Chapter 2: Literature review

This chapter discusses the general factors that affect avian diversity and communities within riparian corridors.

2.1. Factors affecting avian diversity and communities in riparian ecosystems

Woinarski, *et al.* (2000) completed a riparian study in Australia that showed that species richness and bird abundance were significantly greater among riparian areas than in non-riparian areas. Gentry *et al.* (2006) also found that neotropical migrants occurred in riparian habitats and were absent in the surrounding woodlands, which suggested that riparian corridors are especially important habitats for breeding birds in south-eastern south Dakota (Gentry *et al*. 2006). Similar results were also found in a number of studies (Gentry *et al*. 2006;Green & Baker 2003;Knopf *et al*. 1988;Martin *et al*. 2006;Palmer & Bennett 2006;Rottenborn 1999;Smith & Wachob 2006;Woinarski *et al*. 2000). These studies clearly indicate that riparian ecosystems have a strong influence on avian diversity and communities.

Factors that influence avian diversity and communities in several ways are time, space, habitat types, food and feeding, nesting sites, water availability, competition, predation, learning, and the presence of other species (Begon *et al*. 1996;Borgmann & Rodewald 2004;Chouteau 2006;Cody 1985;Doherty *et al*. 2000;Seoane *et al*. 2004;Steyn 1996;Wiens 1989a;Wiens 1989b), which will be discussed next.

2.1.1. Time

Avian diversity and communities change over time in response to the following (Doherty *et al*. 2000;Wiens 1989b):

1. Habitat changes
2. Changes in habitat selection behaviour
3. Community and diversity variations in nearby habitat patches
4. Fluctuations in food
5. Site tenacity (birds stay in a particular habitat)

6. Weather conditions during seasons
7. Migration
8. Breeding
9. Variation in predation and parasitism
10. A lack of saturation of suitable habitats

These factors also interact and influence avian diversity and communities.

2.1.2. Space

Riparian habitats are influenced by the geomorphic and hydrologic processes of riparian ecosystems, which control the valley, floor landforms, channel structure, as well as the riparian vegetation; all of these factors affect the physical habitat within riparian ecosystems (Gregory *et al*. 1991). Additionally, climate, topography, natural disturbances (e.g. flooding, fires, frost and drought) and anthropogenic activities (e.g. farming, residences, industry, fires, grazing and pollution) have profound affects on riparian habitats, by forming complex mosaic patches of different habitat types (Naiman *et al*. 1993;Seoane *et al*. 2004;Wakeley *et al*. 2007;Wiens 1989b). Therefore, climate, topographic variations, disturbances and anthropogenic activities influence the vegetation structure on a spatial scale, which consequently alters the relationships with birds (Naiman *et al*. 1993;Seoane *et al*. 2004;Wakeley *et al*. 2007;Wiens 1989b).

2.1.3. Riparian Habitats

The relationship between species and their habitats has been a central issue in ecology and considered important for conservation management and planning (Seoane *et al*. 2004). Supporting this, a study done by Chouteau (2006) indicated the importance of habitat types and structures on the foraging ecology of two *Coua* species (*Coua coquereli* and *Coua gigas*) in the dry forests of Madagascar. He found the change in habitat type or structure to be an important consideration for the conservation of these birds. The study by Chouteau (2006) and other similar studies indicate the significant effects of habitat structure on foraging behaviour of birds.

Habitats have certain levels of complexity, heterogeneity, and qualities. Habitat complexity refers to the level or strength of interaction between species and their environmental factors, while habitat heterogeneity refers to spatial and temporal changes across a landscape (Doherty *et al*. 2000). Habitat heterogeneity can also be regarded as habitat diversity. The overlap of habitats on a spatial scale increase heterogeneity that may enhance species richness (Doherty *et al*. 2000). Habitats with high heterogeneities on a spatial scale also create opportunities for many species to shift. Habitat complexity can also be defined by the species or species assemblages using the habitat (Doherty *et al*. 2000).

2.1.3.1 Riparian vegetation structure

Several studies showed that avian diversity varies according to vegetation structure (Brand *et al*. 2008;Diaz 2006;Malan *et al*. 2007;Posa & Sodhi 2006;Powell & Steidl 2000;Simons *et al*. 2006;Vidaurre *et al*. 2006;Wakeley *et al*. 2007). Seoane *et al.* (2004) identified vegetation structure as a source of potential predictors as they considered it as a more direct link with reproductive needs (such as nesting sites) and food availability of species than topography or climate.

The prominent vegetation classes are trees, shrubs, grass, reeds, herbs and sedges (Tainton 1999). Reeds and sedges are normally found along waterbodies, wetlands and riparian areas, while trees, shrubs, grass, and herbs are normally found in the terrestrial setting (Lachavanne & Juge 1997;Naiman *et al*. 1993;Naiman & Decamps 1997;Tainton 1999). Therefore, vegetation structure is often more diverse in riparian ecosystems than the surrounding terrestrial matrix (Lachavanne & Juge 1997;Naiman et al. 1993;Naiman & Decamps 1997;Tainton 1999).

The co-occurrence of different vegetation types (such as trees, shrubs, grass, reeds, herbs, and sedges) in most areas determines riparian vegetation structure. Heterogeneity and complexity increase as the number of vegetation types increase, and this increases niche diversity (Diaz 2006).

Figure 2.1 illustrates vegetation structures that can occur along riparian habitats. These habitats have varying heterogeneity and complexity, and the niche diversity varies accordingly.

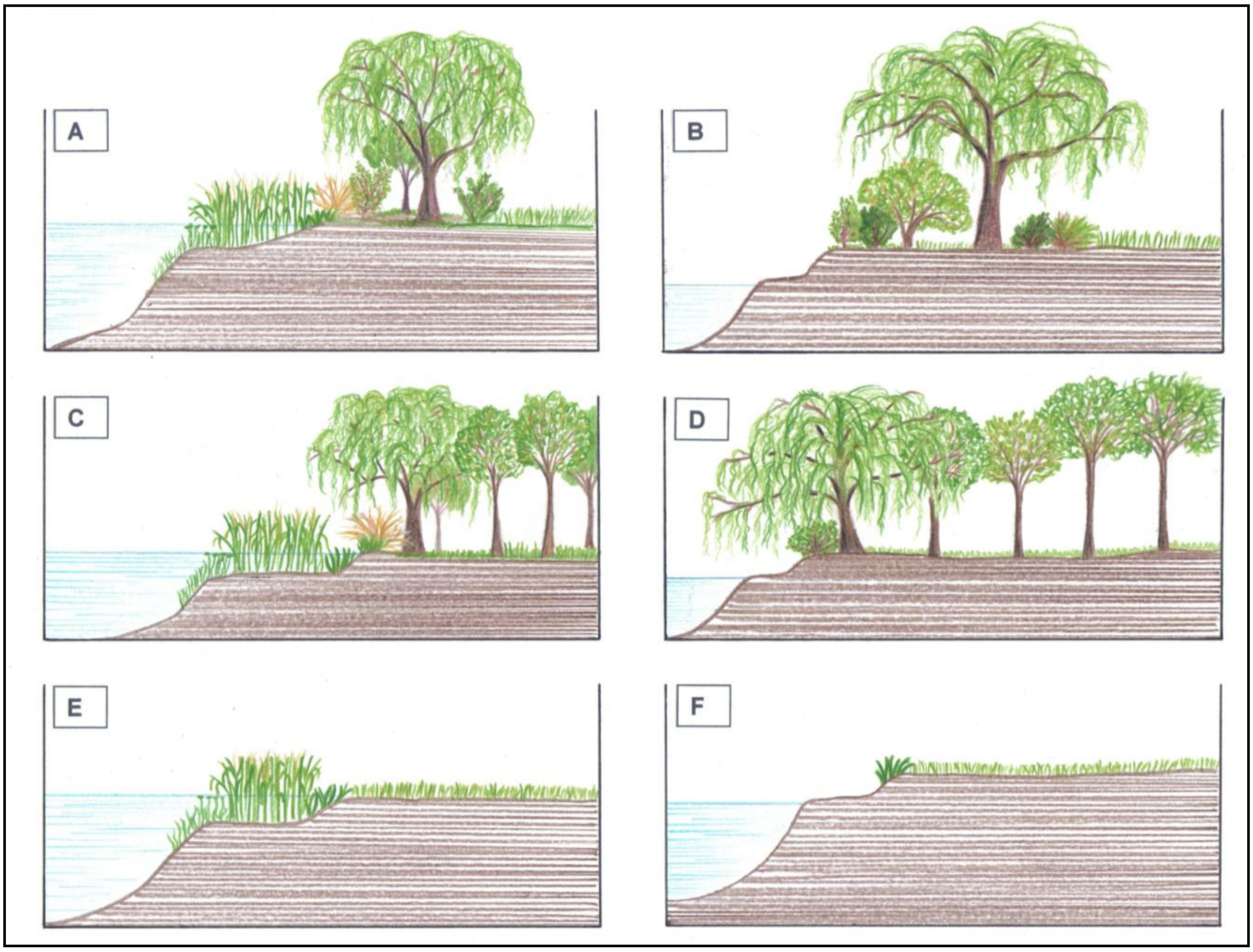

Figure 2.1 Vegetation structures that can occur along riparian habitats (adapted from Lachavanne and Juge (1997)).

A and B: Grass- and woodland, C and D: Woodland, E and F: grassland. Aquatic vegetation such as reeds and sedges occur in A, C and E, and not in B, D and F, due to the geomorphic and hydrologic processes on the valley and floor of the riparian landforms.

Riparian vegetation is also affected by geomorphic and hydrologic processes (Gregory *et al*. 1991;Wakeley *et al*. 2007). These processes influence riparian vegetation in a direct manner, or by influencing the valley and floor of the riparian landforms, which in turn influence the plant successional processes that finally influence the riparian vegetation (Gregory *et al*. 1991). This is also shown in Figure 2.1.

Soils along riparian ecosystems are often fertile and the water table is near the surface. Figure 2.2 also shows surface filtering (run-off), especially where the terrestrial setting has a slope. Rainwater flows down the slope towards the stream channel. These areas favour riparian vegetation, due to the availability of water. Riparian vegetation also reduces soil erosion and improves the water quality along riparian ecosystems (Deschenes *et al*. 2003;Henningsen & Best 2005;Tainton 1999).

Riparian vegetation within riparian habitats, such as indicated in Figure 2.2, influences in-stream biota and processes (Karakatsoulis *et al*. 2005;Naiman *et al*. 1993). These in-stream biota and processes influence the feeding and nesting site availability for birds (Karakatsoulis *et al*. 2005). Vegetation regulates light and temperature regimes, provides nourishment to aquatic as well as terrestrial biota that may serve as food for birds, regulates the flow of water and nutrients from the uplands to the stream channel, and sustains biodiversity by providing a diverse collection of habitat and ecological services (Karakatsoulis *et al*. 2005;Naiman *et al*. 1993). Large wood components also influence sedimentation, morphology of the stream channel and the in-stream habitat (Naiman *et al*. 1993). All these factors mentioned by Naiman *et al.* (1993) and Karakatsoulis *et al.* (2005) combine to create a variety of potential bird habitats. Riparian vegetation also serves as corridors for bird movements between habitat patches (Smith *et al*. 2008) (also see Section 1.1.1).

To summarise, the variety of vegetation types and vegetation structures within the riparian ecosystem affect avian diversity and communities, because it influences habitat quality via the availability of shelter, food, perching sites, and nesting sites.

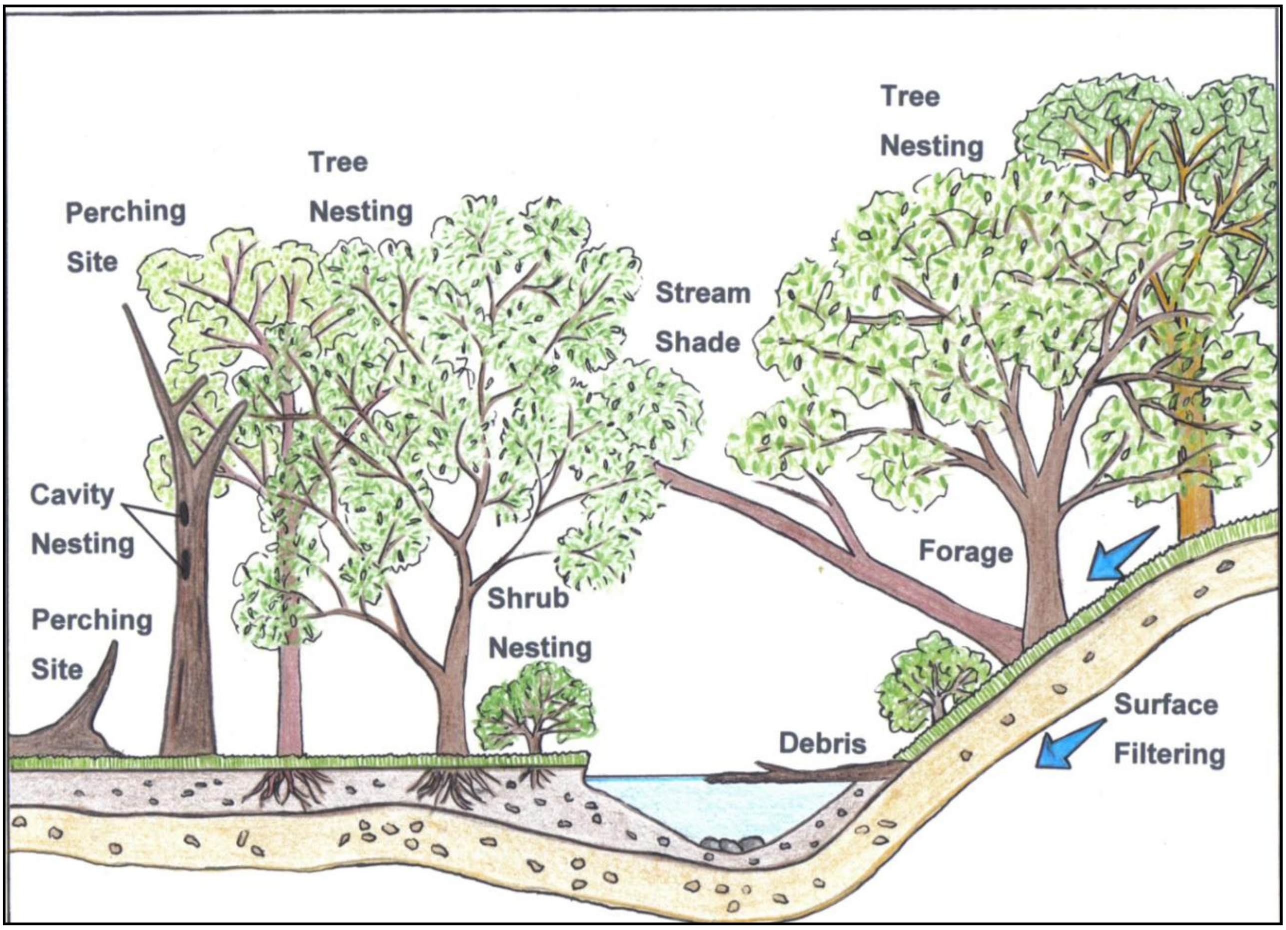

Figure 2.2 Roles that vegetation plays within a typical riparian habitat (adapted from Karakatsoulis *et al.* (1999)).

2.1.3.2. Anthropogenic factors

People have historically settled near streams and rivers for access to drinking water, food, irrigation, transportation, and industry (Pennington *et al*. 2008). Land-use practices such as agriculture and structures such as bridges have been developed over the years along riparian ecosystems.

Soils along riparian ecosystems are often fertile and this increases agricultural opportunities. People have a deep-rooted affinity for watercourses for recreational activities (Miller & Hobbs 2000), adding to the disturbance. Land-use practises in the past and current development threaten the ecological integrity (health, condition, or state) of many riparian ecosystems and associated wetlands (Mensing *et al*. 1998). Riparian habitats have high edge-to-area ratios that make them vulnerable to surrounding landscape changes (Martin *et al*. 2006).

Road and train bridges are common anthropogenic factors along riparian ecosystems for improving transportation over and along riparian ecosystems. Construction of roads and bridges adjacent to streams may jeopardise the integrity, continuity, and stability of riparian ecosystems (Mensing *et al*. 1998).

A study illustrating the above in the Santa Clara Valley in the USA found that bird species richness and density, as well as native vegetation, decreased as the number of bridges per length of river increased (Rottenborn 1999). A study of the Snake River (USA) concluded that overall species richness and diversity declined with increasing residential development (Smith & Wachob 2006). The destruction of riparian vegetation not only caused local extinction, but also reduces the ability of populations to recolonise sites (Knopf & Samson 1994).

However, there are also some advantages to bridges, particularly for birds. Road and train bridges create nesting sites for certain swifts and swallows (Hockey *et al*. 2005;Maclean 1993). Birds such as kingfishers perch from smaller footpath-bridges to catch aquatic prey (Hockey *et al*. 2005;Maclean 1993). Raptors and insectivorous birds perch or roost on other structures such as electricity pylons and fences (Hockey *et al*. 2005;Maclean 1993).

Although not documented, riparian ecosystems in urban environments also attract informal settlers because of proximity to water, urban opportunities, shelter and a general lack of enforcing prohibition of their settlements. These informal settlements have unknown effects on bird communities and diversity.

Knowledge of the effects of anthropogenic factors on avian diversity and community patterns is important for implementing management strategies along riparian habitats.

2.1.4. Food and feeding

Different bird species prefer different food types and therefore use different behavioural strategies for finding it (Begon *et al*. 1996;Cody 1985). Due to species-specific behaviours, different species have different feeding and perching sites (Cody 1985). Consequently, not only the food availability, but also the suitability of feeding and perching sites are important decision-making elements (Section 1.1.5) (Wiens 1989b). Cody (1985) also stated that many species share habitats, but feed among different sites within habitats. Consequently, a variety of feeding sites in a habitat provide opportunities for a greater number of species to utilise this habitat. For instance, thrushes use sight to search for invertebrates and a dense canopy layer may reduce prey detectability (Devereux *et al*. 2006). Other birds such as granivores, wagtails, and pipits also need bare ground for foraging, while several kingfisher species need perching sites from where they can detect their prey (Hockey *et al*. 2005;Maclean 1993).

Studies have shown that riparian ecosystems have greater amounts of food availability for birds than many other terrestrial systems (Murakami & Nakano 2001;Whitaker *et al*. 2000). Large amounts of aquatic and terrestrial insects live and survive in riparian ecosystems and serve as important food sources for insectivores. Murakami & Nakano (2001) completed a study on species-specific behaviour of insectivores on aquatic prey in a riparian forest. They concluded that species-specific behaviours of insectivores could have been responsible for the heterogeneous distribution of insectivores within a riparian forest. Johnson and Sherry (2001) studied the effects of food availability on the distribution of migratory warblers among habitats in Jamaica. They found that a strong association exists between arthropod biomass and warbler abundance on spatial and temporal scales (Johnson & Sherry 2001).

A study along the Snake River in the USA concluded that food generalists and seed eaters were more abundant in areas with a greater number of anthropogenic elements in the landscape, while insectivores preferred riparian forest patches (Smith & Wachob 2006). They also found that aerial insectivores such as bark gleaners, foliage gleaners, and hawking foragers were more abundant in patches with larger trees and less human activities, while ground gleaners were detected along areas with human elements (Smith & Wachob 2006).

Riparian vegetation often has a buffering effect, which reduces negative impacts on animals (Whitaker *et al*. 2000). Whitaker *et al.* (2000) hypothesised that riparian buffer zones provide shelter from strong winds, and therefore act as collecting sites for insects blown in from exposed clear-cuts. Whitaker *et al.* (2000) found greater numbers of insects in the riparian buffer zones than the surrounding clear-cut landscapes, and this was correlated with the greater number of warbler species found along the riparian buffer zones. Therefore, the distribution of insects can affect insectivore distribution patterns (Johnson & Sherry 2001;Murakami & Nakano 2001;Whitaker et al. 2000). Riparian buffer zones harbour a great variety of other food types such as plant seeds, vegetable material, and arthropods (Smith *et al.* 2008). Riparian ecosystems provide habitats for worms, insect larvae, fish, molluscs, crustaceans and amphibians, which are ideal food sources for birds.

The soil within riparian ecosystems has greater moisture levels compared to the surrounding landscapes; therefore, earthworms along riparian ecosystems should occur closer to the surface, which will make them more available for birds in riparian ecosystems than the dryer surrounding landscapes (Green *et al*. 2000).

The availability of food, especially during winter and non-breeding periods, is an important determinant of population size, diversity, and community patterns (Cody 1985;Steyn 1996;Wiens 1989a;Wiens 1989b). During these periods, the demands for nesting sites are irrelevant because they are of lower priority for many bird species. Food and water often also become scarce and more concentrated in certain areas, and many birds will accumulate here.

In summary, food availability, foraging behaviour, and the suitability of feeding and perching sites within habitats influence avian diversity, populations and community composition in riparian habitats.

2.1.5. Nesting sites

Birds have specific nest-site requirements (Cody 1985). Birds construct their nests in trees, shrubs, grass, reeds, cliffs, sand banks, anthropogenic structures and on the ground. Many species can use more than one of these classes for constructing their nests, for example the Reed Cormorant, *Phalacrocorax africanus* builds its nest either in trees or reeds (Hockey *et al*. 2005).

These nesting types indicate that building material is also needed within or close to a nesting site. Therefore, the availability of building material is a resource influencing a bird's decision-making process in selecting an appropriate nesting site. However, not all species construct a nest:

- Brood parasites lay their eggs in the nests of other species, and the host parents raise their young (Steyn 1996). Some parasitic species specialises on a single host species while others can use different hosts (Steyn 1996).
- Several birds may use nests that were constructed by other birds. For instance, the Orange-breasted Waxbill often uses old nests of the Southern Red Bishop, Red-collared Widowbird, or White-winged Widowbird (Hockey et al. 2005;Steyn 1996).
- Several cavity nesting species lay eggs within tree cavities, which they did not excavate (Steyn 1996). These cavities may be natural holes or previously excavated by barbets or woodpeckers (Steyn 1996).

Riparian ecosystems are important breeding sites for birds (Gentry *et al*. 2006;Knopf *et al*. 1988;Wakeley *et al*. 2007). Eighty-two percent of all species in northern Colorado breed in riparian vegetation (Knopf *et al*. 1988). Several species forage in the surrounding uplands of riparian ecosystems, but need the nesting sites provided by riparian vegetation for breeding (Knopf & Samson 1994). This illustrates the importance of riparian ecosystems for providing nesting sites for birds.

To summarise, avian diversity and communities are influenced by the availability and diversity of different nesting sites as well as the availability of building materials for constructing their nests.

2.1.6. Water

Birds and other fauna depend on water for their existence. However, species vary in their needs for water (Hockey *et al*. 2005;Kotler *et al*. 1998;Maclean 1993;MacMillen 1990). For instance, waders feed within water as they forage, granivores need to drink daily (Kotler *et al*. 1998;MacMillen 1990), and many, but not all, insectivores acquire water from their food and are less dependent on open water. The availability of water also influences the availability of food, as open water is a habitat for aquatic insects, tadpoles, fish, and other aquatic animals (Knopf *et al*. 1988;Naiman *et al*. 1993) that serve as food for waders and other birds.

Water regularly flows through riparian ecosystems; therefore, open water is often available to birds and other animals. However, water levels vary from season to seasons and also on a spatial scale, due to rainfall variations (Woinarski *et al*. 2000).

Another factor that influences water quantity and quality in urban riparian ecosystems is the presence and distribution of drainage pipes along the streams (Alberti *et al*. 2003;Kelcey & Rheinwald 2005;Woinarski *et al*. 2000). Water drains via drainage pipes from the surrounding urban areas into the streams, can contaminate the receiving water, and affect water levels (Alberti *et al*. 2003;Kelcey & Rheinwald 2005;Woinarski *et al*. 2000).

Water loss while foraging by birds may affect the overall value of their food intake (Kotler *et al*. 1998). Water is abundant and available along riparian ecosystems allowing foragers to exploit food patches more thoroughly and remain active over a broader range of ambient conditions (Kotler *et al*. 1998). On the other hand, in dryer and more arid landscapes where water is scarce, foragers may alter their activity and avoid certain types of food due to the increased water loss (Kotler *et al*. 1998).

The water in riparian ecosystems also attracts species from more xeric landscapes to obtain water on a regular basis (Knopf & Samson 1994). This attraction of visiting species enhances competition and may attract other predators, which will then influence the native community and diversity along riparian ecosystems.

Water availability along riparian ecosystems can influence avian communities and diversity. However, food availability, nesting sites, competition, or predation may have stronger influences on avian communities and diversity than water availability, because water is often less variable than these other factors on a spatial scale (Woinarski *et al*. 2000).

2.1.7. Competition

Bird species may find certain habitats suitable in terms of structure and productivity levels, but the presence of other species might significantly increase competition by reducing food availability and nesting sites (Cody

1985). Competition is an interaction between individuals where they share and require the same limited resources (Begon *et al*. 1996). Competition leads to a reduction in survival, growth, and reproduction of at least some of the competing individuals (Begon *et al*. 1996). Individuals can compete directly with one another to gain access to resources. In other cases, individuals that compete only respond to the level of resources (Begon *et al*. 1996).

There is also intraspecific and interspecific competition (Begon *et al*. 1996). Intraspecific competition is the competing of individuals within a population, and interspecific competition is the competing of individuals of one species with individuals of another. Interspecific competition can influence the number of species, and intraspecific competition can influence population sizes within habitats, especially within habitats that have limited resources (Begon *et al*. 1996;Wiens 1989b). Wiens (1989b) showed that competition can be responsible for species distributions over different habitats.

Competition for resources tends to increase within areas where migrating species stop-over or over-winter (Skagen *et al*. 2005). The residential and migrating species then compete for food and other resources. Several residential and breeding migrant species also compete for nesting sites during the summer months in Southern Africa (Steyn 1996). Therefore, migration tends to enhance competition within areas where migrant species are present.

Species that are specialists rely on restricted resources or are resident in restricted areas with specific resource conditions (Begon *et al*. 1996;Wiens 1989b). Therefore, specialists are more restricted when selecting their habitats according to food types, nesting sites, perching sites, or roosting sites than generalists. Consequently, competition is more likely to occur among specialists than generalists (Begon *et al*. 1996;Maestas *et al*. 2003;Wiens 1989b).

Competition can therefore influence the number of species and/or the number of individuals within species occurring in riparian habitats, which consequently influence avian diversity and community composition.

2.1.8. Predation

A predator attacks his prey while still alive. Obvious effects of predation are reduction of the preys' population size. Predator numbers within a habitat normally fluctuate with prey population numbers, the prey-predator relationship (Begon *et al*. 1996). For instance, the depletion of a raptor's prey within a habitat will also lead to the declining in raptor populations, which will consequently have an effect on the avian diversity and community structure.

Nest predation is also a predation activity, and is considered as an important force shaping avian communities (Borgmann & Rodewald 2004). Certain bird species, wild- and domestic cats, snakes, iguanas, otters, mongoose, mice, and squirrels are nest predators (Hockey *et al*. 2005;Maclean 1993;Miller & Hobbs 2000). Burchell's Coucal, Brown-hooded Kingfisher, Common Fiscal, and Red-backed Shrike are examples of birds that often prey upon the contents of birds' nests (Hockey *et al*. 2005;Maclean 1993).

Due to the complexity and diversity of riparian ecosystems, predator diversity is also more abundant along riparian ecosystems than the surrounding landscapes (Van der Haegen & DeGraaf 1996). The presence of nest predators, as well as the level of nest predation will affect the avian diversity and communities within riparian habitats.

2.1.9. Learning

Learning can be a relatively permanent change in behaviour as a result of experience (Dugatkin 2003). The ability of organisms to learn provides them with the opportunity to respond to environmental change such as the development of anthropogenic structures (Dugatkin 2003). Birds can learn from their own experience or from the experience of other individuals to adapt their forage and nesting behaviours, to counteract predation, and to adapt within anthropogenic habitats.

2.1.10. Presence of other species

Several species occur in areas due to the presence of other species. For instance, predators select habitats according to prey availability (Section 2.1.8), certain species use the nests of other species to breed (brood parasites and species utilised old nests) (Section 2.1.5), and some carnivores kleptoparasitise food from other carnivores (Hockey *et al*. 2005).

2.2. Conclusion

From the above it is clear that riparian avian diversity and communities are influenced by time, space, habitat types, food and feeding, nesting sites, water availability, competition, predation, learning, and the presence of other species. Birds select their habitats according to their species-specific behaviours, and they use these factors in their decision-making process to select an appropriate habitat (Section 1.1.5). This indicates that different species are likely to be associated with different habitats. Consequently, avian diversity and communities vary among habitats.

The general introduction (Chapter 1) and literature review (Chapter 2) will help to explain the results (Chapter 4) needed to verify the hypothesis listed in Section 1.3. Chapter 3 will give insight of the study area and the procedures for obtaining the results.