p < 0.0001$), when comparing summer vs winter species richness (Table 8).

The number of species observed at each sample unit in summer and in winter was used to calculate the percentage difference between the wet and the dry season (Table 8 and Figure 36).

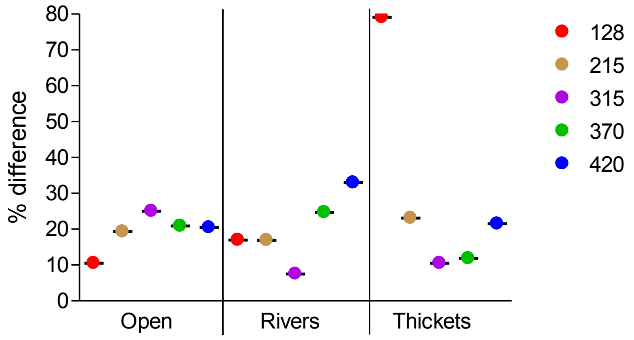

Figure 36 Percentage (%) difference between summer and winter species richness by habitat, with site as series

Percentage difference between summer and winter species richness (Figure 36) was close to the median (20), except at 128 thickets where there was a 79% difference between summer and winter species richness (Column statistics: minimum = 8%, maximum = 79%, mean = 23%, SD = 17).

Summer and winter abundance

Table 8Table 9 lists the number of individuals per species observed during each season.

Table 9 Seasonal abundance

The site, habitat, total number of individuals observed over three years of sampling, number of individuals observed during three summers of sampling, number of individuals observed during three winters of sampling, and percentage difference between summer and winter bird numbers are given.

Site	Habitat	Summer # birds	Winter # birds	% difference Summer-winter
128	**Open**	443	239	46%
	River	810	574	29.1%
	Thicket	254	40	84.3%
215	**Open**	501	227	54.7%
	River	566	743	-31.3%
	Thicket	357	206	42.3%
315	**Open**	724	365	49.6%
	River	959	1193	-24.4%
	Thicket	386	329	14.8%
370	**Open**	605	514	15%
	River	802	637	20.6%
	Thicket	598	366	38.8%
420	**Open**	1001	829	17.2%
	River	825	629	23.8%
	Thicket	848	716	15.6%

A paired t-test was carried out with the number of birds observed in summer and winter at the sample units (Table 9). A significant difference was found (paired t-test p < 0.05, mean of differences = 138, one-tailed p < 0.0001) when comparing bird numbers of summer vs winter (Table 9).

The number of individuals observed at each sample unit in summer and in winter was used to calculate the percentage difference in abundance between the wet and the dry season (Table 8, Table 9 and Figure 37).

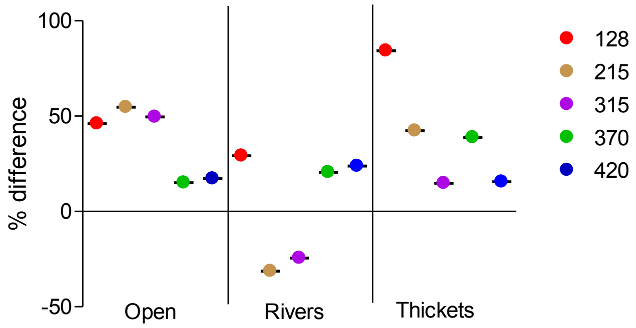

Figure 37 Percentage (%) difference between summer and winter abundances by habitat, with site as series

Figure 37 shows that the percentage difference between summer and winter abundance was close to the median (24), with three exceptions. Similar to the trends in seasonal difference of species richness (Figure 36), there was an increase in bird numbers at 128 thickets in summer (84% difference). Two negative values, at Rivers of 215 (-31%) and 315 (-24%), indicated more birds were observed at these sample units in winter than in summer (Column statistics: minimum = -31%, maximum = 84%, mean = 26%, SD = 29).

Mantel tests to establish association between summer and winter bird assemblages

Two Mantel tests were carried out with PC-ORD to investigate the association between summer and winter bird assemblages; one for species richness and one for abundance.

The Mantel test for species richness (number of species observed at each sample unit) was done using presence/absence values. The main matrix (summer) had 15 sites and 173 species. The second matrix (winter) had 15 sites and 135 species. Relative Sorenson was used as the distance measure for both matrices and the method was randomisation (Monte Carlo). Results showed a p = 0.001 and a Standardised Mantel statistic of r = 0.71. There was therefore a high association between summer and winter species richness.

The Mantel test for abundance was done using values for the number of individuals per species observed at each sample unit. The main matrix (summer) had 15 sites and 173 species. The second matrix (winter) had 15 sites and 135 species. Relative Sorenson was used as the distance measure for both matrices and the method was randomisation (Monte Carlo). Results showed p = 0.001 and a Standardised Mantel statistic of r = 0.81. There was a high association between summer and winter bird abundance.

Year-to-year seasonal consistency in species richness

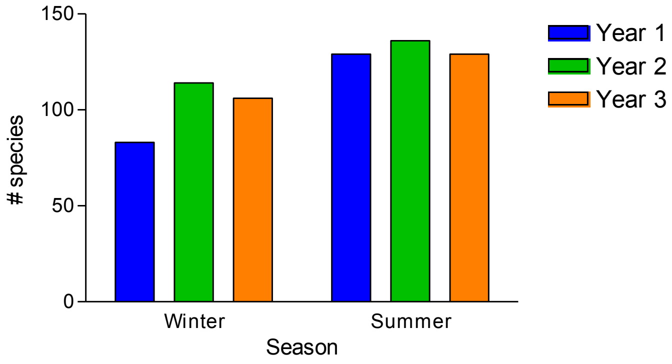

Figure 38 Species richness per season per year. The aggregate number of species observed during each survey is shown.

The number of species observed during each of the six surveys was used to compare the consistency of bird species composition in summer from year to year, and in winter from year to year (Figure 38). There was no significant difference in species composition between the three summer surveys or between the three winter surveys (1-way ANOVA, Bonferroni post-test, p > 0.1).

4.6.6 Guilds

To support multivariate analyses, species were classified into seven nesting and twelve feeding guilds (0) according to their preferred nesting sites and feeding behaviours (Hockey *et al*, 2005). Birds use various substrates for their nesting sites, including vegetation, the ground, rocks, cliffs and anthropogenic structures. The availability of suitable nesting sites and food resources are important considerations in analysing the effect of aridity on avian communities, because birds rely on habitat for their nests and food, and in turn, habitat is partially affected by rainfall.

Table 10 Species with their common names, nesting guilds, feeding guilds and mean body mass.

Scientific names are omitted due to space, they can be found in Table 3. Br migr = breeding migrant, non-br migr = non-breeding migrant, Nom = nomadic, Res = resident. Parasitic breeders are classified under their host nesting guild. “Cavity” refers to both cavity users and cavity makers. Species that eat either meat or insects, as well as at least two types of vegetation matter are classified as omnivores. Species that show seasonal movements are classified as both nomadic and resident.

Common name	**Nesting guild**	**Feeding guild**	**Movements**	**Mean body mass (kg)**
Acacia Pied Barbet	Cavity	Omnivore	Res	0.0335
African Fish-Eagle	Tree-shrub	Carnivore	Nom/Res	2.5
African Golden Oriole	Extralimital	Insectivore/Frugivore	Non-br migr	0.075
African Grey Hornbill	Cavity	Omnivore	Nom/Res	0.155
African Harrier-Hawk	Tree-shrub	Carnivore	Nom/Res	0.8
African Hawk-Eagle	Tree-shrub	Carnivore	Res	1.45
African Hoopoe	Cavity	Insectivore	Nom/Res	0.057
African Pipit	Ground-grass	Insectivore/Granivore	Nom/Res	0.0245
African Quailfinch	Ground-grass	Insectivore/Granivore	Nom	0.011
African Red-eyed Bulbul	Tree-shrub	Omnivore	Nom/Res	0.031
Amur Falcon	Extralimital	Carnivore	Non-br migr	0.14
Ant-eating Chat	Ground	Insectivore/Frugivore	Res	0.0475
Ashy Tit	Cavity	Omnivore	Nom/Res	0.0195
Augur Buzzard	Tree-shrub	Carnivore/Insectivore	Res	1.007
Banded Martin	Constructed	Insectivore	Br migr	0.026
Barn Owl	Cavity	Carnivore/Insectivore	Res	0.41
Barn Swallow	Extralimital	Insectivore/Frugivore	Non-br migr	0.018
Barred Wren-Warbler	Tree-shrub	Insectivore	Res	0.014
Bearded Woodpecker	Cavity	Carnivore/Insectivore	Res	0.083
Black Cuckoo	Tree-shrub	Carnivore/Insectivore	Br migr	0.09
Black-chested Prinia	Tree-shrub	Insectivore	Nom/Res	0.009
Black-chested Snake-Eagle	Tree-shrub	Carnivore	Nom	1.5
Black-faced Waxbill	Tree-shrub	Omnivore	Res	0.009
Black-headed Heron	Tree-shrub	Carnivore/Insectivore	Res	0.505
Black-shouldered Kite	Tree-shrub	Carnivore	Nom	0.25
Blacksmith Lapwing	Ground-grass	Carnivore/Insectivore	Nom/Res	0.165
Black-throated Canary	Tree-shrub	Omnivore	Nom/Res	0.013
Black-winged Pratincole	Extralimital	Insectivore	Non-br migr	0.042
Bronze-winged Courser	Ground-grass	Insectivore	Res	0.155
Brown Snake-Eagle	Tree-shrub	Carnivore	Nom/Res	2
Brown-crowned Tchagra	Tree-shrub	Carnivore/Insectivore	Res	0.0325
Brown-throated Martin	Ground	Insectivore	Nom/Res	0.0125
Brubru	Tree-shrub	Insectivore	Res	0.024
Buffy Pipit	Ground-grass	Insectivore/Granivore	Nom/Res	0.029
Burchell's Sandgrouse	Ground-grass	Granivore	Nom/Res	0.196
Burchell's Starling	Cavity	Omnivore	Res	0.105
Burnt-necked Eremomela	Tree-shrub	Insectivore/Nectarivore	Res	0.009

Common name	Nesting guild	Feeding guild	Movements	Mean body mass (kg)
Cape Bunting	Ground-grass/shrub	Omnivore	Res	0.02
Cape Clapper Lark	Ground-grass	Omnivore	Res	0.028
Cape Crow	Tree-shrub	Omnivore	Res	0.5
Cape Glossy Starling	Cavity	Omnivore	Res	0.09
Cape Penduline-Tit	Tree-shrub	Insectivore/Granivore	Nom/Res	0.0075
Cape Sparrow	Tree-shrub	Insectivore	Res	0.029
Cape Turtle-Dove	Tree-shrub	Omnivore	Nom/Res	0.15
Cape Wagtail	Ground-grass/shrub	Carnivore/Insectivore	Nom/Res	0.02
Capped Wheatear	Extralimital	Omnivore	Non-br migr	0.025
Cardinal Woodpecker	Cavity	Insectivore/Frugivore	Res	0.03
Chat Flycatcher	Tree-shrub	Carnivore/Insectivore	Nom/Res	0.037
Chestnut Weaver	Tree-shrub	Granivore	Nom/Res	0.03
Chestnut-backed Sparrowlark	Ground-grass	Insectivore/Granivore	Nom/Res	0.022
Chestnut-vented Tit-Babbler	Tree-shrub	Omnivore	Res	0.016
Cinnamon-breasted Bunting	Ground-grass	Insectivore/Granivore	Br migr/Res	0.015
Common Fiscal	Tree-shrub	Omnivore	Res	0.04
Common House-Martin	Extralimital	Insectivore	Non-br migr	0.013
Common Quail	Ground-grass/shrub	Omnivore	Br migr	0.095
Common Scimitarbill	Cavity	Insectivore/Nectarivore	Res	0.0325
Common Waxbill	Ground-grass/shrub	Omnivore	Res	0.008
Common Whitethroat	Extralimital	Omnivore	Non-br migr	0.015
Crested Francolin	Ground-grass	Omnivore	Res	0.35
Crimson-breasted Shrike	Tree-shrub	Insectivore/Frugivore	Res	0.05
Crowned Lapwing	Ground-grass	Insectivore	Res	0.185
Damara Hornbill	Cavity	Carnivore/Insectivore	Nom/Res	0.205
Desert Cisticola	Ground-grass/shrub	Insectivore	Nom/Res	0.009
Diderick Cuckoo	Tree-shrub	Insectivore	Br migr	0.035
Double-banded Courser	Ground-grass	Insectivore	Nom/Res	0.09
Double-banded Sandgrouse	Ground-grass	Granivore	Nom/Res	0.23
Dusky Sunbird	Tree-shrub	Insectivore/Nectarivore	Nom/Res	0.008
Eastern Clapper Lark	Ground-grass	Insectivore/Granivore	Nom/Res	0.03
Eurasian Golden Oriole	Extralimital	Insectivore/Frugivore	Non-br migr	0.064
European Bee-eater	Extralimital	Insectivore	Non-br migr	0.052
Familiar Chat	Ground-grass	Omnivore	Res	0.022
Fawn-coloured Lark	Ground-grass	Insectivore/Granivore	Res	0.023
Fork-tailed Drongo	Tree-shrub	Carnivore/Insectivore	Res	0.045
Freckled Nightjar	Ground-grass/shrub	Insectivore	Res	0.08
Gabar Goshawk	Tree-shrub	Carnivore	Res	0.165
Golden-breasted Bunting	Tree-shrub	Omnivore	Res	0.02
Golden-tailed Woodpecker	Cavity	Insectivore	Res	0.07
Great Sparrow	Tree-shrub	Insectivore/Granivore	Res	0.032
Great Spotted Cuckoo	Cavity	Carnivore/Insectivore	Br migr	0.17
Greater Honeyguide	Ground	Insectivore	Res	0.05

Common name	Nesting guild	Feeding guild	Movements	Mean body mass (kg)
Greater Kestrel	Tree-shrub	Carnivore/Insectivore	Nom	0.285
Greater Striped Swallow	Constructed	Insectivore	Br migr	0.027
Green Wood-Hoopoe	Cavity	Omnivore	Res	0.0765
Green-winged Pytilia	Tree-shrub	Insectivore/Granivore	Nom/Res	0.015
Grey Go-away-bird	Tree-shrub	Omnivore	Nom/Res	0.27
Grey-backed Camaroptera	Tree-shrub	Insectivore	Res	0.0105
Grey-backed Cisticola	Tree-shrub	Insectivore	Nom/Res	0.01
Grey-backed Sparrowlark	Ground-grass	Insectivore	Nom	0.017
Grey-headed Kingfisher	Ground	Carnivore/Insectivore	Non-br migr	0.045
Groundscraper Thrush	Tree-shrub	Insectivore	Res	0.074
Hamerkop	Tree-shrub	Carnivore/Insectivore	Nom/Res	0.51
Harlequin Quail	Ground-grass	Insectivore	Br migr/Res	0.08
Helmeted Guineafowl	Ground-grass	Insectivore	Res	1.44
House Sparrow	Tree-shrub	Omnivore	Res	0.0255
Icterine Warbler	Extralimital	Insectivore/Frugivore	Non-br migr	0.012
Jacobin Cuckoo	Tree-shrub	Insectivore	Br migr	0.083
Kalahari Scrub-Robin	Ground-grass/shrub	Omnivore	Res	0.02
Karoo Long-billed Lark	Ground-grass	Omnivore	Res	0.04
Karoo Scrub-Robin	Ground-grass/shrub	Insectivore/Frugivore	Res	0.019
Klaas's Cuckoo	Tree-shrub	Omnivore	Br migr	0.026
Kori Bustard	Ground-grass	Omnivore	Nom	9
Kurrichane Buttonquail	Ground-grass	Insectivore/Granivore	Nom	0.0425
Lappet-faced Vulture	Tree-shrub	Carrion	Nom/Res	6.5
Lark-like Bunting	Ground-grass	Carnivore/Granivore	Nom	0.015
Laughing Dove	Tree-shrub	Omnivore	Nom/Res	0.1
Lesser Grey Shrike	Extralimital	Insectivore	Non-br migr	0.046
Lesser Kestrel	Extralimital	Carnivore	Non-br migr	0.148
Lesser Masked-Weaver	Tree-shrub	Omnivore	Nom/Res	0.02
Lilac-breasted Roller	Cavity	Carnivore/Insectivore	Nom/Res	0.105
Long-billed Crombec	Tree-shrub	Omnivore	Res	0.012
Long-billed Pipit	Ground-grass	Insectivore	Res	0.03
Long-tailed Paradise-Whydah	Tree-shrub	Insectivore/Granivore	Nom/Res	0.0205
Ludwig's Bustard	Ground-grass	Omnivore	Nom	3.6
Marico Flycatcher	Tree-shrub	Insectivore/Frugivore	Res	0.024
Marico Sunbird	Tree-shrub	Insectivore/Nectarivore	Res	0.011
Monotonous Lark	Ground-grass	Insectivore/Granivore	Nom/Res	0.024
Monteiro's Hornbill	Cavity	Omnivore	Nom	0.35
Mountain Wheatear	Ground-grass/shrub	Insectivore/Granivore	Nom/Res	0.035
Namaqua Dove	Tree-shrub	Granivore	Nom/Res	0.04
Northern Black Korhaan	Ground-grass	Omnivore	Res	0.731
Orange River Francolin	Ground-grass	Omnivore	Res	0.425
Pale-winged Starling	Tree-shrub	Omnivore	Res	0.1
Pearl-breasted Swallow	Constructed	Insectivore/Granivore	Br migr/Res	0.012

Common name	**Nesting guild**	**Feeding guild**	**Movements**	**Mean body mass (kg)**
Pearl-spotted Owlet	Cavity	Carnivore/Insectivore	Res	0.065
Plain-backed Pipit	Ground-grass	Insectivore/Granivore	Res	0.0265
Pririt Batis	Tree-shrub	Insectivore	Res	0.0115
Purple Roller	Tree-shrub	Omnivore	Res	0.165
Rattling Cisticola	Tree-shrub	Insectivore	Res	0.015
Red-backed Shrike	Extralimital	Omnivore	Non-br migr	0.029
Red-billed Buffalo-Weaver	Tree-shrub	Omnivore	Nom/Res	0.08
Red-billed Hornbill	Cavity	Omnivore	Nom/Res	0.14
Red-billed Spurfowl	Ground-grass	Omnivore	Nom/Res	0.43
Red-breasted Swallow	Constructed	Insectivore	Br migr	0.031
Red-crested Korhaan	Ground-grass	Omnivore	Res	0.675
Red-faced Mousebird	Tree-shrub	Frugivore	Res	0.055
Red-footed Falcon	Extralimital	Carnivore	Non-br migr	0.163
Red-headed Finch	Tree-shrub	Insectivore/Granivore	Nom	0.024
Rock Kestrel	Tree-shrub	Carnivore/Insectivore	Nom/Res	0.215
Rock Martin	Constructed	Insectivore	Br migr/Res	0.022
Rockrunner	Ground-grass/shrub	Insectivore	Res	0.028
Rosy-faced Lovebird	Cavity	Granivore	Nom	0.055
Rufous-eared Warbler	Tree-shrub	Insectivore/Frugivore	Nom/Res	0.01
Rufous-naped Lark	Ground-grass	Insectivore	Res	0.042
Ruppell's Korhaan	Ground-grass	Omnivore	Res	1.1
Sabota Lark	Ground-grass	Omnivore	Nom/Res	0.025
Scaly-feathered Finch	Tree-shrub	Granivore	Nom/Res	0.0115
Scarlet-chested Sunbird	Tree-shrub	Insectivore/Nectarivore	Nom/Res	0.0135
Sclater's Lark	Ground-grass	Insectivore/Granivore	Nom/Res	0.02
Secretarybird	Tree-shrub	Carnivore/Insectivore	Nom/Res	4
Shaft-tailed Whydah	Tree-shrub	Granivore	Nom/Res	0.015
Shikra	Tree-shrub	Carnivore/Insectivore	Nom/Res	0.132
Short-toed Rock-Thrush	Ground-grass/shrub	Omnivore	Nom/Res	0.06
Sociable Weaver	Tree-shrub	Omnivore	Res	0.027
South African Cliff-Swallow	Constructed	Insectivore	Br migr	0.021
Southern Grey-headed Sparrow	Cavity	Omnivore	Nom/Res	0.024
Southern Masked-Weaver	Tree-shrub	Omnivore	Nom/Res	0.034
Southern Pale Chanting Goshawk	Tree-shrub	Carnivore	Nom/Res	0.82
Southern Pied Babbler	Tree-shrub	Carnivore/Insectivore	Res	0.075
Southern Red Bishop	Tree-shrub	Insectivore/Granivore	Res	0.023
Southern White-crowned Shrike	Tree-shrub	Insectivore/Frugivore	Nom/Res	0.07
Southern Yellow-billed Hornbill	Cavity	Omnivore	Res	0.19
Speckled Pigeon	Tree-shrub	Granivore	Res	0.35
Spike-heeled Lark	Ground-grass	Omnivore	Nom/Res	0.025
Spotted Eagle-Owl	Ground-grass	Carnivore	Res	0.7
Spotted Flycatcher	Extralimital	Omnivore	Non-br migr	0.015
Stark's Lark	Ground-grass	Omnivore	Nom	0.019

Common name	Nesting guild	Feeding guild	Movements	Mean body mass (kg)
Steppe Buzzard	Extralimital	Carnivore	Non-br migr	0.73
Steppe Eagle	Extralimital	Carnivore	Non-br migr	2.75
Swallow-tailed Bee-eater	Ground	Insectivore	Nom/Res	0.023
Tawny Eagle	Tree-shrub	Carnivore	Res	2
Temminck's Courser	Ground-grass	Insectivore	Nom/Res	0.07
Three-banded Plover	Ground-grass	Insectivore	Br migr/Res	0.034
Tractrac Chat	Ground-grass	Insectivore	Nom/Res	0.02
Violet-backed Starling	Cavity	Insectivore	Br migr	0.045
Violet-eared Waxbill	Tree-shrub	Insectivore	Nom/Res	0.012
Wattled Starling	Tree-shrub	Insectivore	Nom	0.07
White-backed Mousebird	Tree-shrub	Herbivore	Res	0.044
White-backed Vulture	Tree-shrub	Carrion	Res	5.5
White-browed Sparrow-Weaver	Tree-shrub	Omnivore	Res	0.047
White-tailed Shrike	Tree-shrub	Insectivore	Res	0.0275
White-throated Canary	Tree-shrub	Omnivore	Nom/Res	0.027
White-throated Swallow	Constructed	Insectivore	Br migr	0.023
Willow Warbler	Extralimital	Insectivore	Non-br migr	0.009
Yellow Canary	Tree-shrub	Omnivore	Nom/Res	0.0175
Yellow-bellied Eremomela	Tree-shrub	Omnivore	Nom/Res	0.009
Yellow-billed Kite	Extralimital	Carnivore	Non-br migr	0.767
Yellow-crowned Bishop	Tree-shrub	Omnivore	Nom/Res	0.015
Zitting Cisticola	Tree-shrub	Insectivore	Res	0.009

4.7 Multivariate analyses

Due to the complexity of the data (17 286 individuals, 188 species, three years of surveys, 15 sample units and six environmental variables) multivariate statistics (NMS) were used to analyse avian community patterns.

Envronmental variables with quantitative values

- Rainfall: mean annual rainfall (mm) at each site.
- Vegetation height: mean vegetation height (m) at each sample unit.
- Mass: total bird biomass (kg) at each sample unit
- Altitude: GPS altitude (m)

Environmental variables with categorical values

- Site: R 128 = Rooiklip, W 215 = Weissenfels, C 315 = Claratal, N 370 = Neudamm, O 420 = Okasewa.

  Numbers, as mean anual rainfal, corresponds with the aridity gradient.
- Habitat type: O = Open areas, R = River, T = Thicket

Sample units are a combination of site and habitat: abbreviation for site is followed by abbreviation for habitat type, e.g. RO = Rooiklip Open, OT = Okasewa Thicket

4.7.1 Species richness

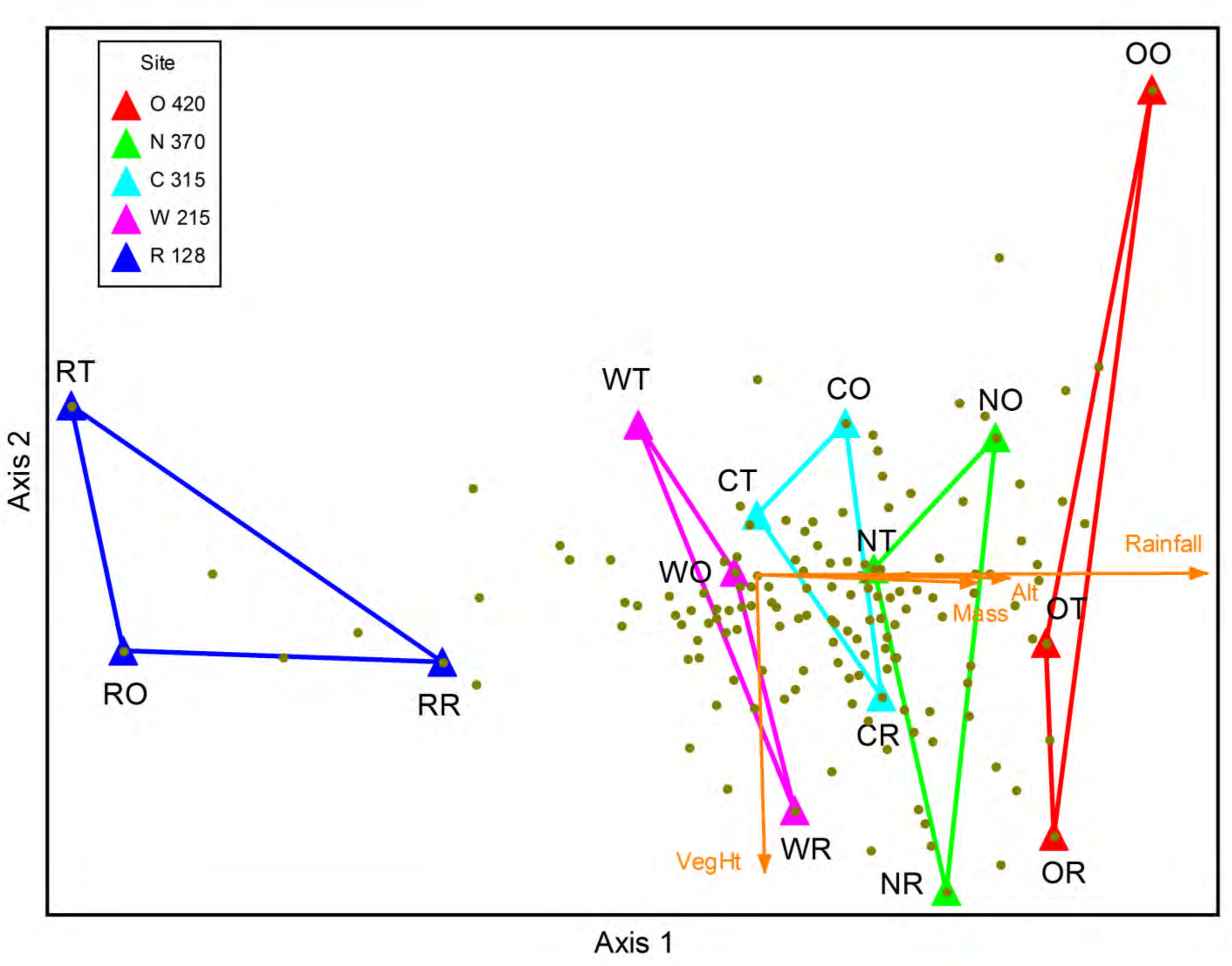

Figure 39 NMS biplot of species presence/absence with sample units and environmental factors rainfall, vegetation height, mass and altitude. Green dots represent species (without names, for clarity), and convex hulls indicate the five sites.

Distance measure = Relative Sorenson. Final stress = 6.9. Two dimensions were derived. r²: axis 1 = 74.6%, axis 2 = 19.4%, cumulative = 94%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The ordination in Figure 39 is an NMS biplot of species richness. Presence/absence scores for bird species were used in the main matrix; 1 = presence, 0 = absence. 188 species were arranged in columns and 15 sample units in rows. The second matrix contained 15 sample units in rows and six environmental factors in columns. Categorical environmental factors were site and habitat. Quantitative environmental factors were mean vegetation height, rainfall, total bird biomass and altitude.

In this ordination, axis 1 ($r^2 = 0.746$) associated with rainfall ($r^2 = 0.834$), altitude ($r^2 = 0.468$) and mass ($r^2 = 0.410$). Axis 2 ($r^2 = 0.194$) associated with vegetation height ($r^2 = 0.548$). Only two dimensions were derived (Figure 39).

Sample units ordinated seperately from left to right according to increasing rainfall (Figure 39). The vegetation height vector is perpendicular to the rainfall vector, indicating that rainfall and vegetation height were independent of each other, whereas mass and altitude co-varied strongly with rainfall. Although axis 2 explained only 19.4% of the total variance, vegetation height played an important role in bird community composition ($r^2 = 0.548$). WR, CR, NR and OR (river species ordination points) are at the bottom of the ordination and of their respective convex hulls, where plants were tallest. Similarly, open habitats CO, NO and OO, dominated by grass, are at the negative side of the vegetation height vector, where plants were shortest. Thickets CT, NT and OT are in the middle, close to the origin of the vegetation height vector.

There is no overlap in the convex hulls of any of the five sites, signifying that each site had more in common with itself than with any other site regarding bird species composition. Most of the species ordinated towards the mesic side of the rainfall vector and the taller side of the vegetation vector, between the river and thicket habitat types. There was a clustering of species around the origin of the vectors, and another clustering of species between CR and NT.

The most arid site, R 128, ordinated towards the far negative side of the rainfall ($r^2 = 0.834$), mass ($r^2 = 0.410$), and altitude ($r^2 = 0.468$) vectors. Twelve species ordinated at or close to the convex hull of R 128. Several more dry-tolerant species ordinated on the arid side of the rainfall vector, closer to W 215 than to R 128. The 12 species that ordinated closest to R 128 were Barn Owl, Cape Bunting, Common House-Martin, Freckled Nightjar, Klaas's Cuckoo, Mountian Wheatear, Ruppell's Korhaan, Speckled Pigeon, Spotted Eagle-Owl, Steppe Eagle, Tractrac Chat and Violet-backed Starling.

4.7.2 Abundance

The number of individuals of each species observed was entered for each sample unit in the main matrix. The second matrix had environmental variables: site, habitat type, rainfall, altitude, vegetation height and mass.

Bird abundance per sample unit in ordination space

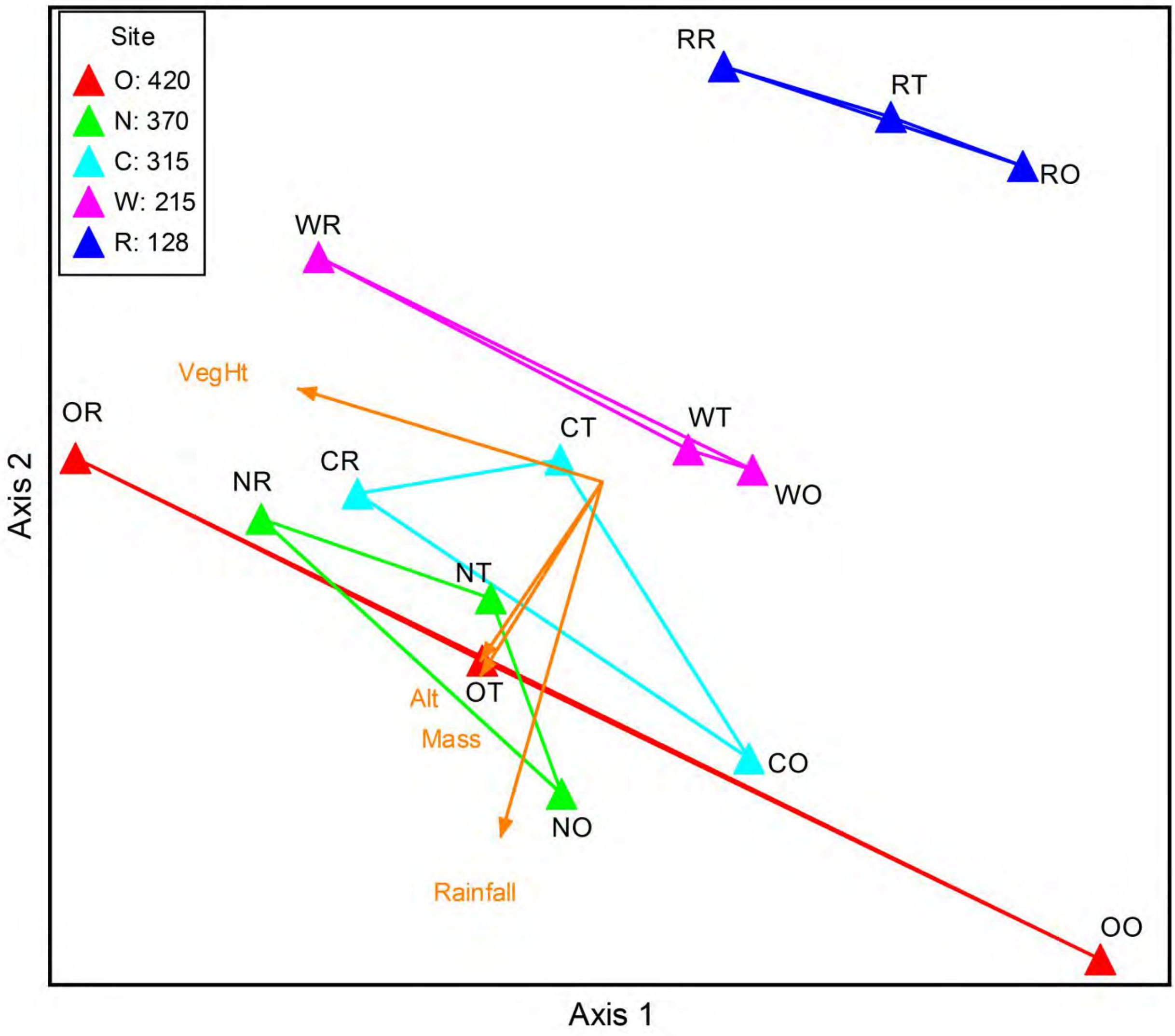

Figure 40 NMS biplot of sample units with environmental factors rainfall, altitude, mean vegetation height and total bird biomass. Convex hulls indicate the five sites.

Distance measure = Relative Sorenson. Final stress = 10.37. Two dimensions were derived. r^2: axis 1 = 49.8%, axis 2 = 37.8%, cumulative = 87.6%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The biplot in Figure 40 is an NMS ordination of sample units using abundance data. Species were not shown here, in order to give a clear visual representation of trends in the distribution of sample units in ordination space (species ordination is in Figure 41). Sample units distributed in ordination space according to environmental variables, in essence, similar to Figure 41.

Vegetation height (r^2 = 0.592 on axis1, r^2 = 0.181 on axis 2; Table 11) determined the ordination of habitats: the rivers (OR, NR, CR, WR, and RR) ordinated where vegetation was highest, open areas were at the opposite end, and thickets in the middle (Figure 40). Overlap between the convex hulls of O 420 and N 370 indicated similarity in the ecology of the two sites. The very long convex hull and distances between the three habitats at O 420 signified variation in vegetation height. Open habitat at site OO had shorter vegetation than open habitat at the other sites.

The vegetation height vector was perpendicular to the rainfall vector, indicating that these two factors were independent from each other. They played an almost equal part ($r^2 = 0.592$; Table 11) in explaining the distribution of sample units in ordination space. Mass and altitude co-varied with rainfall. Mass $r^2 = 0.237$ on axis 1, $r^2 = 0.377$ on axis 2. Altitude $r^2 = 0.238$ on axis 1, $r^2 = 0.351$ on axis 2 (Table 11).

For R 128, the three habitat types had more in common with one another than with the same habitat at any of the other four sites (Figure 40). The position of R 128, distinct from the other sites, was also noticeable in Figure 39. The flat convex hulls of R 128, W 215 and O 420 indicated correlation with the rainfall vector ($r^2 = 0.592$ on axis 2) at these three sites.

Correlation between ordination and environmental data

Table 11 Pearson and Kendall correlations with ordination axes

Axis	1		2	
	r^2	tau	r^2	tau
Rainfall	0.127	-0.329	0.592	-0.576
Alt	0.238	-0.309	0.351	-0.35
VegHt	0.592	-0.587	0.181	0.317
Mass	0.237	-0.371	0.377	-0.562

Species abundance with sites

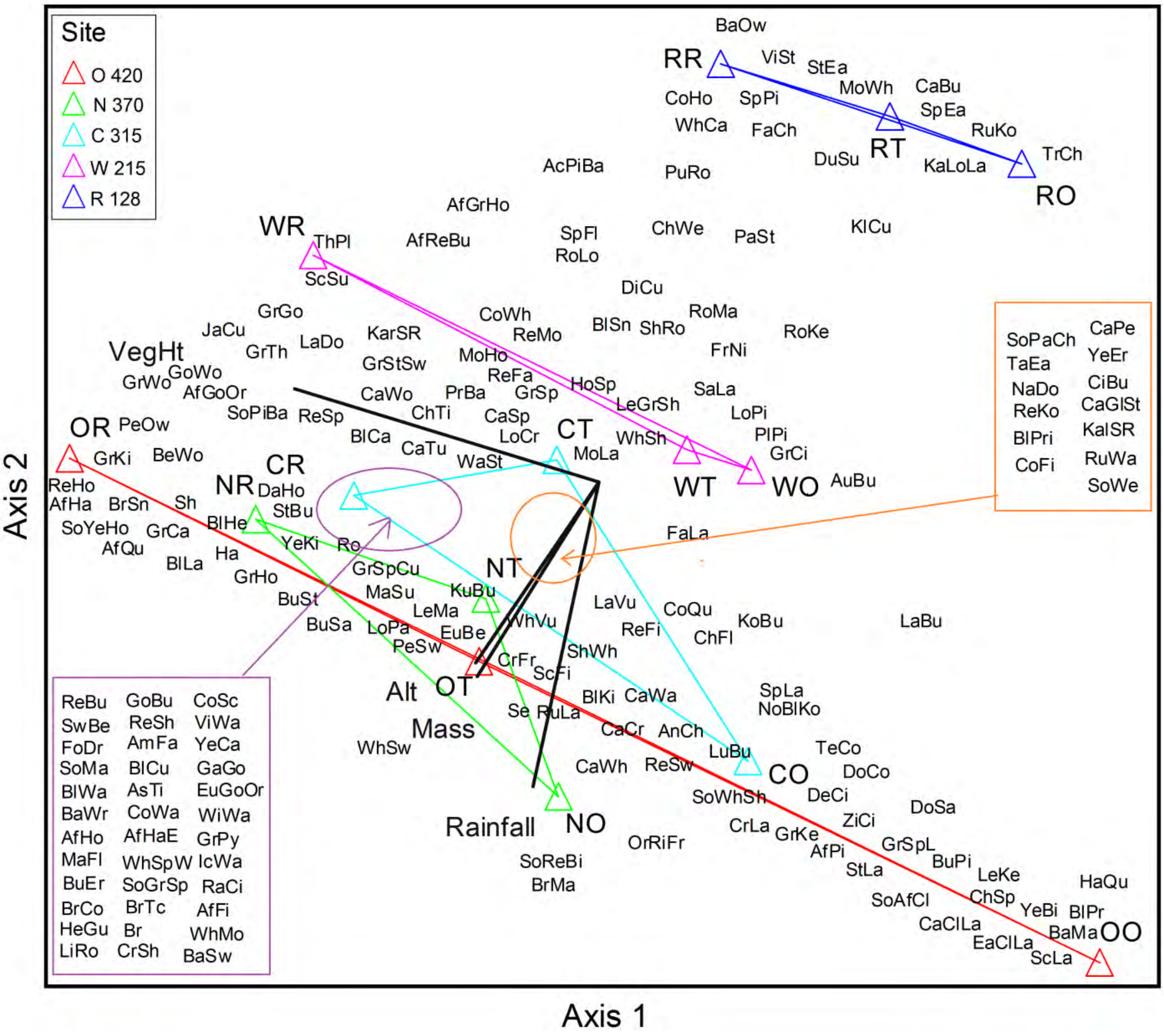

Figure 41 NMS biplot of bird abundances and sites with environmental factors rainfall, altitude, mean vegetation height and total bird biomass. Bird species abbreviations are given, and convex hulls indicate the five sites.

Distance measure = Relative Sorenson. Final stress = 10.37. Two dimensions were derived. r²: axis 1 = 49.8%, axis 2 = 37.8%, cumulative = 87.6%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The biplot in Figure 41 is the NMS ordination presented in Figure 40 with species name abbreviations added. Species names and abbreviations are given in Table 3.

In this ordination (Figure 41; only two axes derived), rainfall and vegetation height played an almost equal part (r^2 = 0.592; Table 11) in explaining the species distribution in ordination space. Mass and altitude co-varied with rainfall. Mass r^2 = 0.237 on axis 1, r^2 = 0.377 on axis 2. Altitude r^2 = 0.238 on axis 1, r^2 = 0.351 on axis 2 (Table 11).

Species preferring shorter vegetation ordinated towards the right (Figure 41). Birds more tolerant of dry conditions ordinated towards R 128 and conversely for O 420 and N 370. Dry tolerant birds included Barn Owl, Cape Bunting, Common House-Martin, Dusky Sunbird, Freckled Nightjar, Klaas's Cuckoo, Karoo Long-billed Lark, Mountian Wheatear, Ruppell's Korhaan, Spotted Eagle-Owl, Steppe Eagle, Tractrac Chat and Violet-backed Starling. Some birds preferring wetter sites were Black-shouldered Kite, Brown-throated Martin, Capped Wheatear, Orange River Francolin, Pearl-spotted Owlet, Rufous-naped Lark, Southern Red Bishop, White-backed Vulture and Zitting Cisticola.

Species abundance with habitat

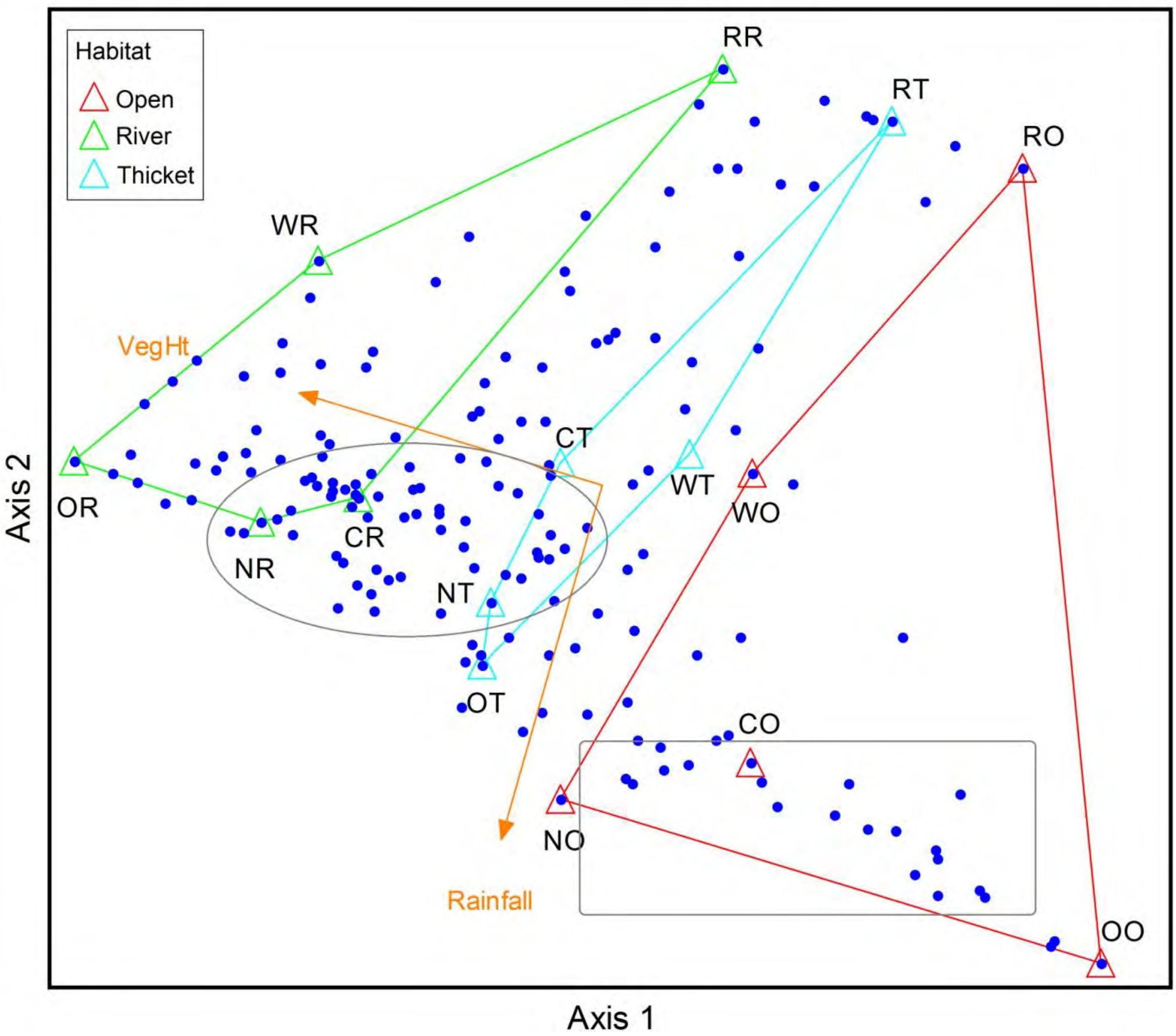

Figure 42 NMS biplot of bird abundances with the three habitat types, and environmental factors rainfall and mean vegetation height. The oval indicates a dense cluster of species between rivers and thickets. The rectangle indicates species associated with open habitat type. Convex hulls indicate the habitat types.

Distance measure = Relative Sorenson. Final stress = 10.37. Two dimensions were derived. r^2: axis 1 = 49.8%, axis 2 = 37.8%, cumulative = 87.6%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The biplot in Figure 42 is the same NMS ordination presented in Figure 41 but with convex hulls for habitat types.

No overlap between the convex hulls of the three habitat types (Figure 42) suggests that each habitat had a set of ecological factors driving a characteristic species composition distinct from every other habitat, but patterns of community composition differed as influenced by rainfall. Bird numbers increased from arid to mesic along the rainfall vector ($r^2 = 0.592$) and from open to river along the vegetation height vector ($r^2 = 0.592$ on axis 1, $r^2 = 0.181$ on axis 2; Table 11). The largest number of birds ordinated between rivers and thickets at the three more mesic sites (Figure 42, oval cluster). A second cluster (rectangle) was characteristic of the open habitat of the three more mesic sites.

4.7.3 Indicator Species Analysis

Table 12 Observed indicator values (IV's) of birds in the habitats and sites

The 45 species that had IV's of 30 and higher are listed and significance is denoted by asterisks: * $p \le 0.1$, ** $p \le 0.05$. Sites are arranged from east (mesic) to west (arid). Scientific names are omitted due to space. They can be found in Table 3.

Common name	Abbreviation	Observed Indicator Values (IV's)							
		Habitat			Site				
		Open	River	Thicket	420	370	315	215	128
African Golden Oriole	AfGoOr		60*						
African Grey Hornbill	AfGrHo		60*						
African Hawk-Eagle	AfHaE			37.5					
Augur Buzzard	AuBu	40							
Bearded Woodpecker	BeWo		80**						
Black-chested Snake-Eagle	BlSn		46.2						
Blacksmith Lapwing	BlLa		40						
Brown Snake-Eagle	BrSn		40						
Buffy Pipit	BuPi				57.1				
Burchell's Starling	BuSt					66.7**			
Burnt-necked Eremomela	BuEr		33.3						
Cape Bunting	CaBu								66.7
Cape Crow	CaCr				66.7				
Cape Sparrow	CaSp		30						
Common Whitethroat	ChSp							66.7	
Freckled Nightjar	FrNi			40					
Golden-tailed Woodpecker	GoWo		40						
Great Spotted Cuckoo	GrSpCu					83.3**			
Greater Kestrel	GrKe				100**				

Common name	Abbreviation	Observed Indicator Values (IV's)							
		Habitat			Site				
		Open	River	Thicket	420	370	315	215	128
Green Wood-Hoopoe	GrWo		40						
Grey-backed Camaroptera	GrCa		32.7		60.6				
Grey-headed Kingfisher	GrKi		40						
House Sparrow	HoSp							56.4	
Jacobin Cuckoo	JaCu		40						
Klaas's Cuckoo	KlCu								84.6**
Kori Bustard	KoBu	46.7							
Lesser Kestrel	LeKe	35.6							
Lilac-breasted Roller	LiRo		80**						
Long-billed Pipit	LoPi	30							
Orange River Francolin	OrRiFr	31.4				38.1			
Pearl-spotted Owlet	PeOw		60*						
Red-breasted Swallow	ReSw				80**				
Red-faced Mousebird	ReMo		30						
Red-footed Falcon	ReFa							51.3	
Scarlet-chested Sunbird	ScSu		40						
South African Cliff-Swallow	SoAfCl				66.7				
Southern White-crowned Shrike	SoWhSh				66.7				
Stark's Lark	StLa	40							
Steppe Eagle	StEa								66.7
Violet-backed Starling	ViSt								100**
White-backed Mousebird	WhMo		40			44.4			
White-throated Swallow	WhSw					66.7			
Willow Warbler	WiWa		50*						
Yellow-billed Kite	YeKi		51.4						
Yellow-crowned Bishop	YeBi				66.7				

Site 315, in the middle of the aridity gradient, did not have any species with IV ≥ 30 and $p \leq 0.05$ (Table 12), while 420 at the highest end of rainfall gradient had most with eight. There were 20 indicator species for river, six for open, and two for thicket.

Greater Kestrel and Violet-backed Starling had the highest IV’s, both 100, and with $p \leq 0.05$ (Table 12). Greater Kestrel was observed only at 420 and in all three habitat types, indicating a lower tolerance for arid conditions. Violet-backed Starling was observed only at 128 and in all three habitat types, suggesting that it is a strong indicator for species that can adapt to arid conditions. Species with high IV’s for both habitat type and aridity were Grey-backed Camaroptera (Rivers and 420), Orange River Francolin (open and 370) and White-backed Mousebird (Rivers and 370).

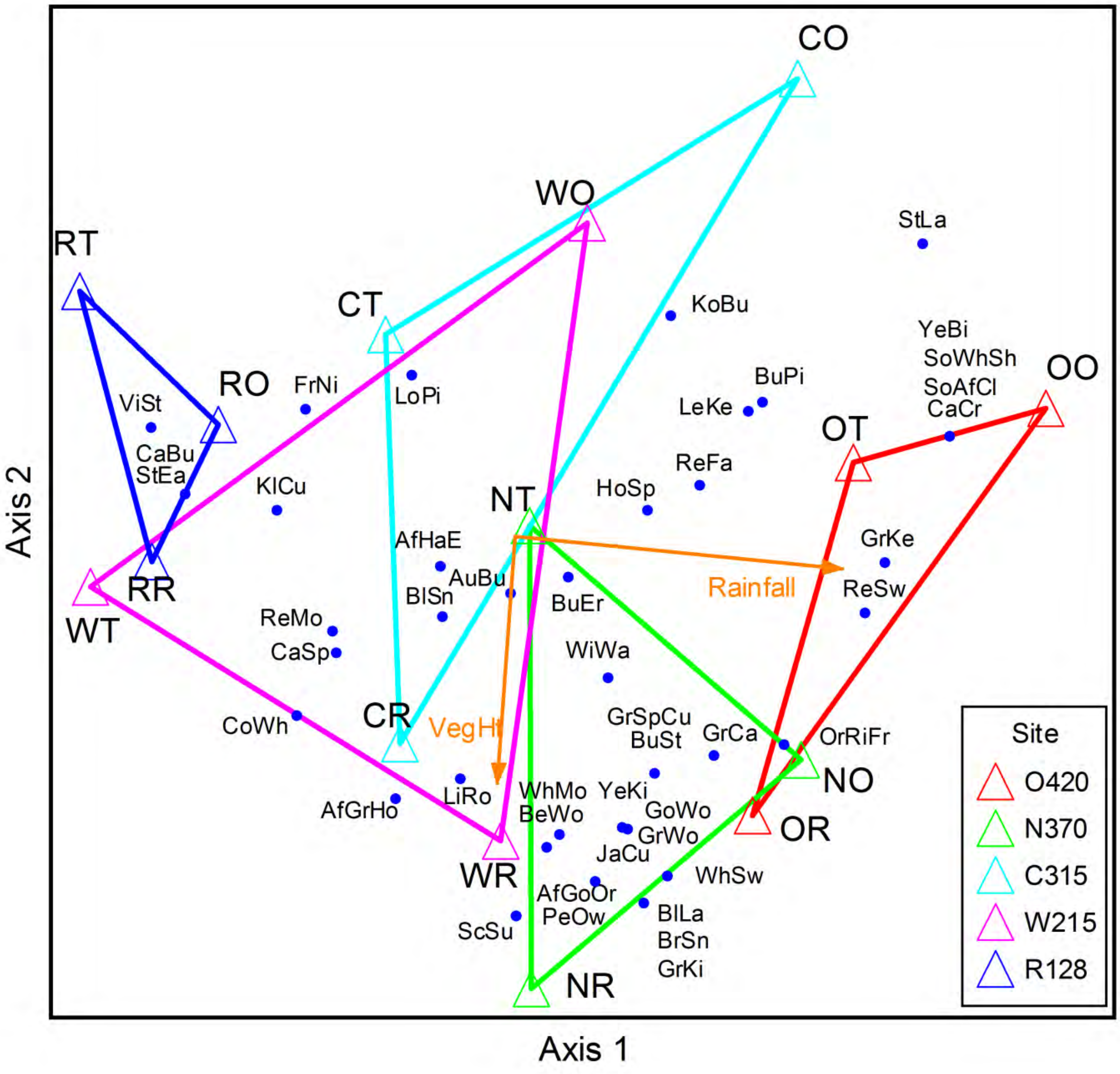

Figure 43 NMS ordination of the presence/absence of the 45 indicator species with sample units and environmental factors rainfall and vegetation height. Convex hulls indicate the different sites.

Distance measure = Relative Sorenson. Final stress = 7.8. Three dimensions were derived but only two are shown. r^2: axis 1 = 25%, axis 2= 28.3%, axis 3 = 17.6%, cumulative = 70.8%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 43 is an ordination of 45 species with IV's of 30 and higher and significance of $p \leq 0$. Presence/absence (1/0) values were used in the main matrix and the second matrix had environmental variables habitat type, site, vegetation height, and rainfall.

The sites were arranged along axis 1, explaining 25% of species distribution in ordination space (Figure 43). The habitat types separated vertically along axis 2, contributing 28% to species distribution (three dimensions were derived, but only axis 1 and axis 2 are shown). Axis 1 associated with rainfall ($r^2 = 0.678$) and axis 2 with vegetation height ($r^2 = 0.511$). Axis 3 contributed little to the two environmental vectors (rainfall $r^2 = 0.018$ and vegetation height $r^2 = 0.083$).

The river habitat types ordinated to the bottom, the thicket habitat towards the left, and the open habitat type towards the right, for all five sites. The convex hulls overlapped to a greater extent than in Figure 44.

Dry-tolerant indicator species were Cape Bunting, Steppe Eagle and Violet-backed Starling. Birds preferring wetter sites and lower vegetation included Yellow-crowned Bishop, Southern White-crowned Shrike, Cape Crow and Southern African Cliff-Swallow. Indicator species preferring higher vegetation included African Golden Oriole, Black-chested Snake-Eagle, Blacksmith Lapwing, Grey-headed Kingfisher, Pearl-spotted Owlet and Scarlet-chested Sunbird (Figure 43).

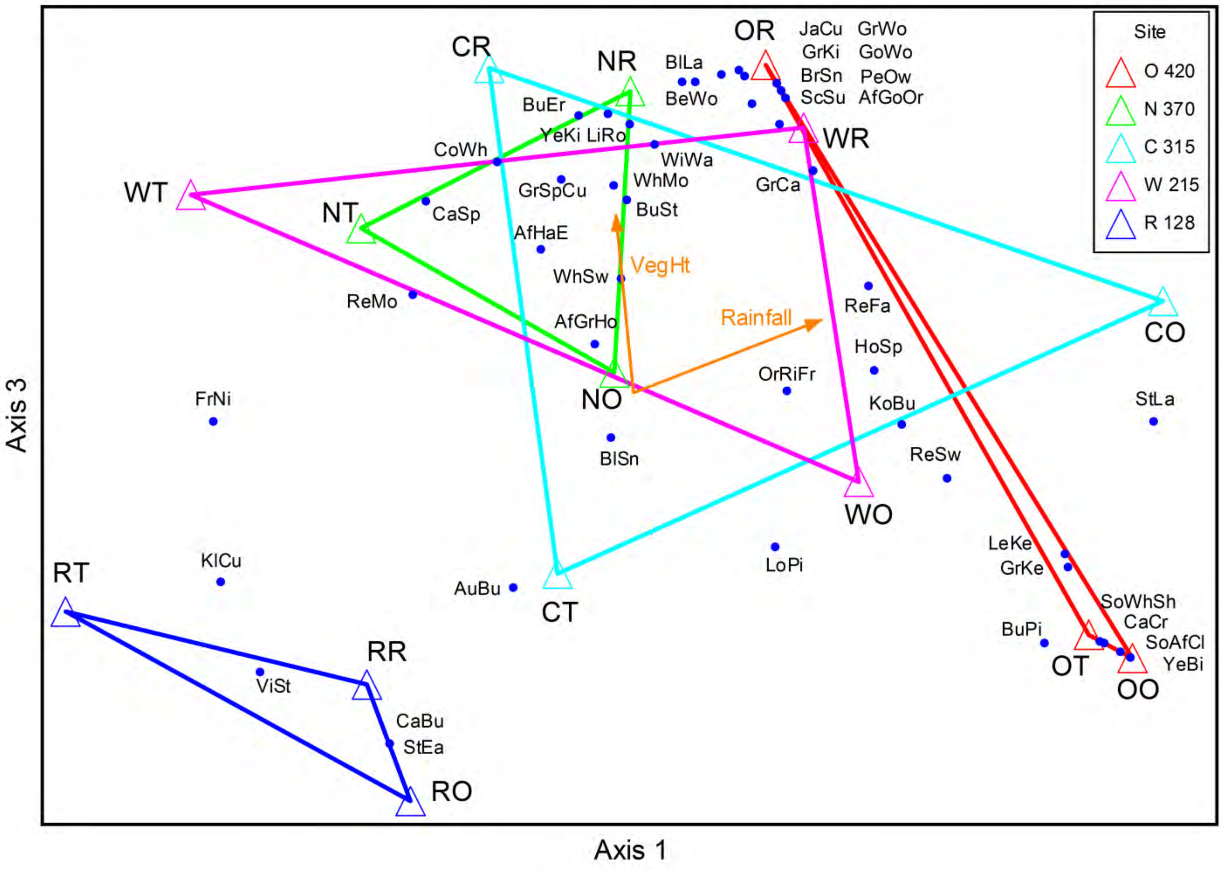

Figure 44 NMS ordination of the abundances of 45 indicator species with sample units and environmental factors rainfall and vegetation height.. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 8.9. Three dimensions were derived but only two are shown. r^2: axis 1 = 28.2%, axis 2= 21.2%, axis 3 = 24.6%, cumulative = 74%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 44 is an ordination of the abundances of 45 species with IV's of 30 and higher and with a significance of $p \leq 0$. Aggregate values (number of observations) were used in the main matrix and the second matrix had environmental variables habitat type, site, vegetation height, and rainfall.

Three axes were derived that played almost equal roles in the distribution of birds in ordination space (axis 1 $r^2 = 0.282$; axis 2 $r^2 = 0.212$; axis 3 $r^2 = 0.246$). Three dimensions were derived, but only axis 1 (rainfall $r^2 = 0.302$; vegetation height $r^2 = 0.034$) and axis 3 (rainfall $r^2 = 0.127$; vegetation height $r^2 = 0.337$) are shown. Assemblages of indicator species in Figure 44 followed the same trends as indicator species community composition based on presence/absence (Figure 43).

4.7.4 Guilds

A separate NMS ordination was done for every guild. Species and guilds are given in 0. Abundance values (number of birds per species observed) were used in the primary matrix for all the guild ordinations. The primary matrix consisted of the species represented in the guild (columns) against 15 sample units (rows). The same secondary matrix with environmental variables of site, habitat type, vegetation height, and rainfall was used for all the guild ordinations. Species names and the abbreviations used in NMS ordinations are given in Table 3.

Nesting guilds

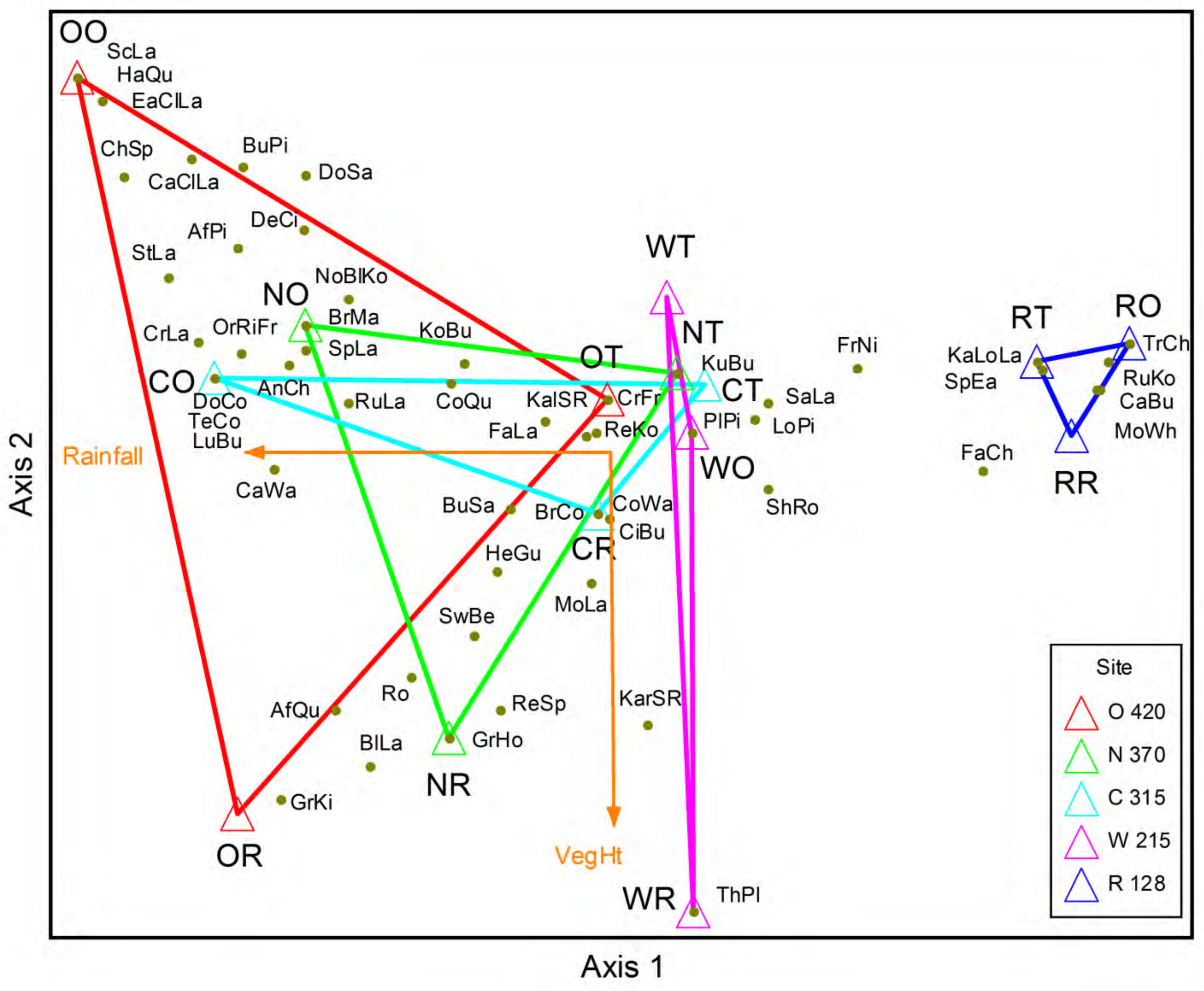

Figure 45 NMS ordination of 55 ground, ground-grass and ground-grass/shrub nesting species with habitats and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Two dimensions were derived. Final stress = 8.6. r^2: axis 1 = 58.4%, axis 2 = 28.5%, cumulative = 87%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket. Data manipulation: two species were removed because they carried greater weight than the others. Grey-backed Sparrow-Lark SD = 128, sum = 696 and Lark-like Bunting SD = 121, sum = 1033, average SD = 10. Average sum = 86.

The NMS biplot in Figure 45 is an ordination of 55 species that nest on or near the ground: ground, ground-grass and ground-grass/shrub nesting species were ordinated together.

Convex hulls of the four more mesic sites overlapped (Figure 45). R 128 ordinated far to the right of the rainfall vector ($r^2 = 0.694$ on axis 1). Vegetation height ($r^2 = 0.709$) correlated with axis 2. Ground, ground-grass, and ground-grass/shrub nesting species clustered at open and river habitat types of the three wetter sites, OO, NO, CO, OR, NR and CR. At the most arid site, seven species ordinated between RO, RR, and RT. They were Tractrac Chat, Ruppell's Korhaan, Cape Bunting, Mountain Wheatear, Spotted Eagle-Owl, Familiar Chat and Karoo Long-billed Lark.

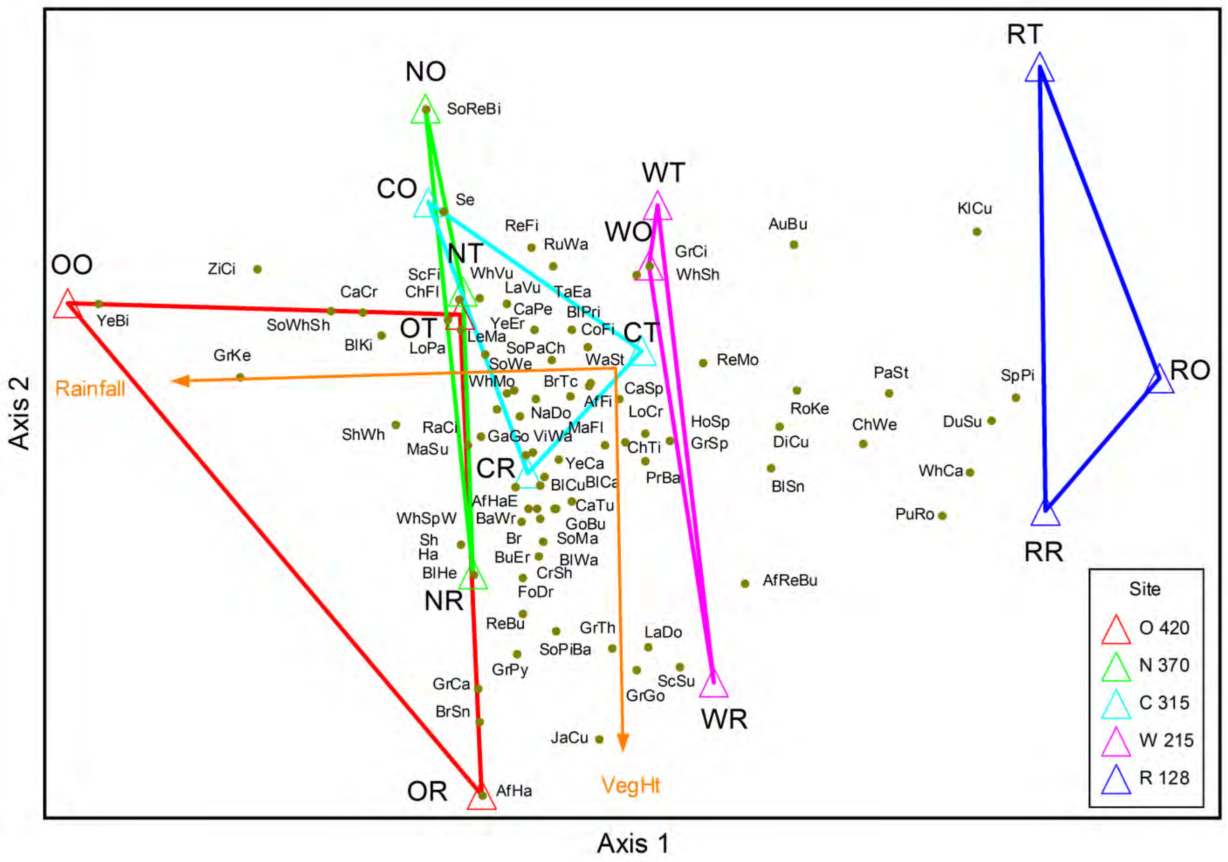

Figure 46 NMS ordination of 83 tree-shrub nesting species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 10.1. Three dimensions were derived. r²: axis 1 = 60.2%, axis 2 = 25.5, axis 3 = 6.9%, cumulative = 92.6%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 46 is an ordination of 83 species that nest in trees, shrubs or a combination of the two.

Rainfall (r^2 = 0.812) explained most of the site separation along axis 1 (r^2 = 0.602). Habitat types separated mostly along axis 2 (r^2 = 0.255), determined by vegetation height (r^2 = 0.700) . Most species ordinated towards river and thicket of the three wetter sites. Some of the species that preferred open habitat were Southern Red Bishop at NO, Grey-backed Cisticola at WO, Yellow-crowned Bishop, and Zitting Cisticola at OO.

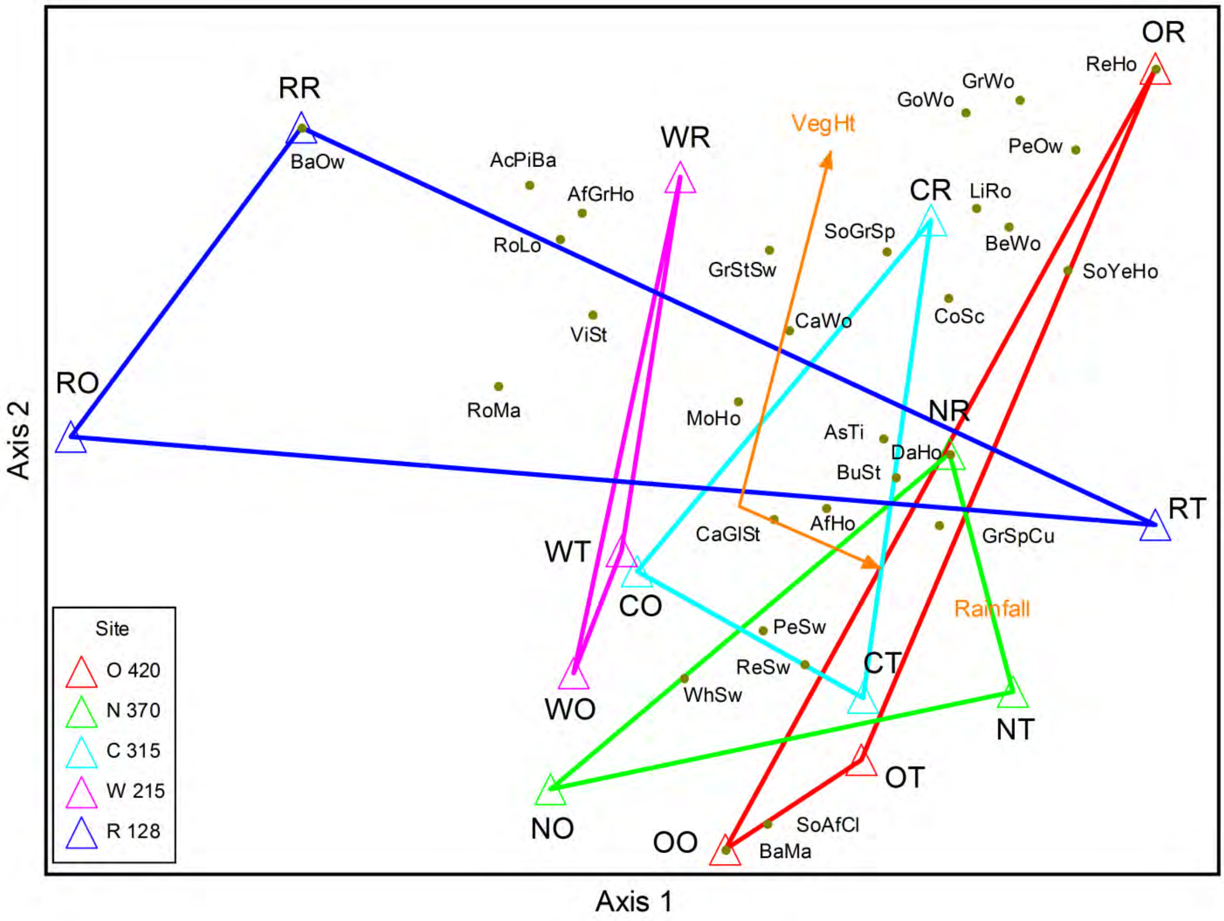

Figure 47 NMS ordination of 29 cavity and constructed nesting species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 11.5. Two dimensions were derived. r²: axis 1 = 56.9%, axis 2 = 29.9%, cumulative = 86.7%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 47 is an ordination of 29 species that nest in cavities or use constructed nests. Constructed nests are used by one martin and five swallow species. The remaining 23 are cavity nesters, including species that make their own cavities and those that use existing cavities.

Axis 1 ($r^2 = 0.569$) explained most of the species distribution in ordination space (only 2 axes were derived) (Figure 47). Species ordinated towards rivers where large trees and dead trees provide opportunities for cavity nesters (vegetation height $r^2 = 0.653$ on axis 2). Banded Martin, South African Cliff-Swallow and White-throated Swallow preferred more open habitat (OO). Pearl-breasted Swallow and Red-breasted Swallow ordinated towards thickets. Rainfall ($r^2 = 0.261$ on axis 1, $r^2 = 0.115$ on axis 2) contributed little towards explaining species distribution in ordination space.

Feeding guilds

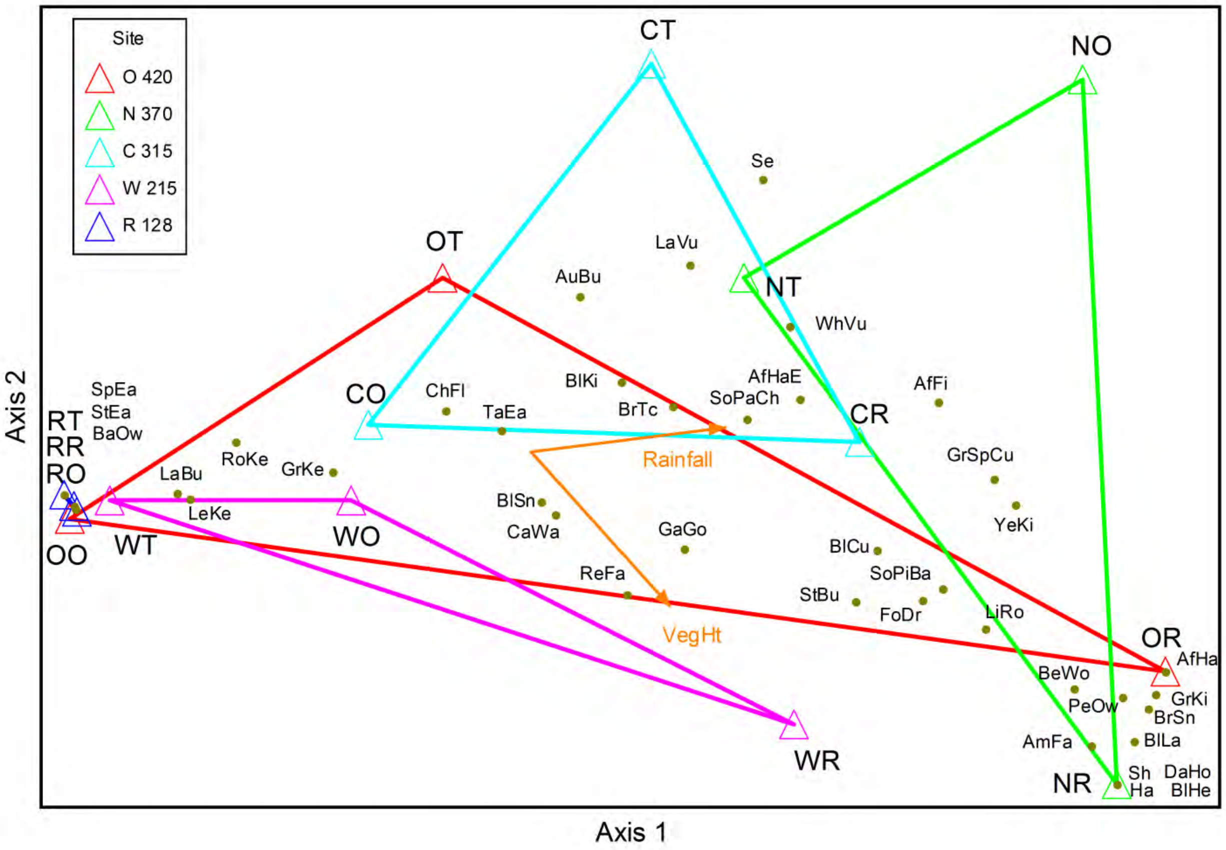

Figure 48 NMS ordination of 40 carnivore, carnivore/granivore, carnivore/insectivore and carrion species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 7.4. Two dimensions were derived. r²: axis 1 = 78.7%, axis 2 = 15.4%, cumulative = 94%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 48 is an ordination of 40 meat-eating species including raptors (carnivores); vultures (carrion); birds like the Lark-like Bunting (carnivore/granivore) that feed on insects as well as seeds and fruits; and carnivore/insectivore species.

Axis 1 (Figure 48, $r^2 = 0.787$) explained most of the species distribution in ordination space (only two dimensions were derived). The rainfall ($r^2 = 0.353$) and vegetation height ($r^2 = 0.251$) vectors correlated with axis 1. Vegetation height ($r^2 = 0.281$) correlated with axis 2, but axis 2 ($r^2 = 0.154$) contributed little to the interpretation of species distribution in ordination space. Lark-like Bunting, Greater Kestrel, Lesser Kestrel and Rock Kestrel preferred open habitat. Dry-tolerant species were Spotted Eagle-Owl, Steppe Eagle, and Barn Owl.

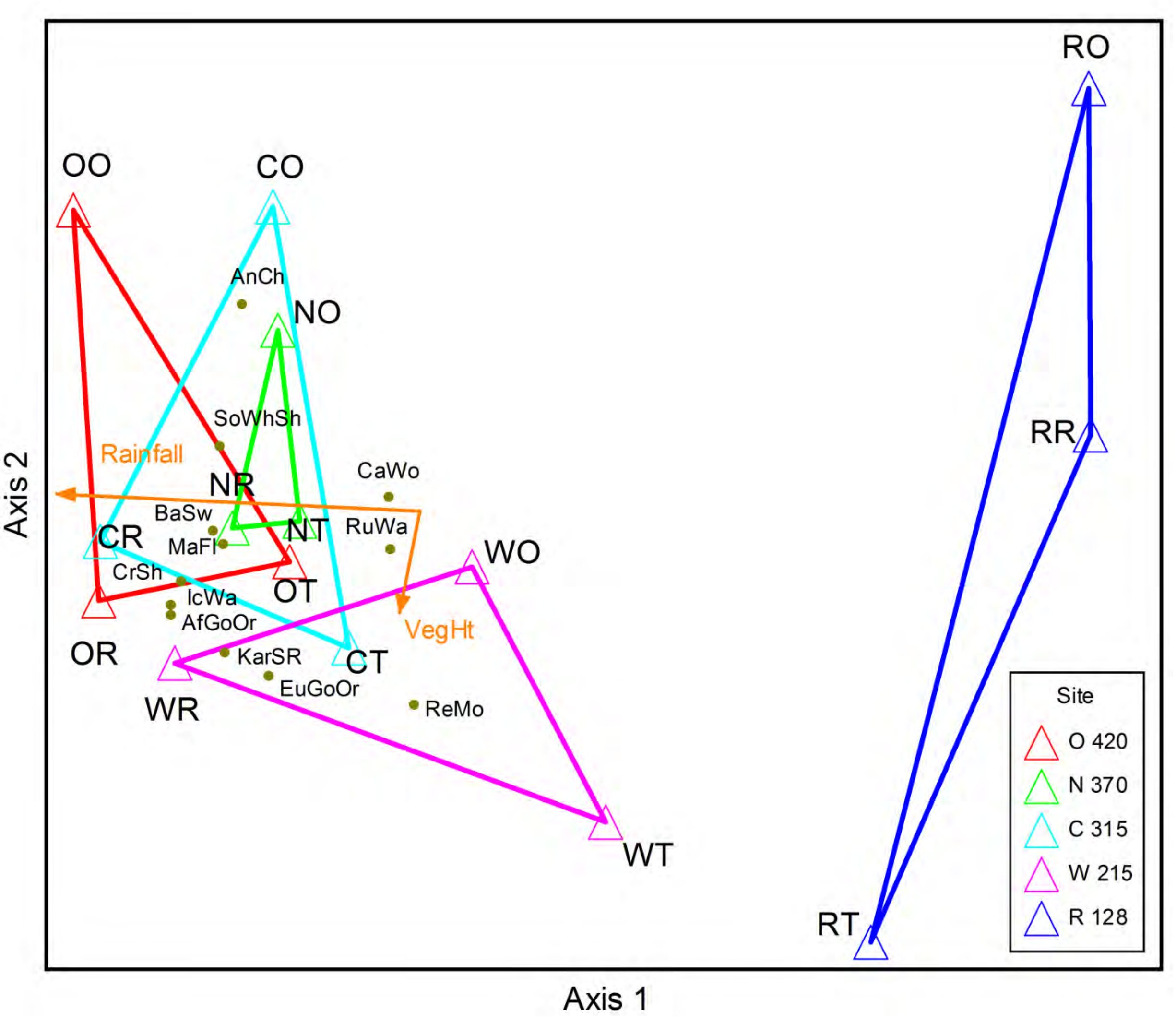

Figure 49 NMS ordination of 12 frugivore and insectivore/frugivore species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Sorenson (Bray-Curtis). Final stress = 10.7. Two dimensions were derived. r²: axis 1 = 62.6%, axis 2 = 20%, cumulative = 82.6%. Sample units:OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 49 is an ordination of 12 frugivore and insectivore/frugivore species.

Axis 1 ($r^2 = 0.626$) explained most of the species distribution in ordination space (Figure 49) (only two dimensions were derived) and it correlated with the rainfall vector ($r^2 = 0.715$ Figure 49). Vegetation height played a lesser part ($r^2 = 0.04$ on axis 1 and $r^2 = 0.198$ on axis 2).

Most species ordinated close together at rivers and thickets (Figure 49), and in the overlap of the convex hulls of the four wetter sites, indicating a relaxed area use where the individuals seem to travel to collect food. All species ordinated far from all habitat types at R 128, indicating fewer species and individuals of this guild associating with this site. Ant-eating Chat ordinated near OO, NO and CO, indicating that it preferred an open habitat type.

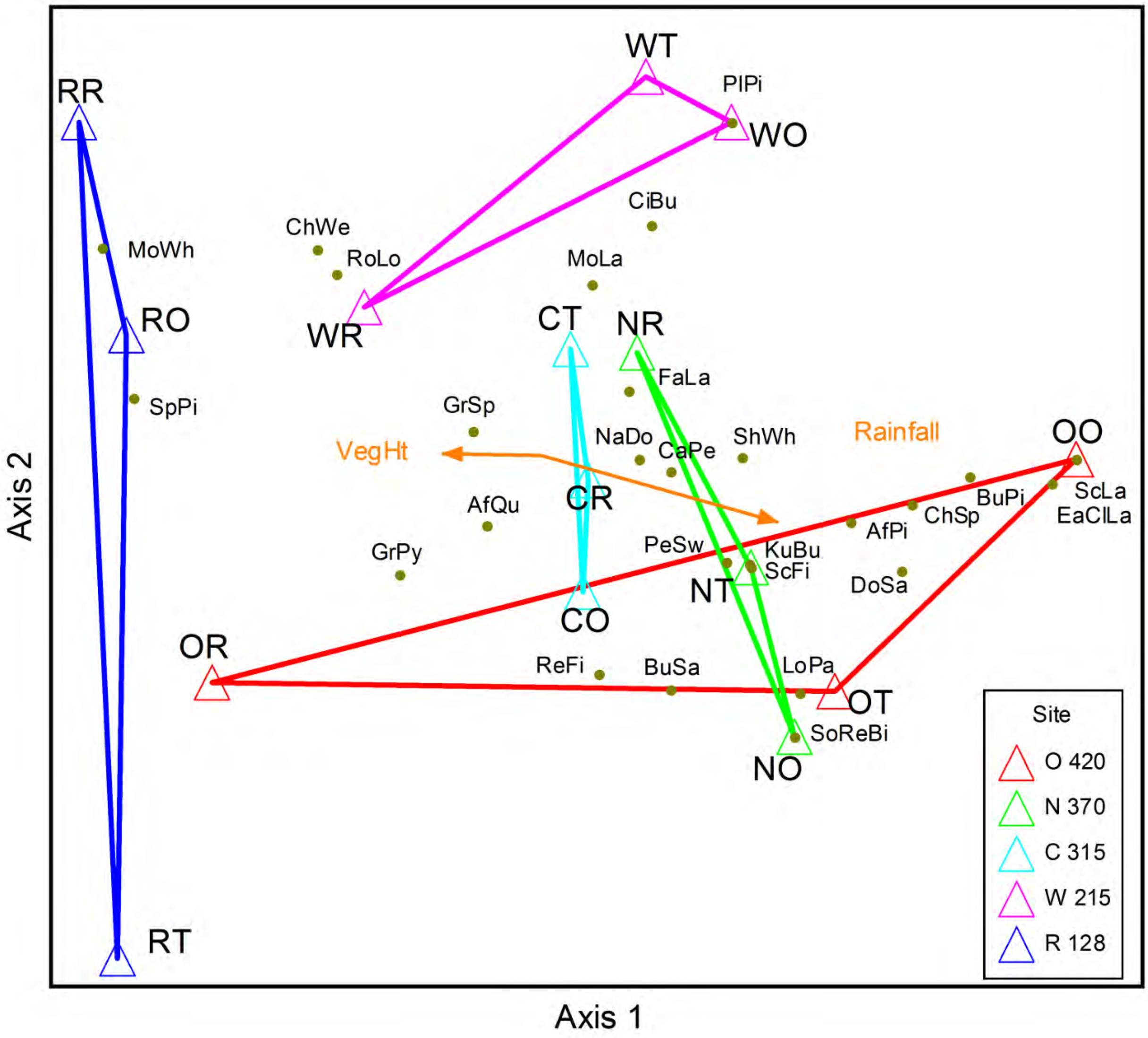

Figure 50 NMS ordination of 27 granivore and granivore/insectivore species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate sites.

Distance measure = Sorenson (Bray-Curtis). Final stress = 11.5. Two dimensions were derived. r^2: axis 1 = 50%, axis 2 = 34.4%, cumulative =84.3%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 50 is an ordination of 27 granivore and granivore/insectivore species. It included the Rosy-faced Lovebird which feeds on seeds, fruits, foliage and flowers.

Axis 1 ($r^2 = 0.5$) and axis 2 ($r^2 = 0.344$) explained the distribution of species in ordination space (Figure 49) (only two dimensions were derived). The rainfall vector explained most of the species distribution in ordination space ($r^2 = 0.474$ for axis 1 and $r^2 = 0.135$ for axis 2). Vegetation height contributed little to interpretation of species ordination ($r^2 = 0.197$ on axis 1 and $r^2 = 0.002$ on axis 2), and was almost opposite of rainfall for this guild. Dry-tolerant species were Rosy-faced Lovebird, Chestnut Weaver, Speckled Pigeon and Mountain Wheatear.

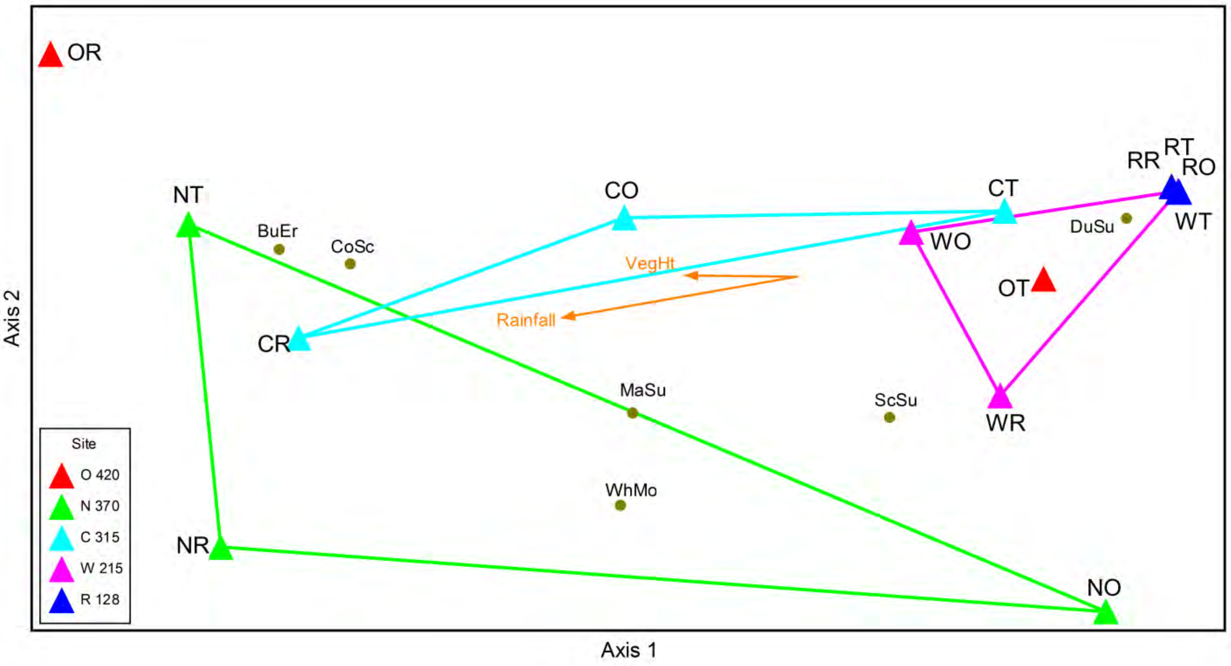

Figure 51 NMS ordination of six herbivore and insectivore/nectarivore species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites, exept for Okesawa (O).

Distance measure = Relative Sorenson. Final stress = 2.3. Two dimensions were derived. r^2: axis 1 = 93.5%, axis 2 = 4.8%, cumulative = 98.3%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket. Data manipulation: one sample unit, OO (open habitat at the most mesic site O 420), had no data and the row was removed from both the main and second matrices. The ordination was carried out with the remaining 14 sample units.

The NMS biplot in Figure 51 is an ordination of one herbivore (White-backed Mousebird) and five insectivore/nectarivore species.

Axis 1 explained almost all the species distribution in ordination space ($r^2 = 0.935$) (Figure 51) and it correlated with rainfall ($r^2 = 0.416$). Vegetation height ($r^2 = 0.198$) co-varied with the rainfall vector (only two dimensions were derived). The three sunbirds ordinated according to the rainfall vector. Marico Sunbird preferred wetter areas, Scarlet-chested Sunbird could handle drier habitats, and Dusky Sunbird was very common at the most arid site, R 128. At R 128, the three habitat types ordinated in one location, together with WT, suggesting that the Dusky Sunbird utilised all habitats available in very arid zones.

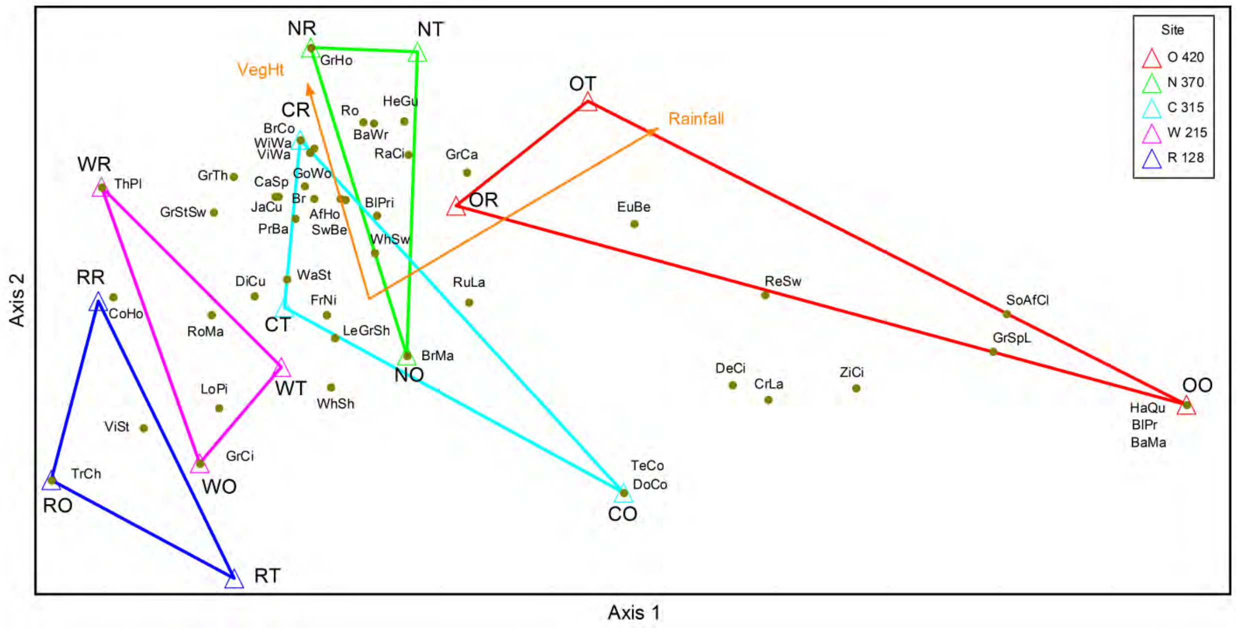

Figure 52 NMS ordination of 46 insectivore species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Sorenson (Bray-Curtis). Final stress = 13.3. Two dimensions were derived. r²: axis 1 = 62.7%, axis 2 = 16.1%, cumulative = 78.8%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 52 is an ordination of 46 insectivore species.

Axis 1 ($r^2 = 0.627$) explained most of the species distribution in ordination space (axis 2, $r^2 = 0.161$, only two dimensions were derived; Figure 52). Species clustered near rivers and thickets of N 370 and C 315. The rainfall vector explained most of the species distribution in ordination space ($r^2 = 0.509$ on axis 1 and $r^2 = 0.300$ on axis 2) while the vegetation height vector explained slightly more variation on axis 2 ($r^2 = 0.377$).

Three species ordinated at R 128, Tractrac Chat, Common House-Martin, and Violet-backed Starling. Species preferring open habitat in wetter areas were Banded Martin, Black-winged Pratincole and Harlequin Quail at OO. The other species preferring open habitat types were Zitting Cisticola, Crowned Lapwing, Desert Cisticola, Double-banded Courser, Temminck’s Courser, Brown-throated Martin and Grey-backed Cisticola.

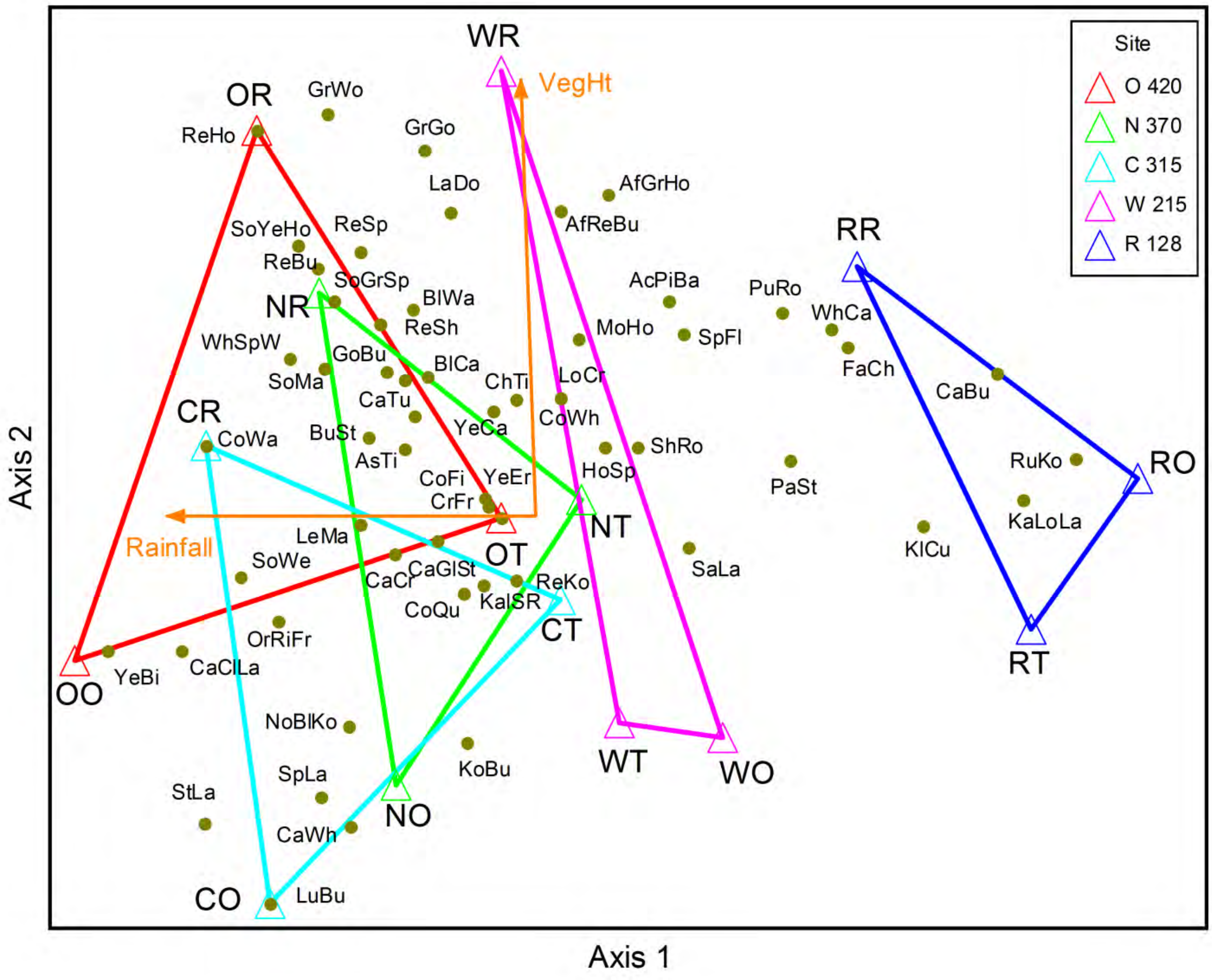

Figure 53 NMS ordination of 57 omnivore species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 10.8. Two dimensions were derived. r²: axis 1 = 49.7%, axis 2 = 36.3%, cumulative = 85.9%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 53 is an ordination of 57 omnivore species.

Axis 1 ($r^2 = 0.497$) and axis 2 ($r^2 = 0.363$, only two dimensions were derived) explained the omnivore ordination in species space (Figure 53). Open habitat ordinated towards the bottom of the diagram, thickets in the middle, and rivers at the top. Rainfall ($r^2 = 0.693$) corresponded with axis 1 and vegetation height ($r^2 = 0.821$) with axis 2.

Omnivore species ordinated in all habitats, clustering at rivers and thickets in the overlap between the convex hulls of O 420, N 370 and C 315 (Figure 53). Species on the arid side of the rainfall vector included Ruppel’s Korhaan, Karoo Long-billed Lark, Cape Bunting, Klaas’s

Cuckoo, Familiar Chat, White-throated Canary, Purple Roller, Pale-winged Starling, Spotted Flycatcher, Acacia Pied Barbet, Sabota Lark and Short-toed Rock Thrush. The convex hull of the most arid site did not overlap with the other sites. The twelve dry-tolerant species seemed to use all three habitat types at the site, whereas the wetter species associated more with a specific habitat type.

Omnivore species that preferred open habitat include Capped Wheatear, Ludwig's Bustard and Stark's Lark. Rivers were preferred by Green Woodhoopoe and Red-billed Hornbill (OR), and thickets (OT/NT overlap) contained Common Fiscal, Crested Francolin, and Yellow-bellied Eremomela.

4.7.5 Movements and migrations

Birds were categorised into four groups based on their movement and migration patterns:

- Breeding migrant and breeding migrant/resident species
- Non-breeding migrant species
- Resident species
- Nomadic and nomadic/resident species

A separate NMS ordination was done for each group. Abundances (number of birds per species observed) were used in the primary matrix for all the movement ordinations. The primary matrix consists of the species represented in each group (columns) against the 15 sample units (rows). The secondary matrix for all the movement ordinations had four environmental variables: site, habitat type, vegetation height, and rainfall. Species names and the abbreviations used in ordinations are given in Table 3.

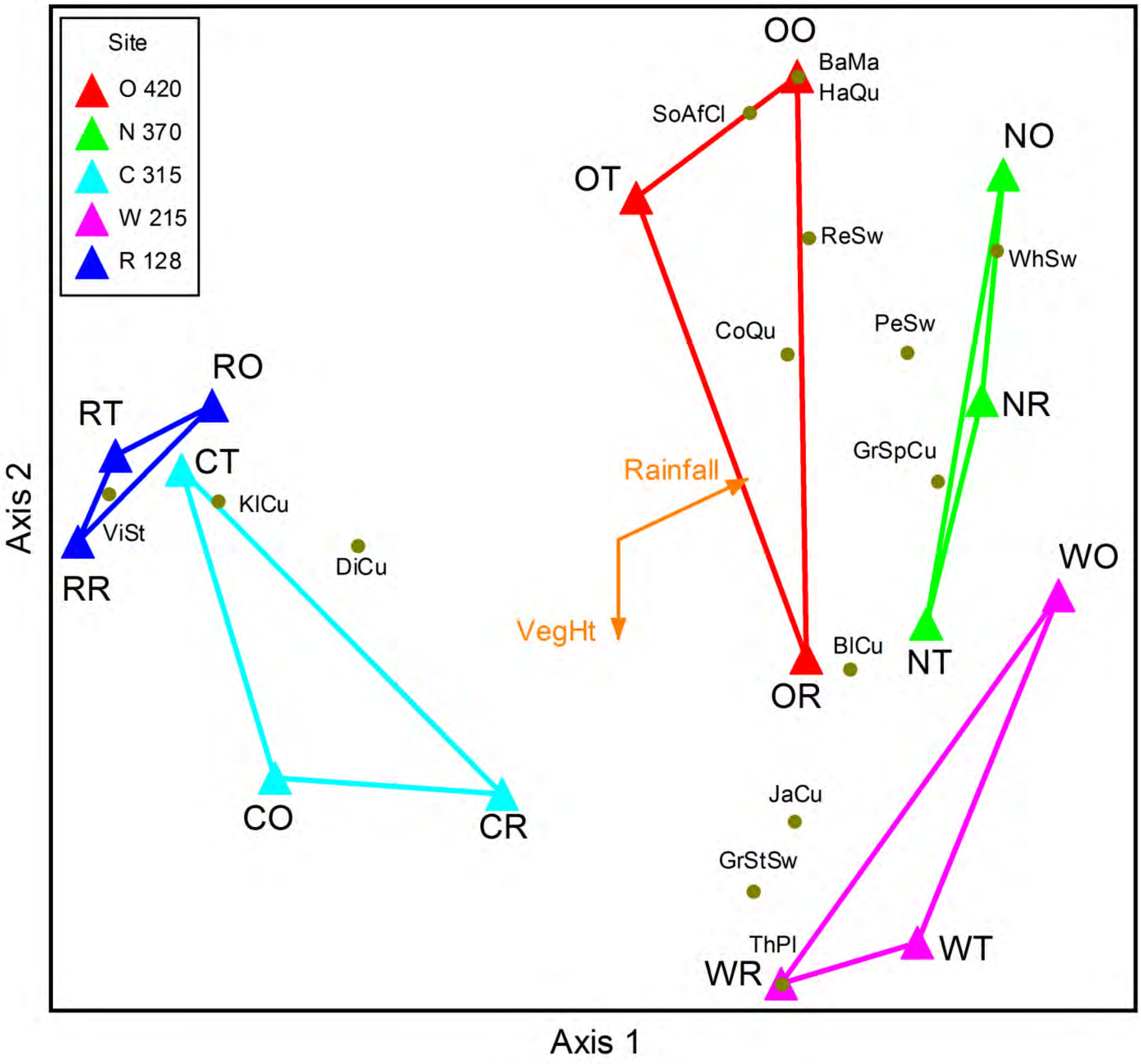

Figure 54 NMS ordination of 15 breeding migrant and breeding migrant/resident species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate sites.

Distance measure = Relative Sorenson. Final stress = 4.3. Three dimensions were derived but only dimensions 1 and 2 are shown. r^2: axis 1 = 46.6%, axis 2 = 32.3%, axis 3 = 16.4%, cumulative = 95.3%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket. Data were manipulated because no useful ordination was initially obtained. Outlier analysis indicated no outliers. Row-column summary indicated two species with much greater SD and sum than average. They were removed before analysis (Figure 54). Rock Martin SD = 26, sum = 348, Cinnamon-breasted Bunting SD = 15, sum = 121, average SD = 4, average sum = 41. Cinnamon-breasted Bunting was common at WO, WT and NR, while Rock Martin was common at RO, RR, WO and WR (Appendix A).

The NMS biplot in Figure 54 is an ordination of 15 breeding migrant and breeding migrant/resident species.

Axis 1 ($r^2 = 0.466$) and axis 2 ($r^2 = 0.324$) explained species distribution in ordination space (Figure 54). Three dimensions were derived, but axis 3 ($r^2 = 0.163$) is not shown. On axis 1, rainfall ($r^2 = 0.261$) explained most of the species distribution and on axis 2, vegetation height ($r^2 = 0.201$) played the greater part.

Open habitat species of the breeding migrant and breeding migrant/resident guild were Banded Martin, Harlequin Quail, South African Cliff-Swallow, Red-breasted Swallow, White-throated Swallow and Pearl-breasted Swallow. Species preferring rivers and thickets were Great Spotted Cuckoo, Diderick Cuckoo, Klaas's Cuckoo, Black Cuckoo, Jacobin Cuckoo, Greater Striped Swallow and Three-banded Plover. Dry tolerant species were Violet-backed Starling, Klaas's Cuckoo and Diderick Cuckoo (Figure 54).

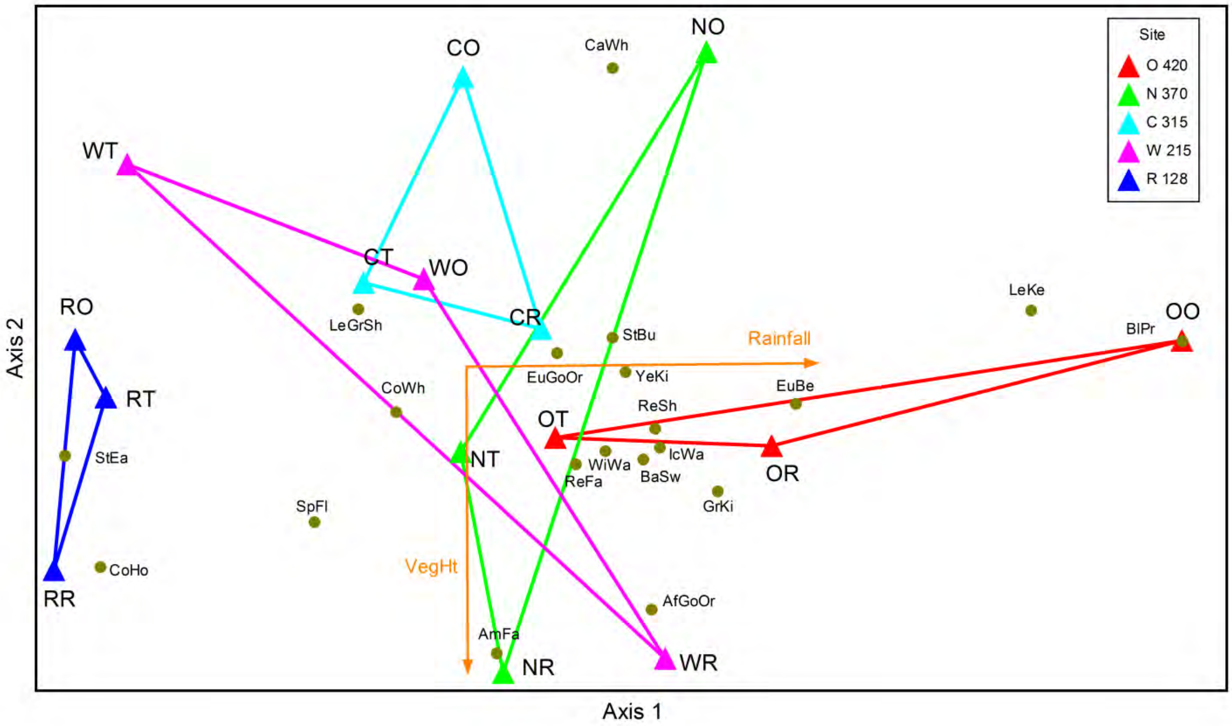

Figure 55 NMS ordination of 20 non-breeding migrant species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 11. Two dimensions were derived. r^2: axis 1 = 60.9%, axis 2 = 22%, cumulative = 82.9%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 55 is an ordination of 20 non-breeding migrant species.

Rainfall ($r^2 = 0.622$) corresponded with axis 1 ($r^2 = 0.609$) and vegetation height ($r^2 = 0.542$) with axis 2 ($r^2 = 0.220$) (two dimensions were derived) (Figure 55). Non-breeding migrant species distribution in ordination space was determined by rainfall and vegetation height combined, with most birds ordinating near rivers and thickets of the three mesic sites, O 420, N 370 and C 315.

Dry tolerant birds were Steppe Eagle and Common House-Martin (Figure 55).Three species preferred open habitat: Capped Wheatear (between NO and CO), Lesser Kestrel and Black-winged Pratincole (near OO).

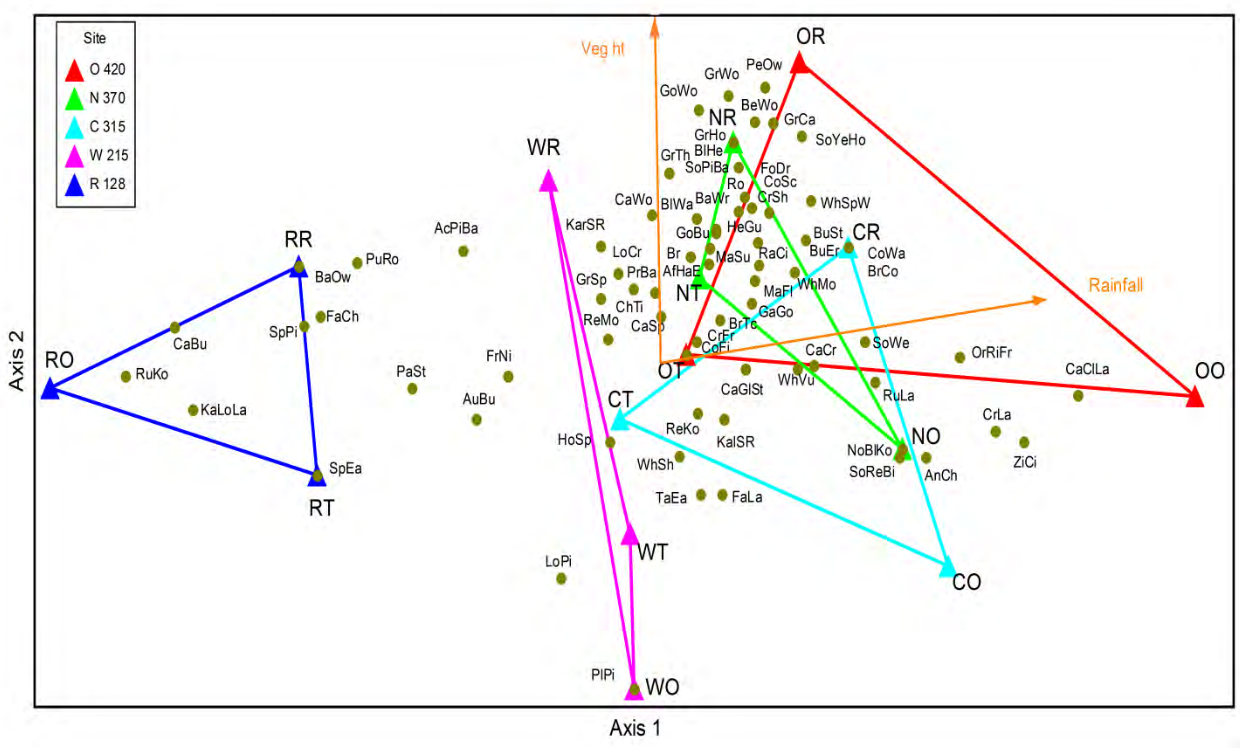

Figure 56 NMS ordination of 73 resident species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate the sites.

Distance measure = Relative Sorenson. Final stress = 8.6. Two dimensions were derived. r²: axis 1 = 71.3%, axis 2 = 14.6%, cumulative = 85.9%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 56 is an ordination of the 73 resident species.

Species distribution in ordination space were explained by a combination of rainfall ($r^2 = 0.672$ on axis 1) and vegetation height ($r^2 = 0.723$ on axis 2) (Figure 56). Two dimensions were derived, with axis 1 ($r^2 = 0.713$) explaining most of the variation. Most resident species ordinated near rivers and thickets of O 420, N 370 and C 315. Dry tolerant resident species were Spotted Eagle-Owl, Ruppel’s Korhaan, Karoo Long-billed Lark, Cape Bunting, Barn Owl, Speckled Pigeon, Familiar Chat, Purple Roller, Pale-winged Starling, Augur Buzzard, Freckled Nightjar and Acacia Pied Barbet.

Resident species preferring open habitat at the three more mesic sites were Cape Clapper Lark, Zitting Cisticola, Crowned Lapwing, Orange River Francolin, Ant-eating Chat, Northern Black Korhaan, Southern Red Bishop, Rufous-naped Lark and Sociable Weaver. Plain-backed Pipit ordinated in drier open habitat, WO (Figure 56).

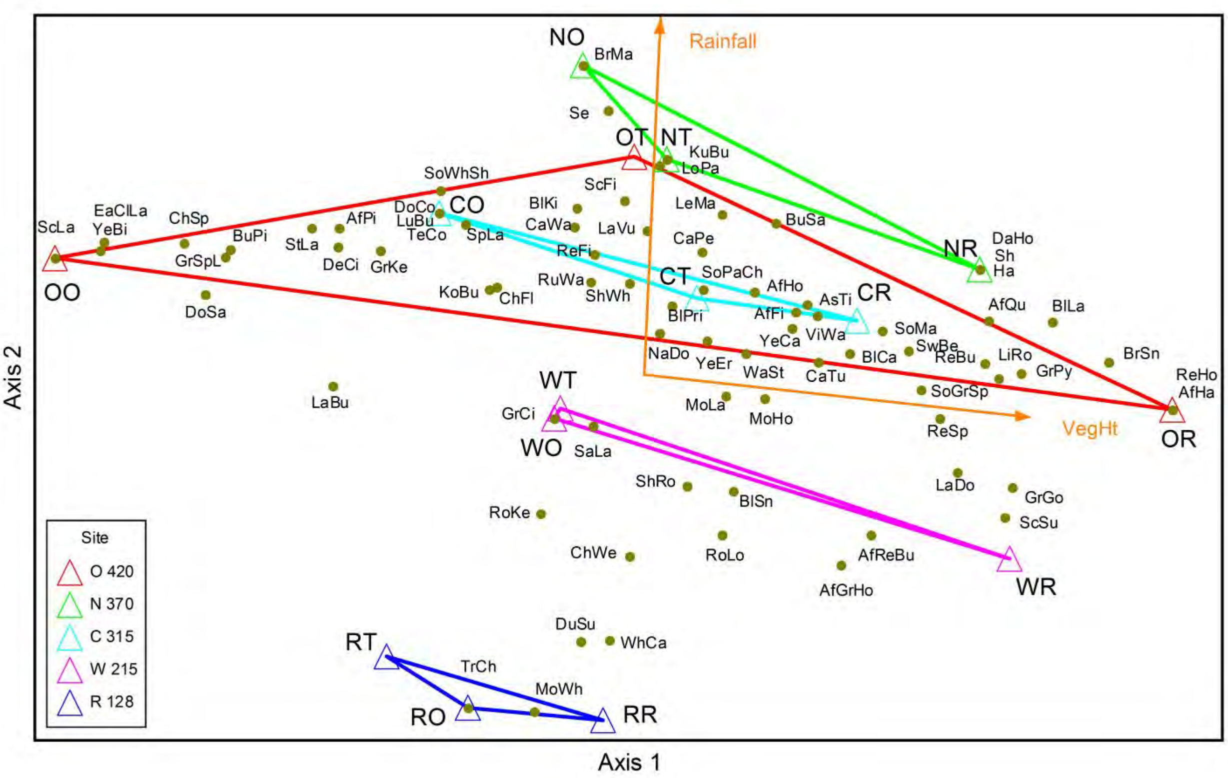

Figure 57 NMS ordination of the 78 nomadic and nomadic/resident species with sites and environmental factors rainfall and vegetation height. Convex hulls indicate sites.

Distance measure = Relative Sorenson. Final stress = 9.4. Two dimensions were derived. r²: axis 1 = 51.5%, axis 2 = 35.5%, cumulative =87%. Sample units: OO: 420 Open, OR: 420 River, OT: 420 Thicket, NO: 370 Open, NR: 370 River, NT: 370 Thicket, CO: 315 Open, CR: 315 River, CT: 315 Thicket, WO: 215 Open, WR: 215 River, WT: 215 Thicket, RO: 128 Open, RR: 128 River, RT: 128 Thicket.

The NMS biplot in Figure 57 is an ordination of the 78 nomadic and nomadic/resident species.

Species distribution in ordination space were determined by a combination of habitat type (vegetation height $r^2 = 0.689$ on axis 1) and rainfall ($r^2 = 0.739$ on axis 2) (Figure 57). Two dimensions were derived.

Nomadic and nomadic/resident species in open habitat ordinated along the rainfall vector with most of them on the wetter side, near O 420, N 370 and C 315 (Figure 57). In rivers and thickets, nomadic and nomadic/resident species ordinated towards the positive side of the rainfall vector, clustering at rivers of the three most mesic sites, OR, NR, and CR. Arid-adapted species ordinated in all three habitat types. At R 128, no species ordinated near thickets.

5 Discussion and conclusions

Avian community patterns are useful indicators of how environmental changes modify the functioning of ecosystems (Hausner *et al,* 2003; Read *et al,* 2000); therefore, the insights gained through studying bird assemblages can be used in the conservation of biodiversity, predict what might happen in the face of climate change, and allow therefore an anticipatory and planning aproach. The focus of this study was to describe how bird assemblages changed along an aridity gradient and between habitat types (section 1.3.1). The effect of rainfall and habitat on avian bird variables (species richness, abundance, diversity, biomass and life history traits) was investigated. The discussion in this chapter will show how the results presented in Chapter 4 provided evidence for the testing of the hypothesis that bird species assemblages are affected primarily by rainfall and secondarily by habitat across an aridity gradient.

The species composition of a local community is determined by the addition of species through colonisation, and by the loss of species through local extinction (Wiens, 1989a). Two factors affecting the gain and loss of avian species in a community, rainfall and habitat, were investigated. Assessing community structures were based on the ecology of bird species and the interactions between the avifauna and ecosystems of the study area.

5.1 Species-accumulation curves

Species-accumulation curves indicate whether the sample size in a community data set is adequate to give reliable results. Figure 19 shows that hardly any new species were added after 40 transects, so the 51 transects sampled were sufficient to investigate the hypothesis that bird communities in arid areas are affected by rainfall and habitat.

5.2 Identifying groups

Each transect had the same length (one km), and each transect sampling was of the same approximate duration. Surveys were assumed to be equal-effort, and therefore considered as comparable between sites and habitats. Sampling was stratified by site according to rainfall and further by habitat according to three structurally different vegetation types. For analysis, an *a priori* grouping was done by combining transect data into sampling units. The cluster dendrograms in Figure 20 and Figure 21, together with MRPP results, indicate sufficient homogeneity between sample units to justify this approach. The individual transect data were therefore combined per habitat, per site.

5.3 Removing non-contributive species

Trends in species richness, abundance and diversity were compared between all observed species included vs non-contributive species removed. Univariate analyses of species richness (Figure 23 vs Figure 27), abundance (Figure 24 vs Figure 29) and bird diversity (Figure 25 vs Figure 32), showed a similarity in trends between all species included, and with non-contributive species removed. This similarity in trends informed the decision to exclude species on ecological grounds (Table 5), and analyses were done with the remaining 188 species.

5.4 Environmental factors

5.4.1 Habitat

Bird species require vegetation patches, each with a particular profile, for their selected habitats, and the variety of patches of vegetation within a habitat determines the variety of bird species breeding there (MacArthur *et al*, 1962). Bird species responding indirectly to changing climates via direct climatic effects on plants (Kissling, 2008) can obscure conclusions on the extent of climatic impact on bird communities; consequently, the effect of aridity on bird communities can only be explored by taking into account the interactions between rainfall and vegetation. Combining climate and habitat variables allows more accurate predictions of the direct and indirect impacts of climate change on avian communities (Barbet-Massin *et al,* 2011; Matthews *et al*, 2011.

The rainfall and vegetation height vectors were perpendicular to each other in all NMS ordinations, except the one for six herbivore and insectivore/nectarivore species (Figure 51). Therefore, rainfall and vegetation height did not co-vary indicating that these two factors were independent of one another, regarding bird community patterns.

Bird community patterns are determined, among other factors, by the vertical structure of vegetation (Seymour & Dean, 2011). In terms of vegetation height, there was strong within-habitat homogeneity regardless of aridity (Figure 18), as expected in a data set based on sampling stratified by habitat. Habitat accounted for more than 92% of variance and $p < 0.0001$ (2-way ANOVA). The NMS ordination of sample units (Figure 40) supported this conclusion and illustrated how habitats correlated with vegetation height and sites with rainfall (Pearson and Kendall Correlations, Table 11). Rivers had the tallest plants, open habitat the lowest and thickets ordinated in the middle of the vegetation height vector. Strong correlation with rainfall was indicated at the driest site, R 128, the wettest, O 420, and the middle site, W 215.

Each of the three more arid sites, C 315, W 215 and R 128, had more in common with itself than with any other site, illustrated by no overlap of their convex hulls with any other site (Figure

40). Environmental factors at N 370 were similar to those at the river and thicket habitats of O 420, but open habitat at O 420 (OO) had different environmental factors than open at the other sites. The effect at OO is discussed in section 5.7. The convex hull of the most mesic site, O 420, (Figure 41) is noticeably longer than those of the other sites and parallel to vegetation height. There is more heterogeneity in the vegetation structure at O 420, which explains the high number of species ordinated along the convex hull. In arid zones: a variety of patches of vegetation is needed to maintain avian diversity (Child *et al*, 2009; MacArthur, 1964); O 420 is an example of patches that support various bird populations.

The NMS ordination of abundance and habitat (Figure 42), showed the rivers ordinating in line with tallest vegetation, open habitat at the opposite end of the vegetation height vector, and thickets in the middle. Each habitat had a set of ecological factors governing bird communities distinct from every other habitat, whereas patterns of species composition were determined by rainfall. The highest number of birds was observed at the three more mesic sites: between rivers and thickets, and then also in open habitat.

5.4.2 Altitude

Altitude *per se* was not investigated as to its effect on avian community patterns. Tingley *et al* (2012) found that climate change caused elevational range shifts in birds (51% of species shifted upslope as predicted), but that changes in temperature or precipitation better accounted for range shifts (82% of range shifts were in a direction predicted by either temperature or precipitation). In this study, altitude co-varied with the aridity gradient in the NMS ordinations. The difference between the highest site (N 370) and the lowest (R 128) was 780 m. R 128, the most arid site, lies at the foot of the Namibian escarpment, while the other sites are on the Khomas Hochland Plateau.

5.4.3 Seasonal variation

There was an across season consistency in bird assemblages during the three years of sampling. No significant difference was found in species richness during winter from year to year or during summer from year to year (1-way ANOVA, $p > 0.1$, $r^2 = 0.335$) (Figure 38). It can be concluded that, during the three years of sampling, no environmental event occurred that had a significant effect on species composition in the study area. There was no severe drought, exceptional rainfall, or temperature event that caused wide-spread range shifts in species.

There was, however, a significant variation in bird assemblages between summer and winter. In summer there were more species than in winter, and there were many more individuals of each species than in winter.There was a difference in species richness of 10-80% between summer and winter (Paired t-test, $p < 0.0001$) (Figure 36). Abundances differed even more between winter and summer, from minus 30% to 80% (Paired t-test P, = 0.0044) (Figure 37). Mantel tests confirmed these results.

Habitat had a significant effect on bird assemblages across seasons because of diminished resources in the dry season. The semi-arid ecosystems of Southern Africa are characterised by wet and dry states that are patchy in time and space (Dean *et al*, 2009). In very arid conditions, bird assemblages in thickets were most affected by the reduced resources available in winter. Species and numbers of birds both declined significantly (difference = 80%) in thickets at the most arid site, R 128 (Figure 36) and (Figure 37). In open habitat at R 128, there was a decline in numbers but not in species, and the seasonal effect in river lines was close to the mean. This suggests that resident birds in very arid zones move from thickets to other habitats when food becomes scarce and utilise resources wherever they find them. The effect of natural population culling (deaths) after the summer breeding season might also play a role, but it has not been studied here. Open areas at the three most arid sites showed a decline in abundance of around 50% during winter, indicating low carrying capacity in this structurally homogenous habitat.

River lines at W 215 (difference = -31.3%) and C 315 (difference = -24.4%) had more birds in winter than in summer (Figure 37), even though there were more species in summer (Figure 36). Abundance by habitat (Figure 29) confirmed this trend: bird numbers remained constant in rivers across the aridity gradient, except at C 315 where there was an increase in the number of individuals per species observed. It is likely that birds move from other habitats, especially from open areas, into dry river lines as resources declined in open areas of W 215 and C 315 (Figure 37). Rivers acting as corridors between patches of suitable habitat enhances the probability of local populations being maintained via migration between patches (Wiens, 1989b).

5.5 Species richness

The most important determinant of community patterns is the species that make up the community (Wiens, 1989a). Rainfall played the most important role in species distribution and there were more species in river lines than in open or thicket habitat types.

Species richness across the aridity gradient remained constant until a certain aridity threshold was reached (1-way ANOVA, p = 0.0066) (Figure 26). There was a sharp decline in mean species numbers at the most arid site, R 128. Habitat structure also played a role in species richness, with rivers remaining more constant than the other two habitat types and thickets losing species rapidly (Figure 27). The importance of dry river lines was emphasized by the fact that rivers had 20 indicator species while open had six and thickets only two (Table 12).

The theory of metapopulations states that the individuals of species are not grouped into isolated populations, but are composed of local populations, connected to each other by a recurrent exchange of migrants (Begon *et al*, 1996). That population dynamics operate within patches and between patches (Begon *et al*, 1996) was evident in this study and especially so in river lines acting as refuges for species and individuals. Large trees provide a variety of resources for birds (Dean, 1999; Steyn, 1996); in the study area, dry river lines are the only habitat type where this can be found.

The impact of rainfall and habitat type on species richness was illustrated by Figure 26 and Figure 27. Rainfall explained 52.4% and habitat type 34.5% of variation. In the NMS ordination of species richness (Figure 39), rainfall was the most significant determinant ($r^2 = 0.834$). The significance of rainfall in the distribution of species was further indicated by the convex hulls of the sites not overlapping. Each site had more in common with itself than with any other site regarding bird species composition. Each site therefore, had its own, discrete, avian composition. Figure 27 suggests a threshold (tipping point) of about 250 mm rain per year below which species richness will decline sharply.

The species that ordinated on the arid side of the rainfall vector (Figure 39) may be important in predicting future changes in bird community composition as a result of climate change. The 12 species that ordinated closest to R 128 were the Barn Owl, Cape Bunting, Common House-Martin, Freckled Nightjar, Klaas's Cuckoo, Mountian Wheatear, Ruppell's Korhaan, Speckled Pigeon, Spotted Eagle-Owl, Steppe Eagle, Tractrac Chat and Violet-backed Starling. Four of these are indicator species for R 128: Cape Bunting, Klaas's Cuckoo, Steppe Eagle and Violet-backed Starling.

5.6 Abundance

If the climate becomes drier and hotter as forecast in climate change scenarios (Hockey *et al,* 2011; IPCC, 2001; IPCC, 2007; McClean *et al,* 2005; Van Jaarsveld & Chown, 2001), it may be predicted that currently mesic sites will lose species while being colonised by dry-tolerant birds from the dry side of the aridity gradient (Figure 41). In-moving species won't be limited because most of them are already present at the currently mesic sites. The effects of bird species dispersal between local populations conform to the stepping-stone model, described by Begon *et al* (1996) as a tool for explaining how dispersal contributes to the colonisation of habitable sites.

Abundance referred to aggregate values and for the purposes of this study was defined as the total number of individual birds per species observed. The total number of birds observed increased from arid to mesic (Appendix A, totals). Habitat type played a more significant role in bird numbers than in species composition. In river lines, bird assemblages were similar regardless of aridity. In thickets and open areas, bird numbers decreased from mesic to arid (Figure 29). Simmons & Seymour (2010) suggested that dry river lines could play an increasingly important role in bird species diversity as global climate change creates more arid regions (Simmons & Seymour, 2008). The findings in this study concurred with theirs.

The mean number of birds per site did not vary significantly across the aridity gradient (Figure 28) (1-way ANOVA, $P=0.294$, Bonferroni post-test, $p > 0.05$ for all pairings). On the other hand, there was a significant difference in bird numbers when comparing the habitat types (Figure 29; 2-way ANOVA, Habitat $p < 0.05$). The NMS ordination of abundance (Figure 41) showed that rainfall and habitat type played an almost equal part ($r^2 = 0.592$; Table 11) in explaining patterrns of abundance.

The overall trend was that riparian habitats contained the highest number of birds; followed by thickets; and open areas had the lowest abundance (r^2: axis 1 (vegetation height) = 0.498, axis 2 (rainfall) = 0.378) (Figure 41). In thicket and open habitats, bird numbers increased from arid to mesic (Figure 29).

In rivers, bird numbers remained constant, except at C 315 in the middle of the aridity gradient where more birds were observed than in the other rivers (Figure 29). Rivers at C 315 and W 215 were the only two sites where more birds were observed in winter than in summer (Figure 37). An explanation for this effect is that birds move into river habitat from surrounding habitats when resources become scarce, as happens in winter. At the two most mesic sites, the effect did not take place, probably because the habitat types are more clearly differentiated (Figure 40) and the decline in resources is not as drastic as in more arid landscapes. The effect did not occur at the most arid site either, because regardless of preferred habitat type, birds utilised the three habitat types at R 128 throughout the year due to scarceness of resources.

The three habitats at R 128 had more in common with one another than with the same habitat at any of the other four sites (Figure 39, Figure 41 and Figure 42). The long distance between the convex hull of R 128 and the rainfall vector (Figure 40, $r^2 = 0.592$) illustrated the impact of very arid conditions on species richness, abundance and diversity, and confirmed the effect of the aridity threshold.

The large number of birds in rivers and thickets of the three more mesic sites highlighted the role of habitat structure in bird assemblages (clusters in Figure 41 and Figure 42).

Heterogeneity in vegetation structure at O 420 (mentioned in section 5.4.1) explained why so many birds were present at this site. In Figure 40 and Figure 42, open habitat at the most mesic site (OO) ordinated far to the bottom right, indicating a strong correlation with short vegetation. Open areas on the farm Okasewa are bush cleared, used extensively for commercial cattle grazing, and consist of grass with scattered small forbs. Open habitats at the other four sites consist of grass, forbs and scattered shrubs or small trees. Figure 28 suggests that abundance will sharply decrease between 420 and 370 mm rain per year.

5.6.1 Total bird biomass

Total bird biomass is a result of abundance rather than a determining factor; therefore variations in bird biomass at the sites are expected to be commensurate with variations in bird numbers. Rainfall explained 84% of the variance in total bird biomass while the role of habitat was negligible (2-way ANOVA, Bonferroni post-test: Habitat $p = 0.62$, Rainfall $p < 0.005$) (Figure 35). The NMS ordination of abundance (Figure 41) confirmed this conclusion with birds clustering in line with the mass and rainfall vectors. Walther & Van Niekerk (2014) found that climate change will have statistically significant effects on body mass frequency distributions.

5.7 Diversity

Diversity measures incorporate species richness, commonness and rarity; consequently, diversity is an indication of the character of a community (Begon *et al*, 1996).

Since avian diversity in general is higher in wet than in dry regions (Hockey *et al*, 2005), bird diversity is expected to decrease from mesic to arid in the study area. Diversity remained constant across the aridity gradient until the aridity threshold was crossed at R 128 (Figure 30), where there was a decline in diversity in all three habitats (Figure 32). Rainfall was the main determining factor for bird diversity (2-way ANOVA, $p < 0.1$, rainfall explained 42% of variance) (Figure 30 and Figure 31).

The aridity threshold at R 128 can be further explored from Figure 32. There was a decline in bird diversity in open habitat and thickets and a lesser decline in rivers. In arid zones, dry river lines contain higher levels of bird diversity than the surrounding landscapes, a factor that should be considered when making conservation decisions at landscape and regional level.

At R 128, bird diversity in rivers and thickets may be affected by records of birds usually associated with open areas (Figure 41). Many species recorded in R 128 river and thicket were observed at a distance of up to 80 m perpendicular from the centre of the transect. Some birds were identified by vocalisation only, particularly the Karoo Long-billed Lark, Ruppel's Korhaan and Sabota Lark. Estimating the perpendicular distance of a bird that was heard and not seen, is less accurate than with visual identification, especially since sound carries far in areas as sparsely vegetated as R 128. It is not conclusive that all the birds recorded in rivers and thickets at R 128 were utilising resources in those habitats. However, it does seem likely, considering that there is less differentiation between the structures of the three habitats at R 128 than at the other sites. This conclusion was substantiated by NMS ordinations of richness with sites (Figure 39) abundance with sites (Figure 41), abundance with habitat types (Figure 42), and indicator species with sites (Figure 43), all of which showed that there were more similarities between the three habitats at R 128 than similarities between R 128 and the other sites.

An increase in species richness (Table 6) and abundance (Appendix A) across the aridity gradient led to the expectation of increased bird diversity at the most mesic site. Nevertheless, there was an unexpected decline in diversity at O 420, especially noticeable in open habitat (Figure 32).

It has already been shown (section 5.3) that the exclusion of occasional migrants and other species did not affect general trends in bird diversity across the aridity gradient. The decline in species richness and diversity in open habitat at O 420 may be explained by two factors: (1) ecology of individual species, and (2) ecology of the site.

(1) Ecology of species (Hockey *et al*, 2005)

Species absent from open at O 420, but present in open at two or more other sites (Table 7):

- Black-chested Snake-Eagle: indicator species for rivers.
- Black-throated Canary: absent in all habitats at O 420. The site falls within its range but it is locally nomadic.
- Dusky Sunbird: abundant at R 128 and decreases at O 420, where it was observed only 4 times in thickets. O 420 is at the eastern edge of its range in Namibia.
- Familiar Chat: abundant at 218, absent in all habitats at O 420. O 420 is at the eastern edge of its range in Namibia.
- Karoo Long-billed Lark: O 420 falls outside its distribution range as does N 370, where one individual was observed.
- Pale-winged Starling: absent in all habitats at O 420, which is at the eastern edge of its range in Namibia.
- Red-footed Falcon: indicator species for W 215. Observed at O 420 river and thicket. Non-breeding migrant from the Palearctic and nomadic in response to local conditions.
- Rosy-faced Lovebird: dry area specialist, absent from very open habitats, dependent on water and strongly nomadic. Absent in all habitats at O 420 and N 370 even though both sites fall within its distribution range.

- White-backed Vulture: roosts in trees, flies during the day. Observed at river and thicket at O 420.

(2) Ecology of O 420

Most of the remaining species from Table 7 (24 out of 35 species, marked with asterisks) prefer a more varied vegetation or topographical structure (Hockey *et al*, 2005) than that offered at O 420 open.

Open areas at O 420 have a flat topography without rocky outcrops, have been bush cleared, are used for cattle grazing and vegetation cover is relatively homogenous. River lines and thickets at O 420 supply the resources these 24 species (Table 7, marked with asterisks) need, whereas at drier sites they utilise an additional habitat (grass-dominated). Heterogeneity of vegetation in the different habitats on the site (personal observation) allows species to remain in their niches. Grass in open areas is short and relatively homogenous; thickets are bush-encroached and cover large surface areas; rivers have a multi-layered structural profile with forbs and shrubs of varying size and mature as well as young trees (Figure 18 indicates tall vegetation in O 420 Rivers).

Indicator species

Rainfall ($r^2 = 0.678$) played a slightly larger role than habitat type ($r^2 = 0.511$) in the distribution of indicator species (Figure 43 and Figure 44). Indicator species for open and thicket had very low recorded values (one and two); the Orange River Francolin had the most with 14 observations. This suggests low niche diversity in open and thicket habitat types in the study area.

5.8 Guilds

Guilds provide a way to explore community features, particularly for comparing communities with different species compositions (Wiens, 1989a). Species belonging to the different nesting and feeding guilds were ordinated with sample units. The results illustrated how aridity and habitat type affected groups of species with similar life history traits. Bird species select habitat types according to their specific physiological and behavioural needs, three of which were explored in guild ordinations: nesting, feeding, and movement. Habitats contain a variety of conditions and resources which provide the niches required by bird species (Begon *et al*, 1996). Available resources varied between sites and habitat types, resulting in niche diversity; which in turn affected avian community composition.

Throughout the discussion of guilds, special reference is made to arid-adapted species, since under climate change scenarios it may be predicted that they would move into currently more mesic sites and replace less dry-tolerant species if the region becomes hotter and drier.

5.8.1 Nesting guilds

Vegetation has a direct link with breeding necessities because it affects the distribution of birds by providing shelter, food and potential nest-sites (Seoane *et al*, 2004). Nesting guilds cannot be used as a tool for examining the distribution of birds without considering food requirements (Dean, 2004; Lovegrove, 1993; Steyn, 1996).

Ground, ground/grass and ground-grass/shrub nesters

Many ground nesting species ordinated in open and river habitat types at the three more mesic sites (Figure 45). Open habitat provides bare ground and grass tufts for species that nest on the ground or at the base of grass, as well as aardvark burrows for species that nest in burrows. River lines provide vegetation for species that nest close to the ground, such as the Karoo Scrub-Robin and Desert Cisticola; and contain warthog holes, gullies, and earth banks, providing nest sites for burrowing species.

At the most arid site there were seven ground nesters, distributed between the three habitats. Habitat structure at R 128 was less differentiated than at the four other sites (Figure 41) and (Figure 42). Ruppell’s Korhaan and Tractrac Chat are near-endemic to southern Africa. Both are habitat-specific birds, the Tractrac Chat preferring open, shrub-covered plains in desert and the Ruppell’s Korhaan preferring gravel plains of the Namib Desert.

Initially, a usefull NMS ordination could not be found and row-column summary indicated two species carrying greater weight than the others, the Grey-backed Sparrow-Lark and Lark-like Bunting. Data was manipulated and these two species were removed before ordination. Of a total of 696 Grey-backed Sparrow-Larks, 630 were observed at the most mesic site, at the end of winter in six flocks in open habitat at O 420. In Namibia the Grey-backed Sparrow-Lark breeds mainly March to June. It is a highly nomadic and partial migrant species. After good rainfall and grass growth it moves to the more arid parts of its range in flocks of up to thousands (Hockey *et al*, 2005). Open habitat at O 420 is relatively homogenous and in addition, food for granivores is scarce at the end of winter. It is unlikely that the flocks of Grey-backed Sparrow-Lark observed at O 420 were breeding at that time of year, suggesting they were moving through the area in search of resources.

The Lark-like Bunting was observed in two flocks containing a combined total of 479 individuals in open habitat at the most mesic site. Laying dates vary with rainfall, in Botswana February to

April and in the Kalahari February to March (Hockey *et al*, 2005). It is highly nomadic in response to rainfall. It can be assumed that the flocks were breeding in the area and were observed at the end of their breeding season, while food resources were still plentiful.

Birds nesting in trees and shrubs

Tree- and shrub-nesting species ordinated in river and thicket habitats (Figure 46) with very few exceptions.

Cavity and constructed nests

Species nesting in cavities and constructed nests ordinated in rivers where large trees and dead trees provide nesting opportunities (Figure 47). There were a few exceptions. The Banded Martin ordinated in open habitat at O 420. It is an intra-African summer breeding migrant and its nest is a burrow in a stream bank, erosion gulley or sand pit (Hockey *et al*, 2005). Two individuals were observed in the same survey (13th March 2010) in a transect adjacent to the river where aardvark and warthog excavations provide nesting opportunities.

The Rosy-faced Lovebird was not observed at the two most mesic sites but was common at the three more arid sites (Figure 47). Its distribution is partially determined by the availability of water (Hockey *et al*, 2005) and although all five sites have surface water in the form of livestock watering holes, the three more arid sites provide better nesting opportunities in rock crevices and Sociable Weaver nests.

Initially, a usefull NMS ordination could not be found and row-column summary indicated three species carrying greater weight than the others, the Cape Glossy Starling, Rock Martin, and Southern Grey-headed Sparrow. Data was manipulated and these three species were removed before ordination. The Cape Glossy Starling occurred in all sites and habitats, uncommon only at the most arid. The total number of individuals observed was much higher than the average for cavity nesters. It is a resident omnivore, so its feeding habits are not dependent on local rainfall events (Figure 47).

The Rock Martin occurred at the low rainfall end of the aridity gradient (Figure 47). Of a total of 348 observations, the majority were observed at the two most arid sites (252 observations). Its preferred habitat is rocky hills and cliffs and it attaches its nest to a vertical surface on a rock face, building, dam wall or bridge (Hockey *et al*, 2005). The topography of R 128 and W 215 is steep, high, rocky cliffs that provide ideal nesting opportunities for the Rock Martin. It is a breeding migrant/resident and feeds on insects (Hockey *et al*, 2005).

The Southern Grey-headed Sparrow was present at all sites and habitats, uncommon only at the most arid (Figure 47). There was a peak in bird numbers in rivers of C 315, in the middle of the aridity gradient: 110 observations out of total 292. Riparian vegetation at C 315 is dominated by tall, mature *Acacia* spp that provide good nesting opportunities for the Southern Grey-headed Sparrow. It is an omnivore and nomadic/resident, indicating that it can adapt to a variety of environmental conditions.

5.8.2 Feeding guilds

Various behavioural strategies are employed by different birds to satisfy their different food preferences (Begon *et al*, 1996). The availability of food is an important determinant of avian population size, diversity, and community patterns (Steyn, 1996; Wiens, 1989a; Wiens, 1989b), especially so in arid zones, where fluctuations in bird abundance are driven primarily by rainfall through its influence on vegetation and invertebrates, which affect food supplies (Dean, 2004).

Carnivore and carrion feeding species

Predators select habitats according to prey availability (Begon *et al,* 1996), and desert raptors are often nomadic, moving rapidly to irruptions of prey items (Dean, 2004). Most carnivores and carrion feeders preferred rivers and thickets at the three more mesic sites (Figure 48), where there is a (presumed) bigger variety of prey species than in open habitats. The Lark-like Bunting, Greater Kestrel, Lesser Kestrel and Rock Kestrel preferred open habitat.

Seven species tolerated arid conditions (Figure 48) and five of them are migrant or nomadic birds. The Barn Owl, Spotted Eagle-Owl, and Steppe Eagle consistently ordinated at the most arid site. They were observed only at R 128 and at low values (Barn Owl one, Spotted Eagle-Owl two, Steppe Eagle two observations). It is highly likely that they were not observed but do occur at the other sites, because all three are common species in Southern Africa, occur in a wide variety of habitats, and are found across the rainfall isohyets of the region (Oberprieler & Cillié, 2009; Pickford *et al,* 1994). For the Barn Owl, a nesting cavity is essential. The Spotted Eagle-Owl is the most common owl in Southern Africa. The Steppe Eagle is highly nomadic while in the region (Oct – March), feeding mainly on termites.

Frugivore and insectivore/frugivore species

There are very few juicy fruits offered by desert plants, so frugivory is not an option in most deserts (Dean & Williams, 2004). Apart from the Red-faced Mousebird (the only “true” frugivore in this study), all the species in this group are insectivores that occasionally eat fruit (Hockey *et al*, 2005). Nine of the twelve species ordinated near rivers and thickets of the four wetter sites (Figure 49). All the species ordinated far from R 128, another encounter with the aridity threshold in terms of its effect on habitat. Vegetation is scattered at R 128 and suitable food resources for frugivores are found only in the river lines. The Ant-eating Chat ordinated in open habitat of the three more mesic sites, its preferred habitat being open arid savanna and semi-arid shrublands (Hockey *et al*, 2005).

Granivore and granivore/insectivore species

Granivory is common in the avifauna in arid ecosystems, but they may also include insects in their diet (Dean, 2004). Seed-eating birds in deserts feed on fresh seed production or wind-blown seeds (Dean & Williams, 2004). The nomadism (Figure 57) of the four arid-adapted granivores (Figure 50) may contribute to their survival in very arid conditions.

The Rosy-faced Lovebird is well-adapted to arid conditions. Its nomadism, varied diet (Hockey *et al*, 2005) and the availability of nesting sites (rock faces and Sociable Weaver nests) may explain its persistence in arid areas.

Herbivore and insectivore/nectarivore species

The six herbivore and insectivore/nectarivore species (Figure 51) were dependent on trees and/or shrubs for their nesting requirements (0). The low species richness of this feeding guild was due to the scarceness of suitable food resources, combined with their nesting requirements.

The Dusky Sunbird ordinated at the most arid site (Figure 51). Of a total of 383 observations, 302 individuals were observed at R 128, mainly in rivers and open habitat. It is a resident (0), although capable of moving large distances in search of resources. Hockey *et al* (2005) suggests they are sedentary in Namibia in regions adjacent to the < 80 mm isohyets, an area within which the study area falls. It likely replaces the Marico Sunbird and Scarlet-chested Sunbird in very arid zones. It utilised all the habitat types, indicating flexibility in procuring food resources.

Insectivore species

Habitats with trees, shrubs and forbs of varying height and foliage structure support more arthropods than homogenous habitats such as grass-dominated open areas. Various studies found that the distribution of arthropods affect avian insectivore distribution patterns (Murakami & Nakano, 2001; Whitaker *et al,* 2000). Insectivorous birds exploit a food resource that is itself nomadic in time and space (Dean, 2004). Local insect events, such as termite emergences after rain, cause local congregations of birds that last for as long as the prey is available.

Insectivore species clustered along the vegetation height vector (Figure 52), and were distributed among mesic and more arid sites, suggesting that habitat played a larger role than rainfall in community composition.

Species preferring open habitat at the wettest site included three migrants: the Banded Martin, Black-winged Pratincole and Harlequin Quail (Figure 52). The Black-winged Pratincole is an extralimital breeder and all observations were at OO in one summer survey, indicating that it was following an insect outbreak.

Omnivore species

Some species usually classified otherwise were categorised as omnivorous in this study, because they include insects and fruit or foliage in their diet when their preferred food resources are scarce, a condition that is common in arid zones. Examples are the White-browed Sparrow-Weaver and Cape Turtle-Dove. The White-browed Sparrow-Weaver's diet in high-rainfall areas consists of more than 90% seeds, whereas in the arid Kalahari 89% of their diet is made up of insects (Hockey *et al*, 2005). The Cape Turtle-Dove is mainly granivorous, but also eats earthworms and arthropods.

Food resources for omnivores are available in all habitat types. Omnivores have a broad feeding range and are opportunistic feeders, which enhance their niche size (Begon *et al*, 1996). Omnivore species ordinated across the aridity gradient and in all habitat types (Figure 53). The convex hulls of the three more mesic sites overlapped at thickets and rivers, indicating similarity between the sites in terms of distribution patterns of omnivores.

Species that occurred to the arid side of the rainfall vector (Figure 53) are of special interest. Twelve dry-tolerant omnivores avoided open habitat types. These 12 species have a variety of nesting requirements: cavity, ground, grass, shrub and tree nesters are represented. Ten of the twelve species are resident.

5.9 Movements and migrations

Flight enables birds to include larger areas in their home ranges (Simmons & Seymour, 2010) and in arid areas mobility is a key to their survival (Dean, 2004). The movements and migrations of birds affect community patterns; consequently it has to be taken into account when studying avian diversity and making conservation management decisions. The high level of endemism in Namibia's arid zones has been used in the past to base conservation decisions on. However, in the case of birds the rarity of species currently in an area should not play a primary role in selecting reserves because birds can migrate and colonise new areas with future climate change (Rutherford, 1999).

Dean (2004) states that the mobility of birds offers them two basic strategies to cope with desert life: moving, or resident and sedentary. Moving species have the further option to migrate seasonally or opportunistically to where resources are available; therefore, mobility affects avian community composition and distribution, and bird species move according to their specific behaviours and needs.

Breeding migrant and breeding migrant/resident species

It is expected that the distribution patterns of this group of birds would be primarily determined by their breeding requirements, with feeding opportunities and general habitat preferences also playing a role. Species showed two distinct habitat preferences: River/thicket, and open (Figure 54). Swallows and a martin ordinated in open habitat, and cuckoos in rivers and thickets.

The three dry-tolerant species were the Violet-backed Starling, Klaas's Cuckoo and Diderick Cuckoo. The Violet-backed Starling was observed in all three summer surveys at R 128. It is a solitary nester, using cavities in trees. While in the region it moves locally, following fruiting trees (Hockey *et al*, 2005). The two dry-tolerant cuckoos are explored here in terms of their habitat preferences and presence of their brood host species in the study area (Hockey *et al*, 2005). The Diderick Cuckoo forages in foliage. Host species present in the study area were Southern Masked Weaver, Chestnut-vented Titbabbler, Golden-breasted Bunting. The Klaas's Cuckoo forages in foliage, and batises, sunbirds and small warblers are its hosts.

Two more species ordinated in rivers, both near WR (Figure 54): Greater Striped Swallow and Three-banded Plover. The Greater Striped Swallow builds a mud nest under rock overhangs, boulders, man-made structures and fallen trees. Its preferred habitat is open grasslands, shrublands and savanna. It forages by circling and gliding over open grassland. The Three-banded Plover favours pools, streams and dams where it forages on open shores. It is a solitary and territorial breeder that makes a scrape in sand or dry mud for a nest. Only one individual was observed: in the river line at W 125 on 10th February 2009, which coincides with its laying months in Namibia (Dec – Mar) (Hockey *et al*, 2005).

The Common Quail and Harlequin Quail ordinated in open habitat on the mesic side of the aridity gradient. Both prefer short, open grassland for foraging and they nest on the ground (Hockey *et al*, 2005).

One martin and four swallows ordinated in open habitat at wetter sites (Figure 54). The Banded Martin OO forages by flying low over grass and nests in burrows. The Pearl-breasted Swallow builds a mud nest in aardvark and porcupine burrows. The nest of the Red-breasted Swallow is in aardvark burrows, fallen trees and termite mounds. The South African Cliff-Swallow is a colonial nester, using man-made structures and sometimes rock crevices. The White-throated Swallow builds a mud nest on a vertical rock face or in a culvert or dam wall (Hockey *et al*, 2005).

Two species were removed before ordination. 1) The Rock Martin, an insectivore, is a partial migrant in parts of its range and resident in others (Hockey *et al*, 2005). The species is discussed in more detail in section 5.8.1, with cavity and constructed nesters. 2) The Cinnamon-breasted Bunting is resident, breeding migrant and locally nomadic in the dry season (Hockey *et al*, 2005). It was absent from the most mesic site, O 420, as well as the middle site, C 315. It was observed in all habitats at the remaining three sites and only during summer, patterns that indicate it is a breeding migrant in this area.

Non-breeding migrant species

The distribution of non-breeding migrants (Figure 55) was determined by a combination of rainfall and habitat, with most species ordinating near rivers and thickets of the three mesic sites. Nesting requirements do not play a role in the distribution of non-breeding migrants and their movement into a region is seasonal. Most of the non-breeding migrants (16 out of 20) were carnivores or insectivores, and they were present in the region in summer; consequently, it can be safely asumed that their local distribution patterns followed emergences of arthropods and the presence of young mammals. In summary, rainfall *per se* did not affect the local distribution of non-breeding migrants as much as habitat.

Dry-tolerant birds were the Steppe Eagle and Common House-Martin (Figure 55). As mentioned before, at R 128 there is convergence in the vegetation structure of the three habitats of R 128.

Three species preferred open habitat: Capped Wheatear (between NO and CO) and Lesser Kestrel and Black-winged Pratincole near OO. The Steppe Buzzard ordinated in low vegetation, corresponding with its preferred habitat of open country. It feeds by gliding down from a perch (Oberprieler & Cillié 2009; Pickford *et al* 1994). The Eurasian Golden Oriole and Yellow-billed Kite ordinated close to Steppe Buzzard. The Eurasian Golden Oriole is a canopy feeder, preferring tall trees (Hockey *et al*, 2005). The Yellow-billed Kite is common in woodlands. It forages aerially and feeds on vertebrates, as well as following insect emergences (Hockey 2005; Oberprieler & Cillié 2009).

The Lesser Grey Shrike, on the low side of the vegetation height and rainfall vectors, ordinated in keeping with its preferred habitat of bare ground with nearby shady trees (Hockey *et al*, 2005). The Common Whitethroat ordinated in river/thicket habitat type, where the undergrowth is suitable for their habit of skulking in low vegetation.

Resident species

Resident birds are species that stay in an arid region and deal with harsh conditions through behavioural and physiological adaptations (Dean, 2004; Lovegrove, 1993). Although they do not move seasonally, resident species in arid ecosystems are not necessarily sedentary. Dean (2004) found marked fluctuations in bird numbers at specific sites, driven primarily by rainfall, that were not entirely due to young birds entering the population.

Although species distribution in ordination space were determined by a combination of rainfall and vegetation height, axis 1 explained 71% of variation and it corresponded with rainfall (Figure 56). This is in contrast with non-breeding migrants whose distribution was determined more by habitat type.

Most of the resident species clustered at rivers and thickets of the three more mesic sites (Figure 56). The twelve dry-tolerant species are likely candidates for moving into currently more mesic areas as conditions become more arid with global climate change.

Some resident species had a preference for open areas at the three more mesic sites. These nine species (Figure 56) may be useful indicators for the impact of land use practises on diversity in bush encroached habitats.

Nomadic and nomadic/resident species

Nomads are species that deal with arid conditions by moving opportunistically in response to local conditions. Coping with an environment that is drying out may be easier for nomadic species (Dean *et al*, 2009).

The distribution patterns of nomadic and nomadic/resident species were determined by a combination of habitat type and rainfall (Figure 57). Most nomadic species ordinated on the wetter side of the rainfall vector in all habitat types, with a cluster at rivers (Figure 57).

5.10 Synthesis

The results of this study, analysing 17 286 individuals and 188 bird species, offer predictions for what will happen with ecosystem processes in arid areas under future climate change scenarios: lower number of species, fewer birds and lower diversity, findings that agree with Parmesan & Yohe (2003) and Hockey *et al* (2011).

There were significantly more birds in wetter areas than in drier areas, and riparian habitat types contained more birds than thickened or open habitat types. Species richness was more in the wet season than in the dry season. There was across season consistency in bird assemblages from year to year, but significant variation in bird assemblages between summer and winter.

Dry river lines considerably increase the species richness in desert areas by creating a more structured plant community (Dean & Williams, 2004). Species richness in rivers remained more constant than in the other two habitats and rivers had twenty indicator species, while open had six and thickets two. When conditions are unfavourable, birds move into river lines from other habitat types.

The loss of bird species from a community is linked to their life history traits (Seymour & Dean, 2010). Hockey *et al* (2011) found that climate change caused habitat generalists in southern Africa to shift their ranges to the south, and migrants and nomads to move south.

Nesting guild ordinations were explained by rainfall and habitat. Species nesting in or on the ground, or using a combination of ground and grass or shrubs for their nests, ordinated mainly in open and river habitats at the three more mesic sites. Species nesting in trees and shrubs ordinated in rivers and thickets of the three more mesic sites and only four species preferred the open habitat type. Species using cavities or constructed nests preferred higher vegetation.

Feeding guild ordinations were also explained by rainfall and habitat. The three more mesic sites contained higher numbers of species from the nesting and feeding guilds, regardless of habitat type, than the two more arid sites. However, habitat played a larger part in explaining community composition of carnivore, carrion-feeding, frugivore and insectivore species.

Breeding migrant and breeding migrant/resident species showed two distinct habitat preferences: river/thicket, and open. Non-breeding migrant species ordinated near rivers and thickets of the three mesic sites, where their food preferences were met. Resident species clustered at rivers and thickets of the three more mesic sites. Nomadic species preferred wetter sites and all three habitat types.

An aridity threshold at a mean annual rainfall of 250 mm seems to have had a significant effect on bird community structures and on avian life history traits. Bird species richness, abundance and diversity remained relatively constant until they declined significantly once the aridity threshold was crossed. Bird species with a combination of life history traits that allow flexibility seemed to be the most likely to persist beyond the aridity threshold. The only four granivores beyond the aridity threshold were nomadic; most of the carnivores were migrants or nomads, and the two resident carnivores were habitat generalists; omnivores utilised all habitat types; ground and tree-shrub nesters were most common; the only nectarivore/insectivore species utilised all habitat types; and there were a similar number of residents and migrants/nomads.

5.11 Climate change implications

Many studies predict that climate change will lead to substantial shifts in species distributions (Barbet-Massin *et al,* 2011; Bellard *et al,* 2014; Tingley *et al,* 2012; Thomas, 2010; Walther & Van Niekerk, 2014). The future distribution and population sizes across many taxa are projected to change substantially (Matthews *et al*, 2011). Barbet-Massin *et al* (2011) predicts a decrease in bird ranges of 25% – 50%, and Bellard *et al* (2014) mention that range shifts have already been observed in more than 1000 species (Parmesan & Yohe, 2003), especially those with high dispersal capabilities like birds. Tingley *et al* (2012) found that 82% of range shifts could be explained by temperature or precipitation. Taking into account increased temperature and decreased precipitation as two measurable results of future climate change, it can be predicted from the results of this study that avian range shifts in the arid savanna of Namibia will occur from west to east, following the expansion of impoverished resources.

Temperature and precipitation are not the only factors of climate change causing range shifts. Land-use scenarios should also be considered to predict the potential effects of global changes on species (Barbet-Massin *et al*, 2011). The significance of vegetation and habitat is highlighted by several studies. Barbet-Massin *et al* (2011) found more accurate models when combining climate and habitat variables, than when using climate alone. Vegetation characteristics can be linked to specific habitat requirements of bird species and land-cover attributes that play an important role in habitat selection (Matthews *et al*, 2011), as this study, based on field data, also found.

The observed shifts associated with recent climate change are likely to have been brought about through both direct and indirect effects of climate (Thomas, 2010). One indirect effect of climate change can be studied through the effect of habitat on avian community structures, but another indirect effect is inter-specific interactions. Species interactions among birds could be modified in the future (Barbet-Massin *et al*, 2011), and the response of some species to climate change may modify interactions at the community level (Bellard *et al*, 2014), causing the disappearance of species following the extinction of their associated species. There is a web of interactions at the community level, and Tingley *et al* (2012) found a complex interplay between species-specific and region-specific factors that structure patterns of breeding range change over long time periods. Species interactions *per se* were not part of the present study, but assemblages were. As was shown here, each site had a discrete avifaunal composition, both in species and in numbers.

Many studies of the impact of climate change on bird communities focus on a predicted decline in species richness. However, dispersal capability could offset this decline to some extent. Long-distance dispersal events, although rare, could be of crucial significance in the current context, as they could make the difference between species survival and extinction; additionally, species also track suitable climatic conditions at the regional scale (Bellard *et al*, 2014). Barbet-Massin *et al* (2011) found that predicted changes were not uniformly distributed and that some regions could have an increase in species richness if colonising species were successful. Thomas (2010) addressed the question of dispersal boundaries. He postulates that some kind of limit, climatic or otherwise, must exist to prevent species from spreading across their current boundaries. One such boundary was observed in this study for the Tractrac Chat and Ruppell's Korhaan, habitat-specific birds restricted to the plains of the Namib Desert margins.

When species don't have the time or means for dispersal, they often survive in refugia when conditions in the surrounding area are unfavourable. The desert and desert margin zones of Namibia can be viewed as such a refuge, especially in the light of Levinsky *et al* (2013) finding that refugia often exhibit high levels of endemism. They identified the Angola-Namibia area and the south-eastern part of South Africa as historic refugia with an unusually high level of aggregation of birds and mammals. On a smaller scale, this study showed that dry river lines acted as refugia for maintaining bird diversity and it can be predicted that riparian habitats would play an even larger role under future climate change scenarios.

Identifying local ecosystems such as rivers that can act as biodiversity sources leads to the question of how to manage conservation in the light of the global nature of climate change. Some authors argue strongly for a continent or subcontinent-wide perspective when developing conservation networks that address climate-change adaptation (Hole *et al*, 2011). However, it may be difficult to mitigate climate change effects by placing protected areas where species are expected to be in the future (Walther & Van Niekerk, 2014). Interactions come into play when making conservation management decisions. Hole *et al* (2011) advise that maintaining overall functional integrity of ecosystems requires addressing crucial ecological and abiotic processes, both within a site and in the wider landscape. Managers will need to account for non-avian species of critical importance to a site's integrity, such as large predators, seed dispersers, and other keystone species (Hole *et al*, 2011). Climate modelling can help to re-evaluate the current set of protected areas, their places, size, layout and design in view of the increasing importance of protecting the heterogeneity of habitats as well as genetic diversity within a species (Bellard *et al*, 2014). Hoffmann & Sgro (2011) urge that areas containing high genetic variation across multiple species should be prioritised when designating areas for reserves. The present study also identified crucial habitat types with less diversity as important. The open areas and thickets at R 128 seem to be crucial in supporting a depleted but unique assemblage, with species seemingly utilising more of the different habitat types than at the more mesic sits.

A growing number of studies show that observed climate-change induced stresses are mediated by species' biological traits (Foden *et al*, 2013). Birds can adapt through physiological alterations or by behavioural modifications of their diet, activity and energy budget (Bellard *et al*, 2014), but changes in habitat distributions are not anticipated to occur equally across all species groups; rather, the impacts of climate change will act on different components of the life history of bird species (Matthews *et al*, 2011). This study showed that movements, diet and nesting requirements affected the adaptability of birds to arid conditions. Locally nomadic species, species with a flexible diet, and species not reliant on habitat types characterised by heterogenous vegetation, are most likely to persist.

Tingley *et al* (2012) argue that the different ecological traits held by diverse species assemblages affect range stability that may result from adaptation of local populations to new climates, an inability to disperse, an insufficient amount of climate change to push species out of their fundamental niche, or a temporal lag in movement response. The present study has identified groups of birds that may be affected by climate change. There were species found at all sites – these may well be less affected by climate change. On the other hand, the species largely restricted to the very arid region seem particularly adapted to the dry conditions. It would be interesting to follow this specific assemblage to see how they adapt to more arid conditions in the ways described by Tingley *et al* (2012).

The assemblage at Rooiklip was at the extreme dry end of the present rainfall gradient, and may not have the potential for further adaptations if it becomes even drier. Nevertheless, these species are likely to experience an increase in range, and disperse accordingly. Regarding the changes due to rainfall and vegetation seen in the present study, it would be safe to assume that fewer species and numbers of birds can be expected under drier conditions, even allowing for the possible effect of dry-adapted species dispersing in the direction of a range expansion. This is because the colonising dry-adapted species would probably not be augmenting populations in the currently more mesic areas, but rather replacing mesic-adapted species that were lost through their dispersal as they followed the contraction of their range.

5.12 Predictions and future research needs

- Range shift of avian species from west to east in response to a drier climate.
- Avifaunal composition changes in species composition and bird numbers following range shifts in response to a drier climate.

- Fewer species and numbers of birds, with a concomitant reduction in diversity in response to a drier climate.
- Changing vegetation characteristics under the effect of climate change will influence habitat selection of birds
- Dispersal boundaries will limit species colonising from west to east in response to a drier climate.
- Dry river lines, as hotspots of bird diversity and refugia for avian diversity, will play an increasingly important role in preventing large-scale extinction in response to a drier climate.
- Protected area networks should be planned with a subcontinent-wide perspective to maintain the integrity of ecosystems
- Life history traits affect the adaptive capabilities of bird species
- Nomadism, flexibility in diet, and adaptability of nesting requirements are traits that will be under selection presure in response to a drier climate.
- Crucial habitat types with less diversity are important for maintaining unique avian assemblages
- Analyses per habitat type and per guild are needed to investigate whether the aridity threshold at a mean annual rainfall 250 mm had a significant effect on bird life history traits

5.13 Conclusion

Through assessment of the impacts of rainfall and habitat on bird variables, the hypothesis of the study was confirmed and it emerged that bird species assemblages were affected primarily by rainfall and secondarily by habitat type.

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Appendix A

Abundance of species included in analyses. Common names and abbreviated names are given but scientific names are omitted due to space and can be found in Table 6. The sites are arranged from arid (west) to mesic (east) and abundance in the different habitats at each site is indicated. Values are number of individual birds per species observed.

		128			215			315			370			420			
Common name	**Abbr**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**TOTALS**
Acacia Pied Barbet	AcPiBa	1	81	1	1	3	1	1	18	1		7	1		10	1	127
African Fish-Eagle	AfFi					1					1						2
African Golden Oriole	AfGoOr					2						1			1		4
African Grey Hornbill	AfGrHo		2			2						1					5
African Harrier-Hawk	AfHa														1		1
African Hawk-Eagle	AfHaE						1			2			2		3		8
African Hoopoe	AfHo		2		1	1	2	1	3	3	3	5	6		2	1	30
African Pipit	AfPi				3		1	16	6	1	13			33		1	74
African Quailfinch	AfQu										1	15		2	15	1	34
African Red-eyed Bulbul	AfReBu	2	28	1	6	92	2		11	4		2	1		3	6	158
Amur Falcon	AmFa									1		18					19
Ant-eating Chat	AnCh							93	15	3	56	6	9	19	4		205
Ashy Tit	AsTi	1		1	5	4	6	1	27	6	4	16	12		9	6	98
Augur Buzzard	AuBu	1									1						2
Banded Martin	BaMa													2			2
Barn Owl	BaOw		1														1
Barn Swallow	BaSw				7	50		9	6	6	13	18	9	12	18	13	161
Barred Wren-Warbler	BaWr					14	1		13	2		15	22	1	12	15	95
Bearded Woodpecker	BeWo					1			1			3			4		9
Black Cuckoo	BlCu				1	5	1		3		1	5	6		4		26
Black-chested Prinia	BlPri	22	49	35	16	12	26	14	80	34	53	29	129	9	25	122	655
Black-chested Snake-Eagle	BlSn	3	1		2	2			1	2		1			1		13
Black-faced Waxbill	BlWa		2		3	42	1		16	5	3	31	14		38	38	193
Black-headed Heron	BlHe											1					1
Black-shouldered Kite	BlKi							2	3		5	2	1	6	2	8	29
Blacksmith Lapwing	BlLa											5			3		8
Black-throated Canary	BlCa	2	11		6	28	16	15	1	4	3	100					186
Black-winged Pratincole	BlPr													68			68
Bronze-winged Courser	BrCo								1								1
Brown Snake-Eagle	BrSn											1			2		3

Appendix A

		128			215			315			370			420			
Common name	**Abbr**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**TOTALS**
Brown-crowned Tchagra	BrTc		4		3	3	2	4	10	3	5	5	6		6	18	69
Brown-throated Martin	BrMa										1						1
Brubru	Br				1	4	3				1	6	1		3	1	20
Buffy Pipit	BuPi									1				5		1	7
Burchell's Sandgrouse	BuSa														10	28	38
Burchell's Starling	BuSt										2	1	1		2		6
Burnt-necked Eremomela	BuEr				1				7				1		3		12
Cape Bunting	CaBu	1	1														2
Cape Clapper Lark	CaClLa										2			13		3	18
Cape Crow	CaCr													1		3	4
Cape Glossy Starling	CaGlSt	2	12	2	31	24	35	39	51	29	29	30	21	18	22	38	383
Cape Penduline-Tit	CaPe	3	2		8	2	18	3	18	18	36	25	11		3	22	169
Cape Sparrow	CaSp		1			2	3		3				3				12
Cape Turtle-Dove	CaTu	12	51	5	17	60	14	25	111	41	19	69	46	35	168	46	719
Cape Wagtail	CaWa							3				1					4
Capped Wheatear	CaWh							25			40					1	66
Cardinal Woodpecker	CaWo	1	3			1			1		2	3	1		5	1	18
Chat Flycatcher	ChFl	1		2		5		3		1	4		1	9		8	34
Chestnut Weaver	ChWe		92	2	15	3			9	12						20	153
Chestnut-backed Sparrowlark	ChSp							1						2			3
Chestnut-vented Tit-Babbler	ChTi		35	2	5	41	22	5	41	26	6	25	30		22	54	314
Cinnamon-breasted Bunting	CiBu	2	1	1	40	3	27				1	43	3				121
Common Fiscal	CoFi		7		1	2	3	2			8	7		2	1	15	48
Common House-Martin	CoHo	1	30	1		1						2					35
Common Quail	CoQu	2			2		1			1	6			3	3	2	20
Common Scimitarbill	CoSc		1		3	5		2	13	2		10	4		19	1	60
Common Waxbill	CoWa								2								2
Common Whitethroat	CoWh					1	1										2
Crested Francolin	CrFr															1	1
Crimson-breasted Shrike	CrSh				2	42	4	1	65	14	4	26	15		68	24	265
Crowned Lapwing	CrLa							59	1		2	6		40	12	3	123
Damara Hornbill	DaHo											1					1
Desert Cisticola	DeCi	1			22	1	13	2	1	6	42		2	81		2	173
Diderick Cuckoo	DiCu	7	16	5		4		2	8	8	1	2	1	1	3	4	62
Double-banded Courser	DoCo							5									5
Double-banded Sandgrouse	DoSa			3										15		4	22
Dusky Sunbird	DuSu	118	157	27	11	28	10	2	5	10	6	2	1			6	383
Eastern Clapper Lark	EaClLa										5			60		1	66

		128			215			315			370			420			
Common name	**Abbr**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**TOTALS**
Eurasian Golden Oriole	EuGoOr						1								2		3
European Bee-eater	EuBe										1		6	6	10		23
Familiar Chat	FaCh	20	45	3	5	9		1	1	1		3					88
Fawn-coloured Lark	FaLa	1	4		20		4	10	3		7			1	4	6	60
Fork-tailed Drongo	FoDr				2	29		3	12		7	22	8	4	34	3	124
Freckled Nightjar	FrNi			1									1				2
Gabar Goshawk	GaGo				1	3	1	1	4			3		1		2	16
Golden-breasted Bunting	GoBu				1	4	5	1	4	2		24	2		3	1	47
Golden-tailed Woodpecker	GoWo					2									3		5
Great Sparrow	GrSp	40	41	15	3	63	4	24	45	44	19	56	28		16	27	425
Great Spotted Cuckoo	GrSpCu										1	2	2		1		6
Greater Honeyguide	GrHo											1					1
Greater Kestrel	GrKe													4	1	2	7
Greater Striped Swallow	GrStSw				1	21	4	1	6				1		4		38
Green Wood-Hoopoe	GrWo					2									5		7
Green-winged Pytilia	GrPy					9			11	1		6			37	8	72
Grey Go-away-bird	GrGo		2		2	60	1		8			6			24		103
Grey-backed Camaroptera	GrCa											1			8	2	11
Grey-backed Cisticola	GrCi				2												2
Grey-backed Sparrowlark	GrSpL	12	6		2	5		38	1	1		1		495	17	118	696
Grey-headed Kingfisher	GrKi											1			4		5
Groundscraper Thrush	GrTh					12			4	1		2			5		24
Hamerkop	Ha											1					1
Harlequin Quail	HaQu													1			1
Helmeted Guineafowl	HeGu					1	1	8	18	1	2	51	15	1	8	22	128
House Sparrow	HoSp				6	5										2	13
Icterine Warbler	IcWa			2		3			5	1		1	4		27	1	44
Jacobin Cuckoo	JaCu					1									1		2
Kalahari Scrub-Robin	KalSR		2	4	65	5	18	21	55	28	19	11	15	3	7	77	330
Karoo Long-billed Lark	KaLoLa	35	5	6	4	1	1			1	1						54
Karoo Scrub-Robin	KarSR					5				3					1		9
Klaas's Cuckoo	KlCu	2	2	7					1				1				13
Kori Bustard	KoBu				3			3		1			1	1			9
Kurrichane Buttonquail	KuBu												3				3
Lappet-faced Vulture	LaVu						1	7	8	11	5		10	1			43
Lark-like Bunting	LaBu	113	127	16	49	23	58	70	19	8			27	482	4	37	1 033
Laughing Dove	LaDo	13	62	2		66		1	24	2	4	23	2		158	10	367
Lesser Grey Shrike	LeGrSh	9	14	8	9	2	12	22	8	12	7	3	8		3	8	125

		128			215			315			370			420			
Common name	**Abbr**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**TOTALS**
Lesser Kestrel	LeKe							1	1					7			9
Lesser Masked-Weaver	LeMa								3		1					3	7
Lilac-breasted Roller	LiRo		1						3			3			5		12
Long-billed Crombec	LoCr	2	1			2			4			2	2			4	17
Long-billed Pipit	LoPi	1	1		8					1						1	12
Long-tailed Paradise-Whydah	LoPa										1				1	17	19
Ludwig's Bustard	LuBu							8									8
Marico Flycatcher	MaFl		1	2	8	17	4	9	58	10	12	21	20		22	12	196
Marico Sunbird	MaSu											1				1	2
Monotonous Lark	MoLa				7	6	2	3				3	1				22
Monteiro's Hornbill	MoHo		12									13	9				34
Mountain Wheatear	MoWh	25	28	2													55
Namaqua Dove	NaDo	10	8	1	9	21	10		28	10	5	11	18	32	16	36	215
Northern Black Korhaan	NoBlKo				3		13	24	4	8	36			27		12	127
Orange River Francolin	OrRiFr										7	1		4	2		14
Pale-winged Starling	PaSt	12	31	2	10	2	10	2	2		1	2	1				75
Pearl-breasted Swallow	PeSw				1	2			1		13	8	3	2	1	4	35
Pearl-spotted Owlet	PeOw					1						2			8		11
Plain-backed Pipit	PlPi				1												1
Pririt Batis	PrBa	1	18	3	2	15	10	2	19	11	1	10	8		11	12	123
Purple Roller	PuRo	4	9						1			1			2		17
Rattling Cisticola	RaCi		1		1		6	5	14	6	14	53	14	3	15	25	157
Red-backed Shrike	ReSh		3		3	3	1		3		1			3	23	10	50
Red-billed Buffalo-Weaver	ReBu					2			4			1	1		6	1	15
Red-billed Hornbill	ReHo														1		1
Red-billed Spurfowl	ReSp		1		2	42	2	2	22		1	4	2	5	35	4	122
Red-breasted Swallow	ReSw										1			2	1	1	5
Red-crested Korhaan	ReKo			1	24	3	28	4	10	25	9	13	14	2	6	20	159
Red-faced Mousebird	ReMo			2		1	1		2	1		1					8
Red-footed Falcon	ReFa				4	6		1							1	1	13
Red-headed Finch	ReFi	1		29				34	15	5	62	7	9	7	13	14	196
Rock Kestrel	RoKe	4	9		1		1	2	1	2			1	2		1	24
Rock Martin	RoMa	57	90	1	29	56	19	12	12	5	26	25	5	9		2	348
Rockrunner	Ro							1				5					6
Rosy-faced Lovebird	RoLo	4	66		1	37	14	14	34								170
Rufous-eared Warbler	RuWa				14		3	2		1	2		6			8	36
Rufous-naped Lark	RuLa		1					15	7	1	54	8	8	6	8	2	110
Ruppell's Korhaan	RuKo	12	3	2													17

		128			**215**			**315**			**370**			**420**			
Common name	**Abbr**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**TOTALS**
Sabota Lark	SaLa	95	59	46	67	7	31	23	45	43	25	13	49	5	1	53	562
Scaly-feathered Finch	ScFi	2	4		39	20	27	83	107	55	236	78	181	82	2	317	1 233
Scarlet-chested Sunbird	ScSu					6						1					7
Sclater's Lark	ScLa													21			21
Secretarybird	Se										1					1	2
Shaft-tailed Whydah	ShWh				3	4	2		8	3	4	18		21	5	9	77
Shikra	Sh											1					1
Short-toed Rock-Thrush	ShRo	4	9	2	4	3	3	1	5	3	1	4			1		40
Sociable Weaver	SoWe				1		4	157	399	21						2	584
South African Cliff-Swallow	SoAfCl													7		3	10
Southern Grey-headed Sparrow	SoGrSp	2	2	1		74	3	4	110	4		24	5	5	51	7	292
Southern Masked-Weaver	SoMa	4	8		3	35		4	192	12		86			44	47	435
Southern Pale Chanting Goshawk	SoPaCh	3			3	3		2	7	3	9	5	4	4	5	3	51
Southern Pied Babbler	SoPiBa					23	1		25	1		1	6		34		91
Southern Red Bishop	SoReBi										2						2
Southern White-crowned Shrike	SoWhSh													1		2	3
Southern Yellow-billed Hornbill	SoYeHo											3	2	2	20	3	30
Speckled Pigeon	SpPi	2	7	4		2											15
Spike-heeled Lark	SpLa				13			62	8	2	19		1	14		1	120
Spotted Eagle-Owl	SpEa			2													2
Spotted Flycatcher	SpFl	4	20	9		7	1		1			9	4		6	2	63
Stark's Lark	StLa							2						1			3
Steppe Buzzard	StBu						1	1							4		6
Steppe Eagle	StEa	1	1														2
Swallow-tailed Bee-eater	SwBe		2		4	15		2	28	6	9	15	1	2	32	2	118
Tawny Eagle	TaEa				2				1							1	4
Temminck's Courser	TeCo							3									3
Three-banded Plover	ThPl					1											1
Tractrac Chat	TrCh	1															1
Violet-backed Starling	ViSt	1	4	3													8
Violet-eared Waxbill	ViWa		11		6	28	7		16	10	9	55	37		7	16	202
Wattled Starling	WaSt		1	10	45	15	15	3	85	15	23	5			14		231
White-backed Mousebird	WhMo					1			2		3	3					9
White-backed Vulture	WhVu				6	1	2	15	16	4	32	9	27		4	8	124
White-browed Sparrow-Weaver	WhSpW		1			8		14	89	4	23	136	18	33	135	21	482
White-tailed Shrike	WhSh			4	3	2	4	4	1	1	3	1			1		24
White-throated Canary	WhCa	13	64		3	4			2				2			7	95
White-throated Swallow	WhSw										2	1					3

		128			**215**			**315**			**370**			**420**			
Common name	**Abbr**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**Open**	**River**	**Thicket**	**TOTALS**
Willow Warbler	WiWa					3			5				1		2	1	12
Yellow Canary	YeCa		1			7		3	4	11		5		2	6	8	47
Yellow-bellied Eremomela	YeEr	1	6	4	2	2	9	2	15	6	5	4	7	2	7	9	81
Yellow-billed Kite	YeKi								3		1	1			2		7
Yellow-crowned Bishop	YeBi													12		1	13
Zitting Cisticola	ZiCi				8		4	17		3	13	2	3	68		4	122
SUBTOTALS		694	1 384	282	728	1 309	563	1 089	2 210	657	1 119	1 439	964	1 830	1 454	1 564	
TOTALS		2 360			2 600			3 956			3 522			4 848			17 286