THE ROLE OF WATERBIRDS IN THE DISPERSAL OF AQUATIC ORGANISMS IN SOUTHERN AFRICA

Chevonne Reynolds

Supervisor:

Professor Graeme S. Cumming

The Percy FitzPatrick Institute of African Ornithology

Department of Biological Sciences

University of Cape Town

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"I think it would be an inexplicable circumstance if water-birds did not transport the seeds of freshwater plants to unstocked ponds and streams, situated at very distant points. The same agency may have come into play with the eggs of some of the smaller fresh-water animals"

Charles Darwin, 1859

DECLARATION

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ABSTRACT

Dispersal is a fundamental process with far-reaching ecological and evolutionary consequences. Not all organisms are capable of dispersing on their own and instead produce propagules that must be transported to new habitat by a vector. Propagule dispersal by frugivorous bird species is well researched, but only very recently has the capacity of highly mobile waterbirds to disperse aquatic organisms received similar attention in the dispersal literature. Dispersal is important for the organisation of communities, and therefore understanding the frequency and scale of waterbird-mediated dispersal provides insight into the structure of wetland communities. Additionally, the study of waterbird-mediated dispersal in arid southern Africa provides an opportunity to expand our knowledge on the persistence of populations of aquatic organisms in heterogeneous environments. Recently, field and laboratory studies have demonstrated the remarkable ability of waterbirds to disperse the propagules of both plants and aquatic invertebrates. However, these studies have largely been based in the northern hemisphere and many have focussed on long-distance dispersal by migratory waterbirds. Therefore, it is difficult to generalise how waterbird-mediated dispersal plays out in different landscapes and throughout the annual cycle. Furthermore, there is still little knowledge of the spatial patterns of propagule dispersal and the mechanisms that cause these patterns to vary in space and over time. This thesis aims to addresses several of these knowledge gaps in waterbird-mediated dispersal and presents the first detailed study of propagule dispersal by waterbirds anywhere in Africa.

In Chapters 2 – 5, I adopt a field- and experimental-based approach to develop a general understanding of waterbird-mediated dispersal in southern Africa. Firstly, making use of faecal samples and feather brushings collected from several waterfowl (duck) species at three locations in South Africa, I determine the quantity and viability of propagules transported via endozoochory and ectozoochory. I then assess the relative contributions of each dispersal mode to the dispersal of plants and aquatic invertebrates in the field. I show that endozoochory is the dominant dispersal mechanism, but it may be complementary to ectozoochory as different propagules are transported via this mode. Secondly, by making use of an experimental feeding trial with two captive waterfowl species, Egyptian Goose and Red-billed Teal, I explore how seed traits mediate a trade-off in recoverability and germinability against gut retention times. I show that small, hard-seeded species are retained for longer and therefore may be dispersed further. Thirdly, I incorporate gut retention time data and Egyptian Goose and Red-billed Teal movement data, acquired from GPS satellite transmitters across five study populations in southern Africa, into a mechanistic model to explore spatial patterns of seed dispersal. The model demonstrates that waterfowl generally facilitate dispersal on the local scale of below 5 km, but on occasion can transport seeds as far as 500 km from a seed source. There was variation in dispersal distances between the vectors and across the study populations and the results indicate that dispersal is affected by both intrinsic and extrinsic drivers of animal movement.

In Chapters 6 and 7, I apply the concept of waterbird-mediated dispersal more broadly to address (1) the role of waterbirds in the dispersal of aquatic invaders; and (2) the determination of seed dispersal functional groups amongst a waterfowl community. I conducted a literature review to objectively describe the role of waterbirds in the dispersal of aquatic weeds. Waterbirds are important vectors of aquatic invasive species and consideration of the spatially explicit manner in which birds move is imperative to our understanding of invasive spread. In the second case, I used diet data from the 16 waterfowl species indigenous to southern Africa to explore whether finer level seed dispersal functional groups were evident. I found support for several functional groups of seed disperser based on unique plant families in the diet and suggest that important functional differences do occur between groups of waterfowl species.

The results of this thesis have shown that waterbirds in the region take up a variety of different propagules, including exotic and terrestrial propagule species, move them over multiple spatial scales and are capable of depositing good numbers of viable propagules in suitable habitat. Furthermore, dispersal is a complicated interaction between the disperser and the vector, and I have shown that both differences in propagule characteristics and vector traits affect spatial patterns of dispersal. I conclude that despite their apparent isolation, important ecological connections exist between wetlands. Waterbirds play an important role in connecting wetlands through dispersal and in doing so influence aquatic community organisation and provide a means of recolonisation in ephemeral habitats. Waterbird-mediated dispersal is thus a significant and perhaps poorly considered mechanism of resilience in aquatic ecosystems.

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Ducks
Seed
Bird
Local
Spread
Scale
Bird
Diet
Aquatic
Ecological
Viability
Plant
Africa
Connecting
Europe
Far
Quantity
Waterfowl
Mode
South Africa
Waterfowl
Experimental
Aquatic
Adaptation
Diet
Spatial
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Egyptian Goose
Red-billed Teal
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Ducks
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Abundance
Anatidae
Ectozoochory
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Red-billed Teal
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Endozoochory
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Seed
Disperse
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Invertebrate
Vectors
GPS satellite telemetry
Model
Function
Connecting
Viability
Movement
Variation
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Papers arising from this thesis

The following manuscript was published prior to submission of this thesis. This manuscript has multiple authors, each of which contributed in some way to its production. C.R. and N.A.F.M. conceived and designed the review. C.R. conducted the review and analysis. All authors contributed to the writing of the paper, which was led by C.R. Contributions: Reynolds 75%, Miranda 15% and Cumming 10%.

Reynolds C., Miranda N.A.F. & Cumming, G.S. (2015) The role of waterbirds in the dispersal of aquatic alien and invasive species. *Diversity and Distributions*, **21**, 744 – 754.

The following three manuscripts have been published whilst awaiting examination of this thesis. In all cases, C.R. undertook all fieldwork, laboratory work, analysis and the writing of the manuscripts. G.S.C., acting in a supervisory capacity aided in the study design and oversaw the data analysis and writing of the manuscripts.

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Reynolds, C. & Cumming, G.S. (2016) Seed dispersal by waterbirds in southern Africa: comparing the roles of ectozoochory and endozoochory. *Freshwater Biology*, doi:10.1111/fwb.12709

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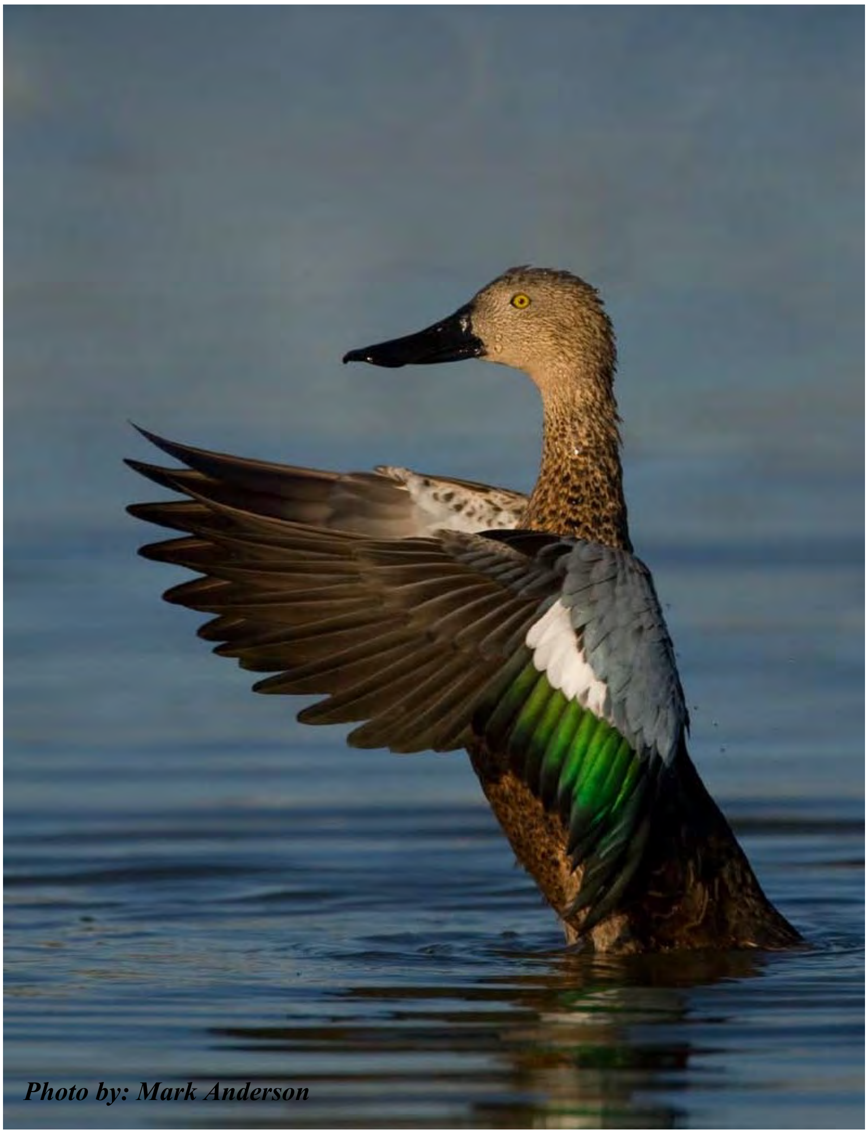
The following manuscript has been accepted for publication whilst awaiting examinaition of this thesis. C.R. undertook all fieldwork, laboratory work, analysis and the writing of the manuscript. G.S.C., acting in a supervisory capacity aided in the study design and oversaw the writing of the manuscript.

Reynolds, C. & Cumming, G.S. (*in press*) Seed traits and bird species influence the dispersal parameters of wetland plants. *Freshwater Biology*

CHAPTER 1

GENERAL INTRODUCTION AND METHODS



Movement is a central component of many ecological and evolutionary processes, and one of the most fundamental features of an organism's biology (Nathan 2008). Dispersal is a particular type of movement of individuals away from the parent or birth place that results in gene flow (Ronce 2007). The ability of organisms to disperse has consequences for individual fitness, population and community dynamics, evolution, and species' distributions (Hanski 1998; Lundberg & Moberg 2003; Trakhtenbrot *et al.* 2005; Ronce 2007; Kremer *et al.* 2012). Given the important ecological and evolutionary outcomes of dispersal, the study of the mechanisms underpinning the dispersal process is an important area of research, and is fundamental to the conservation of biodiversity (Berg *et al.* 2010; Clobert *et al.* 2012). The biosphere is being altered at an extraordinary rate through land-use change, habitat fragmentation, global climate change and alien species' invasion (Chown & Gaston 2008). Therefore, determining the causes and consequences of dispersal is vital for understanding and predicting the response of individuals, populations and species to environmental change (Bowler & Benton 2005; Robledo-Arnuncio *et al.* 2014).

Not all organisms are capable of dispersing on their own (active dispersal). Instead they produce mobile units or propagules, such as seeds, that must be transported to new habitat by a vector i.e. passive dispersal (Howe & Smallwood 1982). Propagules can be dispersed by a variety of dispersal vectors, including wind and water. However, the dispersal of propagules by animals, and vertebrates in particular, is one of the most common mechanism (Howe & Smallwood 1982; Cousens *et al.* 2010). Animal-mediated dispersal is a long-studied and common theme in ecological and evolutionary research (Jordano 1995; Levin *et al.* 2003), and much progress has been made in determining the mechanisms underlying this process. However, the majority of research has focussed on terrestrial ecosystems and on the dispersal of fleshy fruits, nuts and coniferous seeds (Howe & Smallwood 1982; Jordano 1995; Côrtes & Uriarte 2013). In contrast, relatively little is known about animal-mediated dispersal in wetland habitats where waterbirds have recently been shown to be important dispersal vectors of both aquatic plants and macroinvertebrates across multiple spatial scales (Figuerola & Green 2002a; van Leeuwen *et al.* 2012b; Green & Elmberg 2014).

Waterbirds were first proposed as vectors of aquatic plants and invertebrates by Charles Darwin (1859). Despite this distinguished beginning, empirical research on waterbird-mediated dispersal has only gained momentum in the last two decades. This research has highlighted the previously underappreciated role that waterbirds play in the dispersal of aquatic organisms (Brochet *et al.* 2009; van Leeuwen *et al.* 2012b; Viana *et al.* 2013a; Green & Elmberg 2014), and consequently, in wetland community dynamics and ecosystem functioning (Santamaría & Klaassen 2002). However, these studies have largely been based in the northern hemisphere and many have focussed on long-distance dispersal by migratory waterbirds. Therefore, it is difficult to generalise how waterbird-mediated dispersal plays out in different landscapes and throughout the annual cycle. Furthermore, some fundamental questions remain concerning: (1) the relative contribution of different dispersal modes (endo- versus ectozoochory) and different waterbird species to realised dispersal; (2) the effect of the multi-scaled nature of waterbird movement on dispersal; and (3) the role that waterbirds play in aquatic invasive spread. This thesis aims to addresses these knowledge gaps in waterbird-mediated dispersal, drawing on methodologies, frameworks, and theory applied in the broader field of dispersal ecology.

This study specifically investigates the role that waterbirds play in the dispersal of aquatic plants and invertebrates in southern African and uses field, experimental and modelling approaches to determine *what*, *how* and *where* propagules are dispersed. Dispersal is important for the organisation of communities and for the persistence of populations (Leibold *et al.* 2004), and therefore understanding the frequency and scale of waterbird-mediated dispersal provides insight into wetland community structure. Furthermore, understanding the scale of connectivity in wetlands brought about through waterbird-mediated dispersal is imperative in the design of wetland conservation networks (Baguette *et al.* 2013) and in managing the risk of invasive spread (Green 2015).

In southern Africa, where this study took place, the environment is relatively arid with disparity in the magnitude and pattern of precipitation. The high spatio-temporal variability in surface water availability has important consequences for the dispersal of aquatic plants and invertebrates (Levin, Cohen & Hastings 1984; McPeek & Holt 1992; Snyder 2006, 2011), not just through its influence on waterbird vector movement patterns, but on the propagule traits that influence dispersal distances and on the success of propagules arriving at new habitat. Dispersal and dormancy are two of the most common mechanisms for dealing with spatio-temporal variability in the environment (Levin *et al.* 1984; Chesson 2000) and to some extent are considered analogues allowing for the spreading of risk in space and time respectively (Levin *et al.* 1984; Snyder 2006). Naturally, we would expect that dispersal in time would then be able to substitute for dispersal in space (Snyder 2006). However, as the environment becomes increasingly patchy and unpredictable, such as in ephemeral wetlands that characterise arid zones, theory predicts that non-local dispersal and higher dispersal rates in space are favoured (Venable & Lawlor 1980; Comins, Hamilton & May 1980; Levin *et al.* 1984). In patches where local extinction is common larger dispersal distances allow propagules to track favourable patches and recolonise empty areas and lead to the selection of propagule traits that facilitate non-local dispersal (McPeek & Holt 1992; Snyder 2011; Massol & Débarre 2015). Therefore, in southern Africa where hydrological connectivity between wetlands is low and wind dispersal is limited in spatial scale, waterbird-mediated dispersal operating at broader spatial scales offers an important alternative for passively dispersed organisms to track favourable habitat patches. In this context, waterbird-mediated dispersal has an important, but unexplored, role to play in facilitating the persistence of populations in heterogeneous environments. Additionally, by dispersing propagules to recently inundated and newly productive wetland environments waterbirds contribute to the resilience of wetland ecosystems through allowing the opportunity for recolonisation and reorganization following disturbance (*sensu* Nyström & Folke 2001). The study of waterbird-mediated dispersal in southern Africa therefore provides a unique opportunity to expand our knowledge of the persistence of populations in patchy environments.

1.1 BACKGROUND

1.1.1 Dispersal

Dispersal is most commonly defined as movement of individuals or propagules away from the parent or birth place that result in gene flow across space. A propagule is a structure with the capacity to give rise to a new organism and throughout this thesis has been used to refer to seeds, spores, vegetative components, larvae or resting eggs. Dispersal is generally recognised as comprising three distinct stages: (a) departure (emigration); (b) a vagrant or transient stage; and (c) settlement (immigration) (Ronce 2007). Dispersal has important ecological and evolutionary outcomes for all organisms, as it enhances connectivity amongst local populations, allows the recolonisation of empty habitat, and provides the ability to change or expand geographic ranges (Hanski 1999; Kokko & López-Sepulcre 2006). Dispersal has consequences for organisms at individual, population, and species levels. At an individual level variation in morphology, physiology, condition, and age can affect the distance and frequency of dispersal. For example, as individuals age they can accumulate information that may alter their dispersal decisions (Matthysen 2012). Several studies have demonstrated that the selection of breeding sites differs between experienced breeders and inexperienced immatures with consequences for reproduction and survival (Kenward, Walls & Hodder 2001; Parejo, White & Danchin 2007). At the population level, emigration and immigration between habitat patches drives cycles of colonization and extinction and can have both beneficial and detrimental effects on the persistence of spatially structured populations (Bowler & Benton 2005). Movement into declining populations may increase the genetic mixing among populations and help shield them from local extinctions (Baguette *et al.* 2013). On the other hand, high rates of dispersal between populations may promote synchrony amongst subpopulations, which has been shown to increase extinction risks (Heino *et al.* 1997; Bowler & Benton 2005). As the spatial scale of dispersal increases from landscapes to biogeographic regions and from ecological to evolutionary time frames then dispersal can influence organisms at the species level. For example, vicariance, which is defined as the geographical separation of a species leading to speciation (Wiley 1988), is the outcome of processes that restrict the dispersal of individuals within the species ancestral range (Wiens & Donoghue 2004). If dispersal between populations ceases, through limitations imposed by abiotic conditions or other species, these newly isolated populations accumulate novel genetic attributes via genetic drift or natural selection and can then be described as separate species (Wiens & Donoghue 2004). Therefore, the study of dispersal at various levels of organisation can provide important insights into the ecology and evolution of species across multiple spatial and temporal scales.

1.1.2 Why disperse?

Dispersal by definition is the movement of individuals away from the parent or birth place that results in gene flow across space, and is considered a means of increasing fitness in heterogeneous landscapes. The variation in expected fitness between different habitat patches is considered the driving force for the evolution of dispersal (Bowler & Benton 2005). Some of the most commonly considered advantages of dispersal, which affect variation in fitness, include avoiding competition with relatives, reducing risks of inbreeding and/or as discussed earlier spreading risk in spatially and temporally variable environments (Clobert *et al.* 2001; Bowler & Benton 2005; Burgess *et al.* 2015). However, dispersal also has costs, including the energetic and physiological cost of movement itself and/or the development of locomotory appendages in animals. Alternatively, for passively dispersed organisms dispersal represents a risk of digestion or deposition in habitats with unfavourable conditions (Matthysen 2012). Dispersal as a strategy thus requires a balance between the advantages of spatial displacement between related individuals and the costs of such movements (Burgess *et al.* 2015). The readiness of individuals to move is an obvious requirement for the spread of a species (Kokko & López-Sepulcre 2006). However, the decision to disperse is not a simple one and both proximate factors, for example local environmental conditions (Bowler & Benton 2005), and ultimate factors, for example kin selection (Hamilton & May 1977) or bet-hedging in variable environments (Snyder 2011), must be considered when exploring the causes of dispersal

1.1.3 Mechanisms of dispersal

The most basic distinction between mechanisms of dispersal is between active and passive dispersal. Active dispersal occurs when an organism moves between habitat patches by its own locomotion, and is most common amongst animals (Matthysen 2012). Highly mobile animals, such as birds, insects, fish and mammals, can walk, swim and/or fly and are capable of moving large distances in search of suitable habitat. There are also rare examples of active dispersal amongst plant species, for example crevice following plants (Damschen *et al.* 2008) and the forceful ejection of seeds via ballistichory in species such as the kapok tree *Ceiba pentandra* (Howe & Smallwood 1982). In contrast, passive dispersal occurs when an organism cannot move on its own and a vector must facilitate dispersal. Passive dispersal predominates amongst plants in the movement of seeds and vegetative components (Howe & Smallwood 1982), but also plays a role in the movement of the resting egg stages of aquatic invertebrates (Panov, Krylov & Riccardi 2004) and mobile reproductive phases of marine organisms (Burgess *et al.* 2015). Typical vectors include animals (zoochory), wind (anemochory), water (hydrochory) and gravity (barochory) (Howe & Smallwood 1982). Dispersal by humans (anthopochory) must now also be considered a special case of zoochory due to the important role this mechanism has in the transport of invasive species (Wichmann *et al.* 2009).

Passively dispersed propagules may be adapted for movement by a specific dispersal vector and specific adaptive morphologies are characterised into dispersal syndromes (Howe & Smallwood 1982), many of which have been recognised for a long time (Ridley 1930; van der Pijl 1982). For example, winged-pods and plumes are thought to be an adaptation for dispersal by wind, nutritious fruits attract vertebrate dispersers and clinging structures such as hooks and barbs likely facilitate dispersal via ectozoochory (on the feathers and fur) (Howe & Smallwood 1982; Levin *et al.* 2003). Historically, the apparent link between a dispersal syndrome and a particular vector led scientists to believe that dispersal was a well-developed symbiotic relationship (van der Pijl 1982). However, it is now recognised that most propagules are capable of being dispersed by multiple vectors (Ozinga *et al.* 2004), for example animal-dispersed fruits may also be dispersed by hydrochory (Hampe 2004). It is often suggested that these situations result in rare long-distance dispersal events and these non-standard cases of dispersal can have important outcomes for the spatial structure of populations (Higgins, Nathan & Cain 2003). Measuring the spatial patterns of passively dispersed organisms poses an enormous challenge to dispersal ecologists, as models must incorporate movement patterns of different vectors across multiple spatio-temporal scales.

Organisms that rely on passive dispersal cannot move between environments, and thus dispersal is the primary source of habitat selection (Bazzaz 1991; Casas, Willis & Donohue 2012). Directed dispersal is the disproportionate arrival of propagules in sites favourable for the survival of offspring and is considered a form of habitat selection (Howe & Smallwood 1982; Wenny 2001). Propagules may have attributes that facilitate their ability to reach particular habitats. A phenomenal example of this comes from South Africa's Fynbos biome, where the round seeds of the restio *Ceratocaryum argenteum* mimic the appearance and smell of faeces to attract dung beetles that roll them away from the maternal plant and bury them (Midgley *et al.* 2015). This represents the essence of directed dispersal, as in fire prone ecosystems such as the Fynbos, the burying of seeds is a critical strategy to escape the effects of intense fires. Other examples of directed dispersal include the cottony hairs of willows *Populus sp.* that facilitate settlement in favourable riverine habitat by becoming trapped in wet sand (Seiwa *et al.* 2007). Habitat selection has important evolutionary consequences as it reinforces particular dispersing phenotypes, and can accelerate adaptive evolution leading to the multitude of traits that are currently linked to dispersal (Casas *et al.* 2012).

1.1.4 Measuring patterns of animal-mediated dispersal

Animal-mediated dispersal of propagules is perhaps one of the most frequent forms of passive dispersal and includes dispersal by vertebrates, invertebrates (in particular ants or myrmecochory) and humans. In both temperate and tropical regions the majority of trees (60 – 90%) rely on vertebrates for the dispersal of their seeds (Howe & Smallwood 1982; Fleming, Breitwisch & Whitesides 1987). Amongst the vertebrates it is estimated that nearly 33% of extant bird species disperse seeds through the consumption of fruit or the scatter-hoarding of nuts (Wenny *et al.* 2011). Measuring the spatial patterns of animal-dispersed seeds (propagules) is notoriously difficult, but progress is being made by incorporating new technologies and developing new frameworks (Damschen *et al.* 2008; Nathan *et al.* 2008a; Tesson & Edelaar 2013; Kays *et al.* 2015). Typically, animal-mediated dispersal has been measured by either Eulerian (backward tracking) or Lagrangian (forward tracking) methods (Côrtes & Uriarte 2013). These approaches will be discussed with particular reference to seed dispersal, but the methods can be applied to any passively dispersing organism.

Backward tracking or source-based approaches, are concerned with populations of individuals and how they are distributed in relation to the seed source (Muller-Landau *et al.* 2008). Traditionally these methods used seed traps to link the location of seed deposition to a presumed source, and were shown to perform reasonably well for wind-dispersed species, but not for animal-dispersed species (Côrtes & Uriarte 2013). However, in recent years stable isotopes and molecular markers have been used to very accurately assign offspring to the maternal source (Carlo, Tewksbury & Río 2009; García & Grivet 2011). For example, García *et al.* (2009) were able to identify individual source trees for St Lucie Cherry tree *Prunus mahaleb* seeds based on maternally inherited seed tissue. Whilst these molecular techniques are capable of very accurately describing seed rain, a major downfall is that they are incredibly expensive, requiring whole populations of maternal plants to be genotyped.

In forward tracking approaches, the propagules themselves are tracked from the source to the deposition site (Côrtes & Uriarte 2013). Over fine spatial scales, techniques such as observing disperser foraging activities and subsequently actively following or tracking the disperser remotely (e.g. radio-telemetry) have proved useful in determining the spatial patterns of dispersal (Westcott & Graham 2000). Other basic methods include tagging the actual seeds with threads (Forget 1990), painting fruits and seeds with fluorescent paints (Levey & Sargent 2000), or irradiating seeds with a radioactive isotope and using a Geiger counter to track them (Vander Wall 2003). There are also methods to track seeds that employ new technological advances. For example, tiny radio-transmitters attached directly to seeds have been used to track how scatter-hoarding rodents in the Neotropics cache seeds, raid each other's caches and subsequently move and re-cache their own seeds to avoid the raiders (Jansen *et al.* 2012). This study demonstrated that tracking seeds over long periods and including animal behaviour changes our perspective on patterns of seed dispersal. Individually, rodents are considered poor dispersal agents, moving seeds no more than a few meters. However, communities of seed dispersing rodents can be effective long-distance dispersers if seeds are continually moved over short, stepwise distances to avoid thieving (Jansen *et al.* 2012).

The forward-tracking methods described above work well on small scales, but when it comes to tracking seeds over large distances, such as in cases of dispersal by elephants (Campos-Arceiz *et al.* 2008) or migratory birds (Viana *et al.* 2013b), different techniques are needed. Mechanistic models have proved useful in addressing dispersal at larger distances, and aim to incorporate plant and disperser traits and information about the environment into a single predictive model (Cousens *et al.* 2010). However, these approaches are difficult to apply, as they must include traits intrinsic to the dispersal vectors and dispersing propagules, together with environmental factors (Côrtes & Uriarte 2013). The use of high-resolution GPS tracking devices has also proved instrumental in furthering our understanding of dispersal by highly mobile animals. This data can be combined with remotely sensed environmental products and experimental and field based research on seed characteristics to provide new insights into animal-mediated dispersal and its consequences (Cousens *et al.* 2010).

1.1.5 Dispersal in wetlands

Wetlands perform many important functions in the landscape, for example water storage, flood mitigation and water purification, and in doing so are of high value to humans (Mitsch & Gossilink 2000). Furthermore, wetland ecosystems support approximately 6% of all described species despite covering only 0.8% of the planet's surface (Hawksworth & Kalin-Arroyo 1995). More than 10% of all animal species (Dudgeon *et al.* 2006) and approximately 2% of the world's total flora occur in wetlands (Cook 1999). Unfortunately, wetland ecosystems are globally threatened by climate change, invasive species and water extraction (Dudgeon *et al.* 2006; Strayer & Dudgeon 2010). As wetland ecosystems become increasingly fragmented, the ability of wetland species to disperse to new environments will have important consequences for the maintenance of wetland biodiversity (Santamaría & Klaassen 2002).

1.1.5.1 Connectivity in wetlands

Wetlands have typically been viewed as discrete habitat patches surrounded by an uninhabitable matrix. However, wetlands are not isolated spaces but rather a group of complex, dynamic habitat patches with both abiotic and biotic connections (Amezaga, Santamaría & Green 2002). Abiotic or physical connections between wetlands are mainly related to the flow of water, and dispersal can occur between wetland patches in three spatial directions; either longitudinally (downstream movements), laterally (across a watershed) or vertically (surface to groundwater) (Fullerton *et al.* 2010). However, habitat does not need to be structurally connected to be functionally connected (Baguette & Dyck 2007). Some organisms, because of their highly mobile nature, are capable of connecting patches across an inhospitable matrix (Lundberg & Moberg 2003). These kinds of dynamics are evident in wetlands, where wetland patches do not need to be physically connected by flowing water for the biota to move between them (Haig, Mehlman & Oring 1998). Some organisms, such as amphibians, dragonflies and waterbirds, can actively disperse amongst a network of wetland patches (Amezaga *et al.* 2002); whilst others, such as plants and aquatic invertebrates, disperse with the aid of a vector (e.g. wind, bird, mammal or anthropogenic) (Soons 2006; Vanschoenwinkel *et al.* 2008b; Waterkeyn *et al.* 2010; van Leeuwen *et al.* 2012b). Determining the degree to which the biota of wetlands interact with one another and the spatio-temporal scales over which these interactions occur is a fundamental question in community ecology (Heino *et al.* 2015) and an important issue in wetland monitoring and conservation (Roe, Brinton & Georges 2009).

1.1.5.2 Mechanisms of passive dispersal in aquatic organisms

Many plants and aquatic invertebrates lack the ability to move by their own means from one wetland to another. However, despite the apparent isolation of wetland patches, many aquatic plant and invertebrate species have widespread distributions, sometimes spanning several continents (Santamaría 2002). A high capacity for passive dispersal is a key factor explaining the distribution patterns of non-mobile plants and aquatic invertebrates

(Santamaría 2002; Bohonak & Jenkins 2003). Several mechanisms of dispersal can facilitate this process, but not all mechanisms can be considered equivalent in their spatial extent and/or frequency and contribute differentially to eventual dispersal patterns. Hydrochory may facilitate long distance movements, but as already discussed, may not be available as a mechanism in many situations due to lack of hydrological connectivity between waterbodies. Wind dispersal on the other hand is frequent (Soons 2006; Vanschoenwinkel *et al.* 2008a), but only successful over short distances. Human-mediated dispersal can have significant ecological consequences, especially given the relevance of this mechanism for the dispersal of aquatic invasive species (Johnson, Ricciardi & Carlton 2001), but occurs relatively infrequently. Waterbirds disperse propagules in relatively high frequencies and over both long and short distances, and are therefore considered one of the most important natural dispersal agents (Figuerola & Green 2002a).

1.1.6 Dispersal of propagules by waterbirds

Almost 160 years ago, Charles Darwin (1859) attributed the cosmopolitan distribution of many freshwater plants and invertebrates to the waterbird-mediated dispersal of their seeds and eggs. However, only in recent years has this theory been the subject of rigorous scientific inquiry and a number of recent studies have highlighted the remarkable capacity of waterbirds to disperse the propagules of aquatic organisms (Brochet *et al.* 2009; van Leeuwen *et al.* 2012b; Viana *et al.* 2013a; Green & Elmberg 2014). Waterbirds disperse propagules in two different ways. Firstly, propagules may adhere to the feet and feathers of waterbirds as they swim or forage (ectozoochory or external dispersal). Secondly, propagules may survive passage through the gut to be deposited in faecal matter (endozoochory or internal dispersal) (Brochet *et al.* 2010b; Raulings *et al.* 2011). Endozoochory is generally considered the more important mode, at least in terms of the quantity of propagules dispersed (Brochet *et al.* 2010b; Costa *et al.* 2014). However, ectozoochory has been the topic of fewer studies, and its role has possibly been underestimated. Dispersal modes that are less commonly considered are regurgitation of intact propagules (Kleyheeg & van Leeuwen 2015) and propagules taken up as nest building materials (Dean, Milton & Siegfried 1990; Kristiansen 1996).

A recent review implicated waterbirds in the dispersal of 39 species of invertebrate and 97 species of plant worldwide (van Leeuwen *et al.* 2012b), although this number is growing rapidly and is likely out of date. This same review also demonstrated that endozoochory was very common, with over 45% and 32% of faecal samples containing intact plant seeds and invertebrate eggs, respectively. Amongst the most commonly dispersed invertebrate orders are the cladocerans, copepods, anostracans, rotifers and bryozoans, which all produce dormant resting phase eggs that are resistant to desiccation and thus well adapted for external dispersal (Panov *et al.* 2004). However, these eggs are also capable of surviving in high numbers through the gut (Frisch, Green & Figuerola 2007; Green *et al.* 2008) and viable invertebrates propagules have been recovered repeatedly from waterbird faecal matter (DeVlaming & Proctor 1968; Green *et al.* 2008; Brochet *et al.* 2010a). The seeds of many different aquatic and wetland plant species, and surprisingly, many terrestrial plants, are frequently dispersed by waterbirds (Brochet *et al.* 2009; Raulings *et al.* 2011). Waterbirds, especially waterfowl, also forage in terrestrial environments such as agricultural fields and grassland, hence the prevalence of terrestrial seed in the diet, and have been shown to be important dispersers in terrestrial environments (Bruun, Lundgren & Philipp 2008). Furthermore, it has been noted that waterbirds disperse the propagules of exotic plants and invertebrates; however, the role of waterbirds in the spread of invasive species has not received enough attention in the literature (Chapter 6; Green 2015).

1.1.7 Mechanistic approach in the study of waterbird dispersal

Research, particularly over the last decade, has shifted focus from simply determining what waterbirds are dispersing to developing a mechanistic understanding of the processes underlying the patterns of dispersal in these wetland systems (Soons *et al.* 2008; van Leeuwen *et al.* 2013; Viana *et al.* 2013b; Kleyheeg *et al.* 2014). To explore the mechanisms contributing to the spatial patterns of seed dispersal we must recognise all phases of dispersal; (1) emigration, (2) movement, and (3) immigration (Ronce 2007). To apply this framework to waterbird dispersed aquatic organisms we need to explore (1) the uptake of propagules, (2) the transport of propagules, and (3) the deposition of viable propagules in a new site.

1.1.7.1 Emigration - Uptake

The uptake of organisms or propagules by waterbirds can occur intentionally or unintentionally. Birds may actively select propagules as a part of their diet, in which case high numbers may be ingested, or may accidentally encounter them when foraging for other food (i.e. adherence to feathers or accidental ingestion) (Figuerola & Green 2002a). The uptake of propagules via different modes will have varying consequences for spatial patterns of dispersal. Furthermore, the differences between waterbird species vectors is an important determinant in what propagules are taken up as species will have different foraging modes, diet and habitat preferences which will affect the propagules encountered (Green, Figuerola & Sánchez 2002). For example, there seems to be no difference between diving ducks, dabbling ducks and coots in the quantity of propagules dispersed, but the identity of the particular plant and invertebrate propagules that are ingested differs markedly (van Leeuwen *et al.* 2012b). Determining the degree to which particular groups of waterbirds disperse the same (or different) propagules is an important factor in assessing the unique or redundant roles waterbirds play in seed dispersal.

In other systems, the dispersal syndromes that facilitate uptake by a particular vector are more obvious than for waterbird-mediated dispersal and most propagules of aquatic organisms display no obvious adaptations to facilitate dispersal by waterbirds. However, it is noted that the propagules of some aquatic invertebrates may demonstrate a slight adaptation for ectozoochory as some produce spiked structures, for example the statoblasts of bryozoans. Rather than physical structures, the surrounding environment may aid emigration of propagules, for example sticky mud may facilitate the attachment of propagules to the bill and feet, as well as help prevent desiccation (Figuerola & Green 2002a). Overall, however, in wetland systems it appears that propagules are primarily ingested as a food source and their ability to be moved away thus depends on their capacity to survive digestion.

1.1.7.2 Movement - Transport

The distance that propagules can be dispersed is a product of the displacement of the vector and the retention time of the propagule in or on the vector. As discussed above, animal movement is an incredibly complex behaviour and both interspecific (e.g. migratory versus non-migratory bird species) and intraspecific (e.g. seasonal or life history-related) differences in movement can have implications for dispersal at local, regional and even continental scales. The majority of studies addressing waterbird-mediated dispersal of aquatic organisms have investigated dispersal only during migration (Soons *et al.* 2008; Viana *et al.* 2013b a). These studies have shown that migratory waterbirds can facilitate dispersal on a large scale, and whilst we recognise the importance of long-distance dispersal, generally movements over 100 km (Viana *et al.* 2013b), these migratory movements are only a part of the annual cycle of waterbirds. The influence of the daily movements of waterbirds on patterns of dispersal has hardly been investigated (Kleyheeg 2015), and will have particular relevance in regions, such as southern Africa that have no inter-continental migratory waterfowl, although Knob-billed Duck *Sarkidiornis melanotos* is considered an intra-continental migrant (Underhill *et al.* 1999). Thus, determining the spatial patterns of dispersal requires detailed knowledge of the movement and behaviour of birds throughout the annual cycle and across different regions.

Propagule retention time is the other important factor determining the spatial patterns of dispersal. The maximum dispersal distance of a propagule is limited by how long the propagule remains in the gut of a waterbird or attached externally (Clausen *et al.* 2002). Research on the retention times of propagules in the gut of captive waterbirds has provided key insights into the propagule traits (e.g. seed size) that facilitate endozoochory (Soons *et al.* 2008). Recently, additional experiments have investigated the role of vector activity (e.g. swimming versus roosting) in moderating the digestion of propagules (van Leeuwen, Tollenaar & Klaassen 2012a; Kleyheeg *et al.* 2014). However, estimates of the retention times of propagules remain highly variable (Charalambidou *et al.* 2005; Soons *et al.* 2008; Brochet *et al.* 2010c; García-Álvarez *et al.* 2015) and thus more studies are required to establish generalities across propagule species and vectors.

1.1.7.3 Immigration - Deposition

To complete the dispersal process, viable propagules must reach a suitable habitat where they may become established. This is a difficult step of the dispersal process to quantify and few studies have attempted to determine the effects of seed ingestion or external transport on the difficulty of becoming established once dispersed (but see Figuerola & Green 2004). A number of studies have quantified the number of germinating and viable propagules from both ecto- and endozoochory samples (Brochet *et al.* 2010b a; Raulings *et al.* 2011; García-Álvarez *et al.* 2015). It is estimated that between 6.5% and 12% of experimental and field samples contain at least one viable propagule (van Leeuwen *et al.* 2012b). The capacity of propagules to reach new habitat and to establish thus appears high. The study of the scale of deposition and the habitats that are selected by waterbirds will provide key insights into how waterbird-mediated dispersal affects the structure of aquatic communities.

1.2 OUTLINE OF THE THESIS

Remarkably, despite the growing interest in the topic, no previous examples of waterbird-mediated dispersal of aquatic organisms in Africa have been published. In this thesis, I explore the role of waterbirds in the dispersal of aquatic propagules in southern Africa for the first time. Each of the three stages of dispersal described above (Section 1.1.7) is assessed to develop a holistic representation of waterbird-mediated dispersal in the region (Fig. 1). The study of waterbird-mediated dispersal in southern Africa offers an opportunity to expand our current knowledge of this process in novel landscapes and to different waterbird vectors with varying feeding ecologies and movement patterns. In addition, this study will provide insight into wetland community organisation and the persistence of populations in spatio-temporally variable environments.

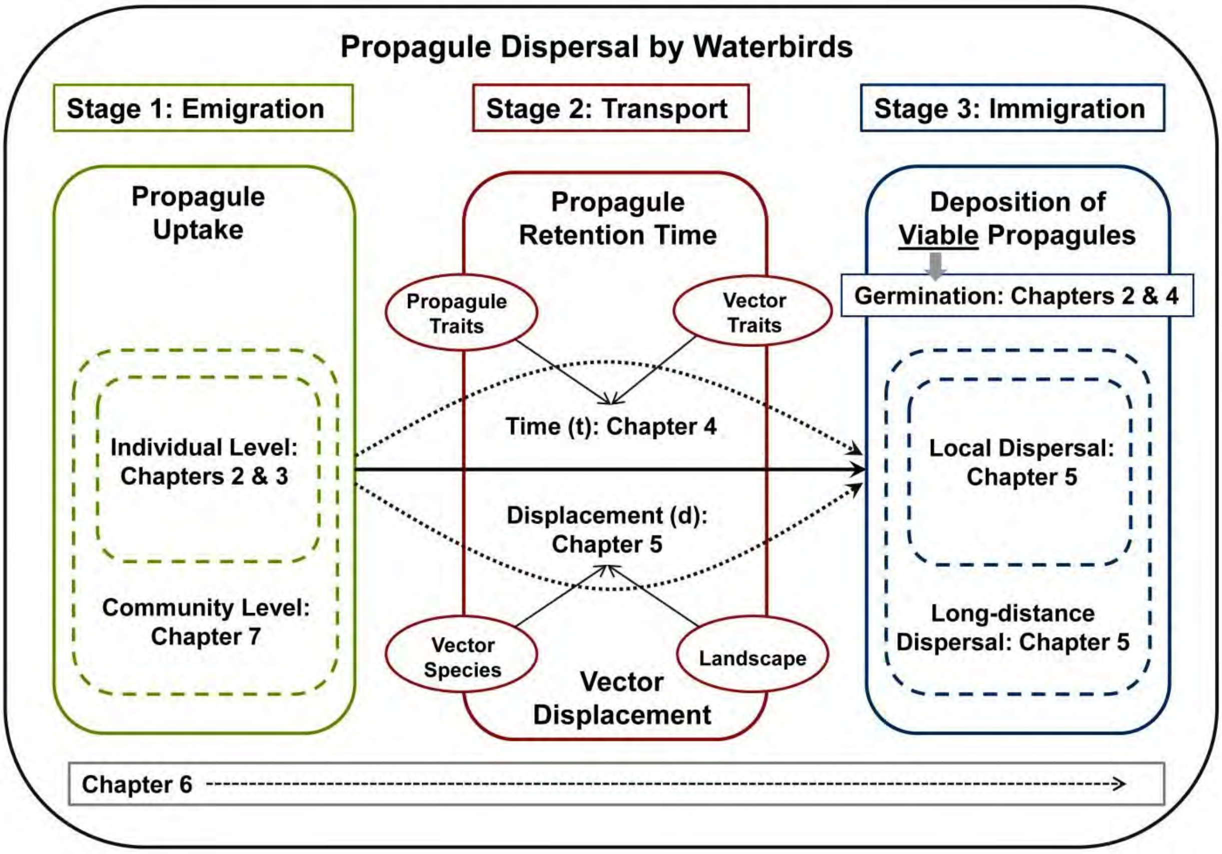


Figure 1 Three stage conceptual framework of propagule dispersal by waterbirds and thesis outline indicating the contribution of each chapter. Each stage is represented in a separate colour. Dashed boxes indicate where a single process has been addressed at different scales or levels.

All waterbird groups (including shorebirds, rails, ibises, flamingos) are important for the dispersal of propagules. However, the waterfowl (ducks, geese and swans in the family Anatidae) are of particular importance because of the high proportion of seeds and aquatic invertebrates in their diet, their general abundance and highly mobile nature (Green *et al.* 2002). I therefore investigated the role of waterfowl in the dispersal of aquatic plants and invertebrates in southern Africa. In this thesis, with the exception of Chapter 6 that addresses the role of various families of waterbirds in the spread of exotic species, I have focussed only on a subset of waterfowl species that are indigenous residents in southern Africa (Table 1). Additionally, whilst parallels can be drawn to the dispersal of aquatic invertebrates in many of the chapters, only Chapter 3 and 6 explicitly address the dispersal of aquatic invertebrates by waterbirds and the majority of chapters are focussed on seed dispersal.

In Chapters 2 – 5, I adopt a field- and experimental-based approach to parameterise a simple mechanistic model to determine patterns of waterfowl-mediated dispersal in southern Africa. Each chapter expands our knowledge of a different stage (and in some cases multiple stages) of dispersal (Fig. 1), to create a detailed picture of propagule dispersal by southern African waterfowl. In Chapters 6 and 7, I apply the concept of waterbird-mediated dispersal more broadly to address (1) the role of waterbirds in the dispersal of aquatic invaders; and (2) the determination of seed dispersal functional groups amongst a waterfowl community. Finally, in Chapter 8, the results are synthesised and evaluated in the context of dispersal ecology, community organisation, and the conservation of freshwater resources. A number of recommendations and priorities for future research are also highlighted in this final chapter.

1.2.1 Chapter description

In Chapter 2, I determine the identity, quantity, and germinability of plant seeds dispersed via ecto- and endozoochory in southern African waterfowl. To determine the extent to which the two modes are complementary, I also test for differences in species composition between the two modes. Chapter 3 comprises a very similar study, but instead focuses on differences in the dispersal of aquatic invertebrates between ecto- and endozoochory. Together these chapters provide an overview of the capacity of southern African waterfowl to disperse aquatic organisms and constitute the most comprehensive comparison to date of dispersal potential between ecto- and endozoochory.

One of the factors influencing the distances that seeds are dispersed is gut retention time, which in turn is affected by both disperser and propagule traits. However, the relative importance of these traits for dispersal is unclear. Chapter 4 experimentally investigates how the seed characteristics of size and hardness mediate trade-offs in recoverability and germinability against increasing gut retention times. A randomised, replicated feeding trail is used to determine the seed passage times and recovery of several different seed species with varying characteristics force fed to two southern African duck species, Egyptian Goose *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha*.

In Chapter 5, a mechanistic model is developed to explore the patterns of seed dispersal by waterbirds in southern Africa. The gut retention data from Chapter 4 is combined with Egyptian Goose and Red-billed Teal movement data from GPS satellite transmitters across five different study populations in southern Africa to explore spatial patterns of seed dispersal. The GPS data afford an excellent opportunity to investigate variation in dispersal patterns between both different species and landscapes.

Waterbirds are commonly cited as dispersal vectors of invasive aquatic species (McConnachie, Hill & Byrne 2004; Green & Figuerola 2005b); however, empirical evidence of this remains scarce**.** Chapter 6 objectively assesses the role of waterbirds in the dispersal of invasive and exotic aquatic species through a comprehensive literature review. In this Chapter, I review evidence for the dispersal of invasive and exotic aquatic organisms for each of the three stages of dispersal.

Chapter 7 explores whether seed dispersal functional groups are evident amongst the southern African waterfowl. This chapter uses diet data from 16 waterfowl species to determine whether meaningful functional groups can be created which capture important ecological variation in seed dispersal function. The analysis is presented in the form of a case study as I suggest that this methodology has usefulness beyond the seed dispersal function of waterfowl.

1.2.2 Study Sites

Data were collected from five different permanent wetland sites in southern Africa (Fig. 2). In each of the chapters, the relevant study sites and co-ordinates utilised are listed. Here I provide additional context for each study site to avoid repeating the same material in each chapter.

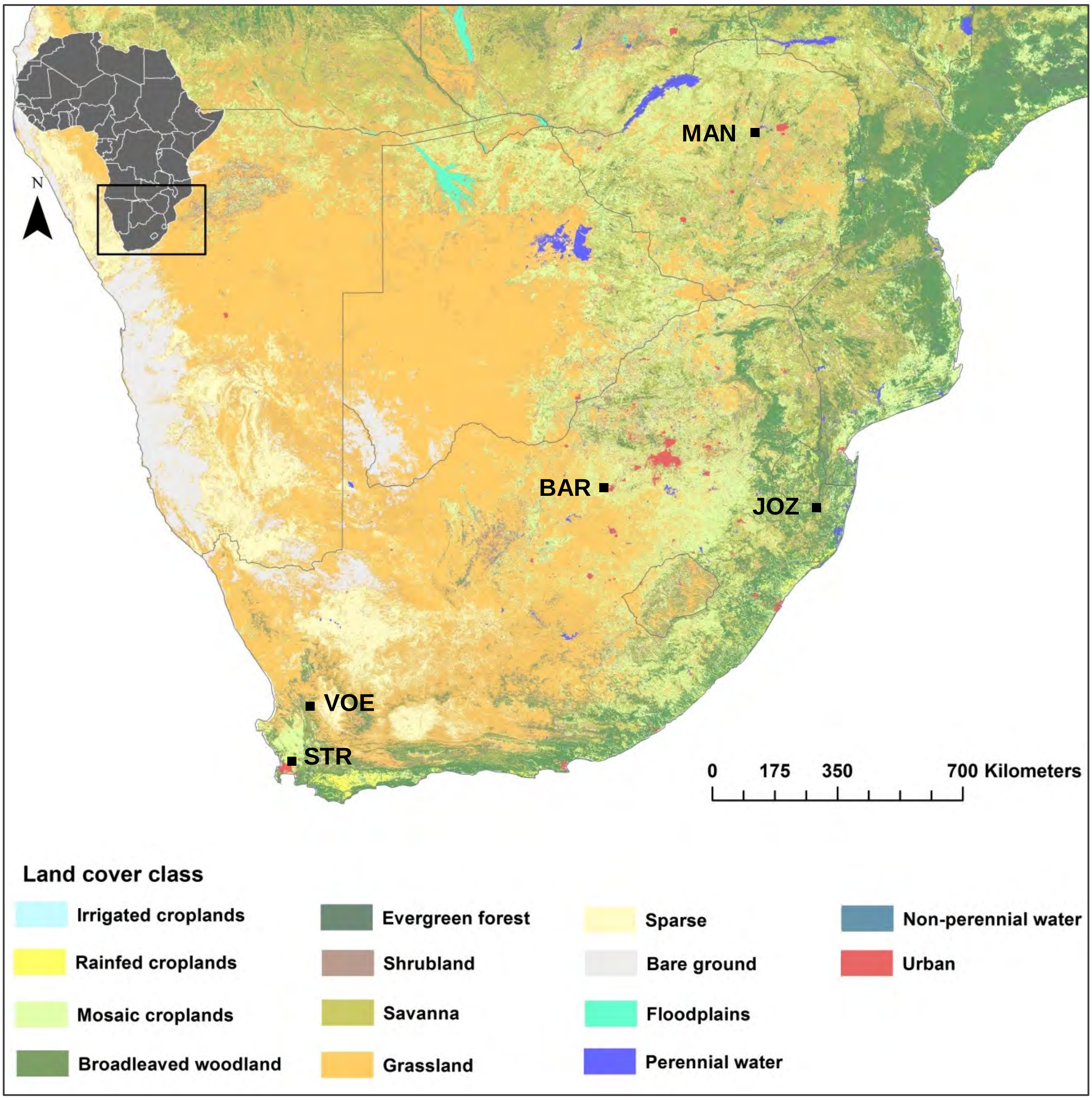


Figure 2 Location of study sites in southern Africa. Land cover data derived from the GlobCover dataset available at 300 m resolution (Arino *et al*. 2012). BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = Strandfontein/False Bay Ecology Park and VOE = Voëlvlei Dam.

1.2.2.1 Barberspan Nature Reserve - 26°35’ S 25°34’ E

Barberspan Nature Reserve is a Ramsar wetland located in the semi-arid, summer-rainfall region of the North West province of South Africa. It is a large, permanent, alkaline pan fed by the Harts River. In the summer months, the pan can cover an area of nearly 2000 ha, but water levels fall substantially during late winter. The surrounding habitat is short, open grassland, but outside of the nature reserve much of this vegetation is now under maize and sunflower cultivation. The pan is an important refuge for waterfowl during the dry months and is used as a stopover site by many migrating waders. It regularly supports in excess of 20 000 waterbirds (Birdlife 2015).

1.2.2.2 False Bay Ecology Park (Strandfontein) - 34°04' S 18°30' E

False Bay Ecology Park is situated on the Cape Flats about 20 km outside of Cape Town, South Africa. The area experiences a Mediterranean-type climate with hot dry summers and wet winters. Strandfontein, situated within the nature reserve, is a wastewater treatment facility supporting a number of nutrient-enriched settling ponds of various sizes and surrounded by a few large, permanent natural waterbodies. The entire wetland complex covers approximately 1800 ha. Aquatic vegetation is sparse, but huge beds of exotic *Typha capensis* dominate the marsh surrounding the wetland. The invasive Water Hyacinth *Eichhornia crassipes* is also found in several pans. Despite problems with invasive weeds and encroachment from the surrounding residential areas, the wetland is highly productive and supports a high diversity of waterbirds (Birdlife 2015).

1.2.2.3 Voëlvlei Dam - 33°21' S 19°02' E

Voëlvlei Dam is a large water storage dam located in the semi-arid winter-rainfall region of the Western Cape, South Africa. The surrounding landscape is mountainous, with viticulture and wheat farms monopolising the valleys. The dam has a surface area of nearly 3100 ha (DWAF 2015). The shoreline is bare and rocky. The site supports huge roosting and moulting populations of Egyptian Goose and Spur-winged Goose *Plectropterus gambensis*.

1.2.2.4 Lake Manyame - 17°49' S 30°36' E

Lake Manyame is the only study site situated outside of South Africa, and is a dam located outside of Harare, the capital city of Zimbabwe. The dam is within a summer-rainfall region and is fed by the Manyame River, which falls within the Zambezi catchment. The surface area of the dam is nearly 8100 ha, although it can experience substantial changes in water levels due to rainfall seasonality. There is a significant amount of agriculture in the region, predominantly commercial tobacco and maize farms and some industrial poultry farms, and the dam is mostly surrounded by agricultural fields. Lake Manyame is a seasonally important site for large aggregations of waterbirds (Cumming, Gaidet & Ndlovu 2012).

1.2.2.5 Jozini Dam - 27°20' S 31°54' E

Jozini Dam is located in the KwaZulu-Natal province of South Africa and experiences summer rainfall. The dam was built in 1974 with the aim of providing irrigation to surrounding agricultural areas and has a surface area of 13 200 ha. The dam is located almost entirely within the Pongola Nature Reserve and the surrounding vegetation ranges from grassland to *Acacia* thornveld. The shoreline of the dam is open and vegetation immediately surrounding the dam is sparse. Populations of waterbirds are highly variable, with low numbers when water levels are high, and with numbers increasing as water levels recede to expose productive mudflats (Henry 2015).

1.2.3 Study Species

Of the Anatidae, (ducks, geese and swans), seven of the ten subfamilies occur in southern Africa: Dendrocygninae, Thalassorninae, Oxyurinae, Anatinae, Tadorninae, Plectropterinae and Aythyinae. The waterfowl are small to very large (Hottentot Teal *Anas hottentota* 33 cm, 250 g to Spur-winged Goose 98 cm, 5.1 kg) with relatively short legs, broad bodies, and medium to long necks. Despite common names such as Egyptian Goose and Spur-winged Goose, all species are actually ducks, and southern Africa boasts no true geese. In southern Africa, the Anatidae includes 16 species occurring as breeding residents, 3 species occurring as occasional vagrants from the northern hemisphere and 1 introduced species (Table 1). A range of different habitats (vegetated pans, open dams, rivers), diets (granivorous, herbivorous, insectivorous, piscivorous), foraging modes (dabbling, diving, grazing) and movement behaviours (sedentary, nomadic, semi-nomadic) are represented (Hockey, Dean & Ryan 2005).

Not all waterfowl species listed in Table 1 could be considered for the field and experimental elements of this study. Field samples were readily obtainable from six southern African duck species that were fairly common and easy to capture, and roosted in sizable, monospecific flocks that aided in the collection of faecal samples. This included three dabbling ducks: Red-billed Teal, Yellow-billed Duck *Anas undulata* and Cape Shoveler *Anas smithii*, two grazing ducks: Egyptian Goose and Spur-winged Goose, and one dabbling-and-diving duck: White-faced Whistling Duck *Dendrocygna viduata* (Table 1). These species exhibit important differences in their feeding ecology, morphology, and habitat preference and are therefore useful for comparing different elements of dispersal.

Table 1 Waterfowl species occurring in southern Africa. * Indicates occasional Palearctic migrants, ** indicates introduced species and bold text indicates species used in this study.

Common name	Scientific name	Foraging Mode
Egyptian Goose	*Alopochen aegyptiaca*	Grazing
Cape Teal	*Anas capensis*	Dabbling
Red-billed Teal	*Anas erythrorhyncha*	Dabbling
Hottentot Teal	*Anas hottentota*	Dabbling
Cape Shoveler	*Anas smithii*	Dabbling
African Black Duck	*Anas sparsa*	Dabbling
Yellow-billed Duck	*Anas undulata*	Dabbling
Fulvous Duck	*Dendrocygna bicolor*	Diving
White-faced Whistling Duck	*Dendrocygna viduata*	Diving
Southern Pochard	*Netta erythrophthalma*	Diving
African Pygmy-goose	*Nettapus auritus*	Diving
Maccoa Duck	*Oxyura maccoa*	Diving
Spur-winged Goose	*Plectropterus gambensis*	Grazing
Knob-billed Duck	*Sarkidiornis melanotos*	Dabbling
South African Shelduck	*Tadorna cana*	Grazing
White-backed Duck	*Thalassornis leuconotus*	Diving
Northern Pintail*	*Anas acuta*	
Northern Shoveler*	*Anas clypeata*	
Mallard Duck**	*Anas platyrhynchos*	
Garganey*	*Anas querquedula*	

Red-billed Teal and Egyptian Goose were chosen for the experimental and GPS tracking components of this study. Most of the GPS satellite tracking data existed prior to the inception of this study and formed part of several previous studies investigating the spatial ecology of southern African waterfowl and avian influenza dynamics in the sub-region (Cumming *et al.* 2011, 2012; Ndlovu *et al.* 2013). Thus, to apply the GPS data in the prediction of the spatial patterns of seed dispersal by southern African waterfowl, I chose to collect gut retention data from these two waterfowl species. Egyptian Goose and Red-billed Teal were perfect comparative species as they range remarkably in size, but have similar diets. Although Red-billed Teal are typically categorised as omnivorous dabbling ducks, and Egyptian Goose as herbivorous grazing ducks, these species show remarkable overlap in diet (Chapter 7). Both species readily consume agricultural grains and grasses (Poaceae) and eat the seeds of wetland plants from the Potamogetonaceae and Polygonaceae families (Halse 1984; Petrie 1996). Additionally, both species are widespread, abundant and relatively mobile (Hockey *et al.* 2005). Finally, the study of seed dispersal by Egyptian Goose is also interesting from a biogeographic perspective, as this species has recently undergone a range expansion and the population numbers are rapidly increasing, especially in areas where it was once scarce (Okes, Hockey & Cumming 2008). This species has been introduced to Western Europe where it is also expanding its range (Lensink 1998). A full analysis of how changes in waterfowl distribution can influence seed dispersal patterns is beyond the scope of this thesis, but it is important to recognise the impact that anthropogenic land-use change and global climate change can have on waterbird distributions and the cascading effects on the functions performed by these animals.

1.2.4 A brief note on chapter structure

Each chapter is written as a stand-alone paper to facilitate the publication of the work. Thus, each chapter comprises an abstract, introduction, materials and methods, results and discussion section. There is some repetition of concepts throughout the introductory sections and a little duplication in the materials and methods sections. I have removed as much repetition as possible; however, in some cases this repetition is essential for the readability of each chapter. Where chapters have been accepted for publication, the text has been edited and formatted to fit with the rest of the thesis.

CHAPTER 2

SEED DISPERSAL BY WATERBIRDS IN SOUTHERN AFRICA: COMPARING THE ROLES OF ECTOZOOCHORY AND ENDOZOOCHORY

Photo by: Anja Terörde

Published: Freshwater Biology

ABSTRACT

Waterbirds are important seed dispersers and may play a vital role in maintaining connectivity among isolated aquatic communities. Whilst considerable progress has been made in our understanding of the dispersal function of waterbirds, the number of studies is still limited and is largely focused on migratory waterbirds in Europe. The first detailed study of seed dispersal by waterbirds in Africa is presented here. I quantified and compared endo- and ectozoochory across six waterfowl species at three widely dispersed sampling locations in South Africa and tested for differences between dispersal agents and sampling sites. I also tested for differences in the plant communities dispersed by endo- and ectozoochory. All intact and germinating propagules found in freshly collected faecal samples ($N = 313$) and feather brushings ($N = 422$) were counted and identified. A total of 1585 seeds from 48 plant taxa were recovered from the samples. 37% of all external brushings and 27% of all faecal samples contained at least one intact propagule and 15% and 8% of the samples contained at least one germinating seed respectively. Sampling site had a strong influence on the presence, abundance and germination of propagules recovered from both external and faecal samples. Additionally, sympatric waterfowl showed differences in the abundance and germinability of plant propagules transported by endozoochory. The presence of at least one propagule was highest in the external samples, but propagule abundance and germination were highest in faecal samples. The community composition of propagules transported by each of these two modes was significantly different, suggesting that endo- and ectozoochory might be complementary dispersal modes. The results indicate an important role for waterfowl in the dispersal of aquatic plants in Africa. While ectozoochory can be an important dispersal mode, its effects may be heterogeneous and unpredictable relative to endozoochory. Endozoochory appears to be the more effective and dominant mode. These results also point to a high capacity for the dispersal of exotic species via both ecto- and endozoochory.

2.1 INTRODUCTION

Birds exhibit the most diverse range of ecological functions amongst the vertebrates (Sekercioğlu 2006). Seed dispersal is considered one of the most important avian ecological functions, with consequences for maintenance of plant diversity, gene flow, and the colonisation and regeneration of deforested, fragmented and marginal habitats (Sekercioğlu 2006). Approximately 33% of extant bird species are responsible for seed dispersal through fruit consumption or the scatter-hoarding of nuts and coniferous seed species (Whelan, Wenny & Marquis 2008; Wenny *et al.* 2011). However, this estimate does not include the potentially valuable contribution of seed-consuming waterbirds to the dispersal of plant propagules (Green & Elmberg 2014).

The presence and activity of waterbirds can have significant positive effects on aquatic biodiversity (Green & Elmberg 2014). In particular, birds may act as important seed dispersers (Figuerola & Green 2002a; van Leeuwen *et al.* 2012b) and play a vital role in maintaining species and genetic diversity among communities in isolated aquatic systems (Amezaga *et al.* 2002). This seed dispersal function is a potentially important source of connectivity, reorganisation and recolonisation, especially in dynamic and ephemeral freshwater systems (Nyström & Folke 2001; Soons *et al.* 2008).

Dispersal by waterbirds has long been an explanation for how organisms reach isolated habitats (Darwin 1859; Ridley 1930), but until recently, was a poorly studied phenomenon (Santamaría & Klaassen 2002). Recent field and laboratory studies indicate that waterbirds are particularly adept dispersers (van Leeuwen *et al.* 2012b; Green & Elmberg 2014). Their frequent multi-scale, directed movements between ecologically similar wetlands and their high abundance make them particularly suitable seed vectors (Figuerola & Green 2002a; Green *et al.* 2002; Nathan *et al.* 2008b). This is especially true relative to the unreliable nature of human vectors (Waterkeyn *et al.* 2010), the finer-scale movements of less abundant aquatic vertebrates such as fish and mammals (Vanschoenwinkel *et al.* 2008b; Pollux 2011), the inherently random nature of wind dispersal (Soons 2006), and the need for physical connectivity for dispersal by water (Boedeltje *et al.* 2003).

Plant propagules are dispersed by birds after passing intact through the gut (endozoochory) or by becoming attached to the feathers, feet and bill (ectozoochory). The latter was widely assumed to be the dominant process, following early observations of pondweeds clinging to waterfowl feathers and seeds sticking via mud to feet (Darwin 1859). However, it is now widely suggested that endozoochory is the more frequent seed dispersal mode (Brochet *et al.* 2010b). Endozoochory by waterbirds has been implicated in the dispersal of over 97 plant species (van Leeuwen *et al.* 2012b), but this number is likely much higher.

Whilst considerable progress has been made in our understanding of seed dispersal by waterbirds over the last decade, the number of studies is still very limited and the focus largely restricted to migratory waterbirds in Europe. No previous quantitative studies of waterbird-mediated seed dispersal in Africa exist (Green & Elmberg 2014). Much of Africa is described as arid or semi-arid and characterised by unpredictable rainfall, temporary wetlands and dry-downs. The role waterbirds play in the recolonisation of these temporary wetlands in arid zones is virtually unexplored, although Green *et al.* (2008) and Raulings *et al*. (2011) provide Australian examples. In this chapter, the first quantitative analysis of the seed dispersal potential of waterbirds anywhere in Africa is presented. I have focused on waterfowl because the Anatidae are considered the most influential dispersers due to their high abundance and the prevalence of plant seeds in their diet (Green *et al.* 2002).

The main objective of this study was to identify, quantify and determine the germinability of plant propagules transported by waterfowl via endozoochory and ectozoochory in arid southern Africa. I determined the abundance and germinability of dispersed propagules to address both the quantity and quality of seed dispersal (Schupp, Jordano & Gómez 2010). Intact propagules passing through the gut or found attached to the feathers and feet of several waterfowl species were collected from three locations in South Africa. I first tested whether the capacity of waterbirds to disperse plant propagules varied between different waterfowl species and across sampling sites. The relative contributions of endozoochory and ectozoochory were then compared in terms of both the numbers of propagules attached to birds and differences in the potentially dispersed plant community.

Published research suggests that endozoochory is the dominant mode of dispersal and that ectozoochory is rare (Brochet *et al.* 2010b; van Leeuwen *et al.* 2012b). A higher presence and abundance of propagules in endozoochory samples was thus predicted. However, since ecto- and endozoochory may be complementary modes of seed dispersal, I also predicted that different plant species would be transported via the different modes. These predictions were tested by quantifying differences in propagule size and plant species composition between faecal and external samples. Although previous studies have attempted to compare ectozoochory with endozoochory (Brochet *et al.* 2010b; Raulings *et al.* 2011), this is the first study to address ectozoochory with sample sizes comparable to those obtained for endozoochory, making for a more representative comparison.

2.2 MATERIALS AND METHODS

2.2.1 Field Sampling

Field samples were collected from three wetlands in South Africa; Barberspan Nature Reserve (BAR) (26°35' S 25°34' E), False Bay Ecology Park (Strandfontein - STR) (34°04' S 18°30' E), and Voëlvlei Dam (VOE) (33°21' S 19°02' E) (Fig. 1). Sampling took place during January/February at Strandfontein and May/June at Barberspan in both 2013 and 2014, but Voëlvlei Dam was only sampled in April 2013 (see Appendix 2A for sampling dates). Sampling months coincided with the peak wing moult period of several southern African waterfowl in these areas and were chosen to support capture of high numbers of waterfowl, especially for the ectozoochory study. Approximately 37% of all captured birds were undergoing moult of their wing feathers, and wing moult status (from here on moult status) was therefore recorded for all birds used in the study to control for this confounding factor.

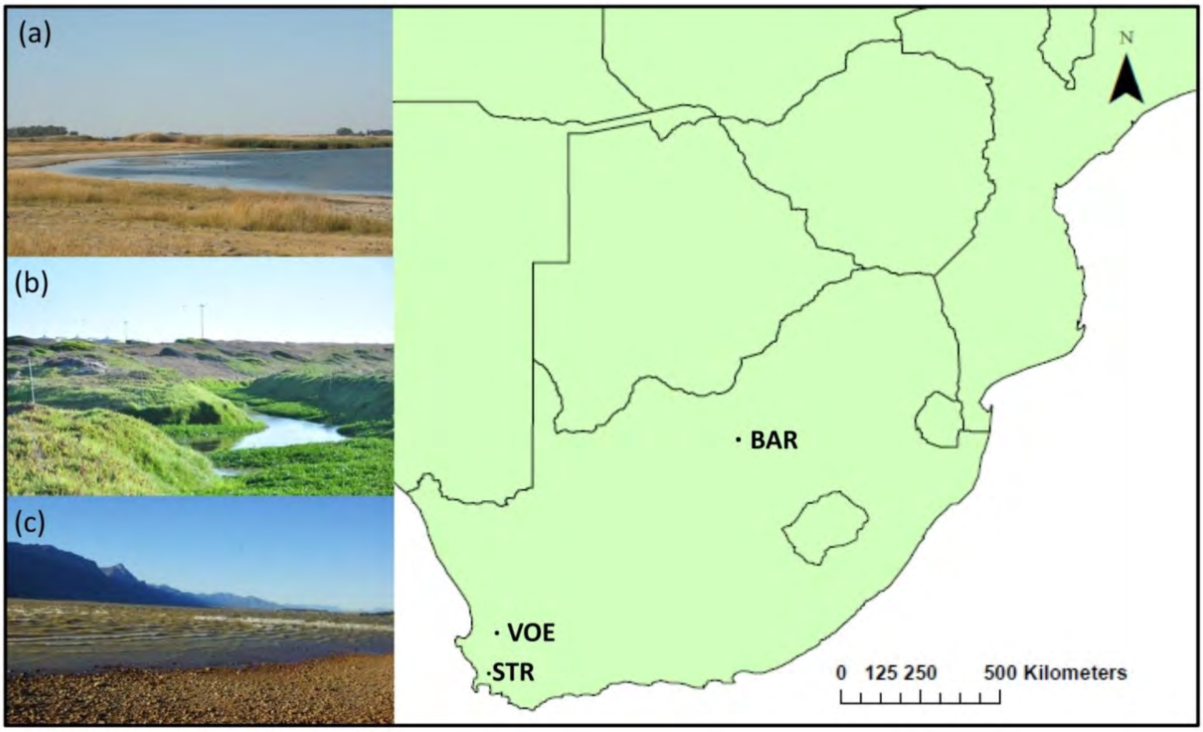


Figure 1 Map of Southern Africa showing the three collection sites; STR=Strandfontein, VOE = Voëlvlei Dam and BAR= Barberspan Nature Reserve. Photographs illustrate the marked difference in vegetation surrounding the waterbodies a) Barberspan, b) Strandfontein and c) Voëlvlei

To study ectozoochory, 422 samples were collected from live ducks captured in baited walk-in traps or mistnets. This total included samples from four common duck species: Red-billed Teal *Anas erythrorhyncha* (*N* = 49), Yellow-billed Duck *Anas undulata* (*N* = 141), White-faced Whistling Duck *Dendrocygna viduata* (*N* = 8) and Egyptian Goose *Alopochen aegyptiaca* (*N* = 224) (Appendix 2A). Captured ducks were removed from the traps and placed into individual clean cloth holding bags. Each captured duck was lifted from the holding bag and brushed over a plastic tray with a fine-toothed comb for three minutes. The feet and bill were then scrubbed with a toothbrush and rinsed with water into the same collection tray (Figuerola & Green 2002b; Brochet *et al.* 2010b). This residue was rinsed onto filter paper, lightly air-dried and stored in a sealed envelope at 4° C until laboratory analysis in August/September of the collection year. The cloth holding bags were washed between each use to ensure that no contamination of the samples occurred. I also excluded seeds of maize *Zea mays* that may have come from bait used in the traps. The bait was high quality crushed maize and was satisfied that it did not contain other weed seed contaminants. The walk-in traps were placed in areas of open shoreline, away from the surrounding vegetation, to limit the number of propagules picked up by birds in the traps.

To study endozoochory 313 faecal samples were collected from six different waterfowl species including Red-billed Teal (*N* = 35), Cape Shoveler *Anas smithii* (*N* = 35), Yellow-billed Duck (*N* = 60), White-faced Whistling Duck (*N* = 8), Egyptian Goose (*N* = 145) and Spur-winged Goose *Plectropterus gambensis* (*N* = 30) (Appendix 2A). Fresh faecal samples were collected from areas where monospecific flocks of birds were observed roosting, with the exception of Red-billed Teal and White-faced Whistling Duck where samples were collected directly from each captured bird. Faecal samples collected from roost sites were easily attributed to individual species based on colour and size. Samples were collected over a 2-hour period from areas of open shoreline and were at least 2 m apart. Due to the large numbers of birds at the study sites, I was confident that each sample was an independent replicate. Faecal samples were collected in individual plastic vials and stored at 4 °C until being analysed in the laboratory in the August/September of the year collected.

2.2.2 Laboratory sampling and germination trials

In the laboratory, individual faecal and feather brushing samples were washed through a set of stacked sieves with mesh sizes 1 mm, 250 µm and 63 µm and the residue on each sieve was examined under a binocular microscope (Nikon SMZ-10, Japan). All intact propagules were removed, counted and stored in distilled water in 2 ml Eppendorf^{TM} tubes at 4 °C until the start of the germination trial. Intact propagules were later photographed and the length measured to the nearest 0.01 mm under a binocular stereoscope (Leica EZ4, Germany). To ensure that additional propagules had not been accidentally overlooked, the residue remaining from sieving was also collected and immediately planted into sterile potting soil in small pots 6 cm in diameter and germination was followed for 3 months. All germinating propagules were added to the total count of intact and germinating propagules for that sample.

Intact propagules were set into germination trials during the October of the year in which they were collected. Individual samples were placed in 5 ml (3.5 cm depth) glass vials half-filled with distilled water, with a maximum limit of 20 propagules per vial for samples where large numbers of propagules were recovered. I did not record which propagules germinated from particular vials in these instances, but was conscious that small differences in the conditions of individual vials might have affected germination. Sample vials were placed into a phytotron unit (Zenith, USA) set at a light:dark cycle of 16:8 h and respective temperatures of 24:16 °C after which germination was monitored for 6 weeks. Germination was checked every 3 days for the first 21 days and then once a week until the trial ended. Water was replenished on each check, the propagules were removed and cleaned with tissue paper, and the vials were cleaned to prevent bacterial and/or fungal growth on the propagules. Germinated propagules were removed and planted into separate pots and grown to aid later identification. Propagules that failed to germinate were stored at 4 °C for one additional month before being set to germinate under the same conditions for a further six weeks. Approximately 2% of propagules germinated during this second trial.

Propagules were identified either from adult plants or directly from seeds with the help of experts and reference plant collections from the field sites. Additional reference texts included guides to the identification of aquatic and wetland plants (Cook 2004; Ginkel & Hitchcock 2011) and grasses (Oudtshoorn 2002) and the Atlas of Seeds (Legagneux, Duhart & Schricke 2007). The alien status and primary habitat requirements for all identified plant species was determined from the Red List of South African Plants database (SANBI 2014) (Table 1).

Table 1 Taxonomy and size of plant species identified in endo- and ectozoochory samples. Plant species found in both, as well as those found exclusively in endo- and ectozoochory samples are indicated. Habitat and status refers to the primary habitat and status listed in the Red List of South African Plants (SANBI 2014). Plant species that have other dispersal traits such as barbs or fleshy fruit are also indicated. See Appendix 2D for photographic inventory of unidentified propagules.

Family	Species	Mode	Status	Habitat	Traits	Length (mm)
Alismataceae	*Alternanthera caracasana*	Both	Alien	Terrestrial	Barbed	2.88
	Alisma plantago-aquatica	Endo	Alien	Aquatic		1.70
Amaranthaceae	*Amaranthus deflexus*	Both	Alien	Wetland		0.84
	Amaranthus hybridus	Both	Alien	Wetland		0.84
Asteraceae	*Bidens pilosa*	Both	Alien	Terrestrial	Barbed	3.36
	Helianthus annuus	Both	Alien*	Terrestrial		1.49
	Xanthium strumarium	Both	Alien	Terrestrial	Barbed	8.00
Caryophyllaceae	Unknown4	Endo				1.20
Ceratophyllaceae	*Ceratophyllum demersum*	Ecto	Native	Aquatic		2.74
Chenopodiaceae	*Atriplex sp.*	Ecto		Wetland		1.35
	Chenopodium sp.	Both		Wetland		0.64
	Unknown3	Ecto				1.10
Cyperaceae	*Cyperus eragrostis*	Endo	Alien	Wetland		5.04
	Eleocharis sp.	Both		Wetland		2.08
	Scirpus sp.	Both		Wetland		2.48
	Unknown5	Endo				1.12
	Unknown11	Ecto				1.22
	Unknown14	Endo				3.00
Fabaceae	*Medicago Arabica*	Both	Alien	Terrestrial		1.22
Juncaceae	*Juncus sp.*	Ecto		Wetland		1.49
Lemnaceae	*Lemna gibba*	Ecto	Native	Aquatic		1.69
Menyanthaceae	*Nymphoides indica*	Endo	Native	Aquatic		1.22
Pinaceae	*Pinus sp.*	Ecto	Alien	Terrestrial		6.00
Poaceae	*Cymbopogon caesius*	Ecto	Native	Terrestrial	Barbed	2.74
	Echinochloa sp.	Ecto		Wetland		2.90
	Panicum coloratum	Endo	Native	Terrestrial		2.50
	Panicum sp.	Endo		Terrestrial		2.08
	Paspalum sp.	Ecto		Terrestrial		3.50
	Themeda triandra	Both	Native	Terrestrial		4.00
	Unknown7	Ecto				1.96
	Unknown8	Endo				2.19
	Unknown9	Both				1.00

	Unknown15	Endo				3.19
Polygonaceae	*Fallopia convolvulus*	Both	Alien	Terrestrial		4.09
	Persicaria lapathifolia	Both	Alien	Wetland		2.06
	Persicaria senegalensis	Ecto	Native	Wetland		2.50
	Rumex sp.	Endo		Terrestrial		1.75
Potamogetonaceae	*Potamogeton nodosus*	Endo	Native	Aquatic		3.55
	Potamogeton pectinatus	Both	Native	Aquatic		2.90
Rosaceae	*Rubus sp.*	Both		Terrestrial	Fleshy Fruits	2.03
Solanaceae	*Solanum nigrum*	Both	Alien	Terrestrial	Fleshy Fruits	1.49
Urticaceae	*Urtica lobulata*	Ecto	Native	Terrestrial		1.60
Zannichelliaceae	*Pseudalthenia aschersoniana*	Endo	Native	Aquatic	Barbed	1.79
Unidentified taxa	Unknown1	Endo				-
	Unknown2	Ecto				1.50
	Unknown10	Both				1.83
	Unknown12	Endo				2.43
	Unknown13	Endo				5.39

*Cultivated species

2.2.3 Statistical analysis

To investigate both quantity and quality aspects of seed dispersal (Schupp *et al.* 2010), I chose to model three measures of dispersal — presence, abundance and germinability of propagules. The differences between sampling location (site) and bird species (Bsp) on the presence, abundance and germinability of propagules transported via either endozoochory or ectozoochory, were examined using generalized linear models (GLMs). Bird capture method (walk-in trap or mistnet) and moult status (yes or no) were also included as factors in models of ectozoochory. For endozoochory samples, the method of faecal sample collection differed between bird species: some samples were collected directly from captured birds, whilst other samples were collected from roost sites. To account for this in endozoochory models faecal sample mass was included as an additional predictor as it was correlated with the method of faecal sample collection (Spearman's Correlation Z = - 0.51; $p < 0.001$). Method of faecal sample collection could not be included as a covariate in the endozoochory models as it was linearly dependent on bird species.

The Julian date within the year (day) when both external and faecal samples were collected – as well as a second order polynomial (day^2) to account for nonlinear patterns – were included as covariates in all original models to take into account differences in propagule availability throughout the sampling season (Brochet *et al.* 2010b). However, due to high co-linearity with location, as indicated by variation inflation factors > 15, these covariates were excluded from subsequent models. The year of collection (2013 or 2014) was also excluded from subsequent models due to similar linear dependence issues with location and bird as described above. The effect of (a) year and (b) day on the presence of propagules in the samples was tested separately using logistic regressions with binomial error distribution for (a) each dispersal mode and (b) site respectively.

All plant species were pooled for GLMs as there was not sufficient data to investigate the effects of the covariates on separate plant species. The effect of the covariates on each of the three dispersal measures was considered separately for ectozoochory and endozoochory and resulted in six individually modelled cases (Table 2). I modelled (1) the presence of at least one intact propagule, using a binomial GLM and logit link function; and (2) the abundance of propagules in the samples, using a negative binomial GLM and log link function. To analyse propagule germination (3) the proportion of germinating propagules, was modelled using a binomial GLM and logit link function and the total number of intact propagules per propagule species was included as a binomial denominator (Brochet *et al.* 2010b). For each of the six cases all possible combinations of the independent variables were tested — 16 possible subsets of 4 predictor variables for ectozoochory and 8 possible subsets of 3 predictor variables for endozoochory. Candidate models were compared using Akaike's Information Criteria (AIC) (Burnham & Anderson 2002). The strongest model has the smallest AIC; if the difference between two AIC values (ΔAIC) was < 2, models were considered to be equivalent. In most cases several equivalent models were found, and so we adopted a model-averaging approach of all candidate models within Δ2 AIC to obtain final parameter estimates, standard errors and confidence intervals (Table 2) (Burnham & Anderson 2002). The parameters of the fitted model were deemed significant if the 95% confidence interval did not include zero. See Appendix 2B for model rankings. Where site and bird species were found to be significant, I calculated the model-averaged effect sizes and confidence intervals between each pair within the group to determine which site or species pairs were significantly different to each other. This approach is the information-theoretic alternative to multiple comparisons (Burnham & Anderson 2002; Burnham, Anderson & Huyvaert 2010). Model selection and averaging were performed using various functions from the R package *AICcmodavg* (Mazerolle 2015).

To compare the relative contribution of endo- and ectozoochory all samples from both external and faecal sampling protocols were pooled. Only Egyptian Goose, Red-billed Teal and Yellow-billed Duck had representative sample sizes for both dispersal modes and were thus included in the analysis. GLMs were used to test the effect of dispersal mode on the (1) presence, (2) abundance and (3) germinability using the same model family and link functions described above and again included the total number of intact propagules per propagule species as a binomial denominator for the germination model. To account for site and bird species effects both were included as control factors in the models.

To test for differences between dispersal modes in the types of propagules transported, I first tested for an effect of propagule size on the mode of transport. Following Brochet *et al.* (2010), a Fisher exact test was carried out (preferred over the χ^2 test in this context due to low expected frequencies in some categories) to compare the proportion of propagules < 1, 1-2, 2-4 and > 4 mm in length in the external and faecal samples. Next, I tested for a difference in the species of propagules transported via the different modes. First, the number of species unique to each mode and the overlapping species was calculated. To determine if there was a significant difference between ecto- and endozoochory in the plant community dispersed I used a Permutation Multivariate Analysis of Variance (PerMANOVA) utilising the *adonis* function from the R package *vegan* (Oksanen *et al.* 2015). PerMANOVA is a non-parametric technique that uses distance matrices to partition variance between samples and permutation to produce a *p*-value. Bray-Curtis distance was used, which is appropriate for data sets with substantial numbers of zero entries, and included bird species and its interaction with dispersal mode as additional factors in the analysis. Only data from the Barberspan site was used for this analysis to ensure that plant species dispersed were likely from only one initial plant community. All statistical analyses were conducted in R version 3.2.2 (R Core Team 2015).

2.3 RESULTS

We collected 1585 intact plant propagules from 48 plant species (Appendix 2C). Of these intact propagules, 213 germinated. Intact propagules were recovered from all locations and all bird species. Approximately half of the identified propagules were from terrestrial plants (16 spp.), and the remainder were either wetland plants that prefer damp habitats (11 spp.) or aquatic plants that have submerged roots (7 spp.) (Table 1). A surprisingly high number of alien plants were also recovered (13 spp.), including weedy exotics such as blackjack *Bidens pilosa* and spotted burclover *Medicago arabica*.

There was no effect of sampling year on the presence of propagules in either the external (χ^2 = 2.84, df = 2, *p*= 0.09) or faecal samples (χ^2 = 0.50, df = 2, *p*= 0.48). Dates of sample collection also had no effect on the presence of propagules in the samples (all $p >$ 0.1), with the exception of faecal samples collected at Strandfontein (χ^2 = 6.30, df = 1, p = 0.01).

2.3.1 Ectozoochory

A total of 255 intact and 76 germinating plant propagules were recovered from the 422 external brushings (Appendix 2C: Table 1). Nearly 37% of all external samples contained at least one intact propagule and 15% contained at least one germinating propagule (Fig. 2a). The average (±SE) number of propagules recovered per “positive” sample was 1.65 ± 0.10 (median = 1.00). Samples from all four bird species at the three locations contained intact propagules, and only samples from Voëlvlei contained no germinating propagules.

I found support for (1) two equally ranked models predicting the presence of at least one intact propagule, (2) one model predicting the abundance of propagules and (3) two equally ranked models predicting the presence of at least one germinating propagule in the external samples respectively (Appendix 2B). The use of a walk-in trap to capture the birds had a significant negative effect on the probability of finding propagules attached and on the abundance of propagules recovered (Table 2). However, this capture method had a significant positive effect on the presence of germinating propagules in the samples. Flightless moulting birds had significantly higher numbers of propagules attached to the feathers, but wing moult status did not affect presence on the feathers or germination. Site was a significant predictor in all three model cases. The presence and abundance of propagules in the Barberspan samples were significantly higher than for the Strandfontein and Voëlvlei sites. Post-hoc testing showed that Strandfontein and Voëlvlei were not significantly different to each other in terms of presence of propagules (*β* ± *SE*: 0.05 ± 0.07; *CI*: 0.08 - 0.18) or abundance (*β* ± *SE*: 0.12 ± 0.08; *CI*: 0.05 - 0.28). The germination probability of propagules was significantly higher for the Strandfontein site. No germinating propagules were found for the Voëlvlei site (Appendix 2C: Table 1), and this site was therefore not included in the germination models. Bird species did not occur in any of the top models, strongly suggesting that few differences occur between duck species in the presence and abundance of propagules transported via ectozoochory.

Intact propagules from 32 plant taxa from 15 families were found externally, and 15 of these species subsequently germinated (Appendix 2C: Table 2). A high number of the identified species (11 spp.) are considered alien in South Africa (Table 1). Three plant species accounted for 64% of all recovered propagules with the majority of these propagules recorded from the Barberspan site. Khaki-weed *Alternanthera caracasana* represented 38% of all propagules recorded externally and was present in 18% of all samples. *A. caracasana* was most commonly recorded in samples from Barberspan and 48% of all these propagules recovered germinated. The next most commonly recovered propagules were those of red grass *Themeda triandra* and willow weed *Persicaria lapathifolia*, respectively representing 14% and 12% of all propagules recorded externally. Only two propagule species could not be identified to at least family level (see Appendix 3D for photographic inventory of unidentified propagules).

2.3.2 Endozoochory

I recovered 1330 intact propagules from the 313 faecal samples; however, 518 of these propagules were recovered from one individual Egyptian Goose sample at Barberspan (Appendix 2C: Table 2). A total of 137 propagules later germinated from the faecal samples. Overall, 27% of samples contained at least one intact propagule and 8% contained at least one germinating propagule (Fig. 2b). The average (±SE) number of propagules found per “positive” sample was 15.83 ± 6.37 (median = 1.00). Intact propagules were found in all six bird species from all three locations and only propagules recovered from White-faced Whistling Duck samples failed to germinate.

I found support for (1) four equivalent models predicting the presence of at least one intact propagule, (2) two equivalent models predicting the abundance of propagules and (3) one model predicting the presence of at least one germinating propagule in the faecal samples respectively (Appendix 2B). The four top models predicting presence of propagules included the null model, suggesting that none of the variables strongly predicted the presence/absence of propagules in the faecal samples (Appendix 2B) and I therefore did not interpret these models. Bird species was a significant predictor for the abundance and germination of propagules (Table 2); in particular, significant differences occurred between Egyptian Goose and other bird species. Post-hoc tests indicated that significant differences between other species pairs did not occur with the exception of a higher probability of propagules germinating in Yellow-billed Ducks samples when compared to Cape Shoveler (*β* ± *SE*: 0.04 ± 0.02; *CI*: 0.01 - 0.07). Faecal sample mass had no effect on the presence and abundance of propagules in the samples. However, faecal sample mass had a significant negative effect on the probability of germination. Finally, sampling site had a significant effect on the abundance and germination of propagules in the samples. The abundance of propagules was highest for Strandfontein and lowest for Voëlvlei, and germination of propagules was lowest for the Barberspan site (Table 2). Post-hoc tests showed that Strandfontein also had a significantly higher abundance of propagules in the faecal samples then Voëlvlei (*β* ± *SE*: 8.87 ± 3.59; *CI*: 1.83 - 15.92), but there was no difference between this pair in terms of germinating propagules.

Intact propagules of 34 plant species from 14 families were recorded in the faecal samples, from which 15 species subsequently germinated (Appendix 2C: Table 2). Again, a high number of alien species were recorded in the samples (12 spp.) (Table 1). The propagules recovered in the highest abundance were the seeds of nutgrass *Cyperus eragrostis*, representing 40% of all propagules collected, however most of these seeds were collected from one individual Egyptian Goose sample. Similarly *Panicum sp.* and black nightshade *Solanum nigrum* respectively represented 21% and 11% of all recorded propagules but were found in only a few samples. Furthermore, 76% of *S.nigrum* propagules germinated. Recovery of large numbers of propagules was not the norm and the majority of samples contained only a few intact propagules (median = 1.00). Species including *P. lapathifolia* and sago pondweed *Potamogeton pectinatus* were recovered in low quantities i.e. approximately 3% of all intact propagules, but were present in multiple samples. Four of the propagule species could not be identified to at least family level (Appendix 2D).

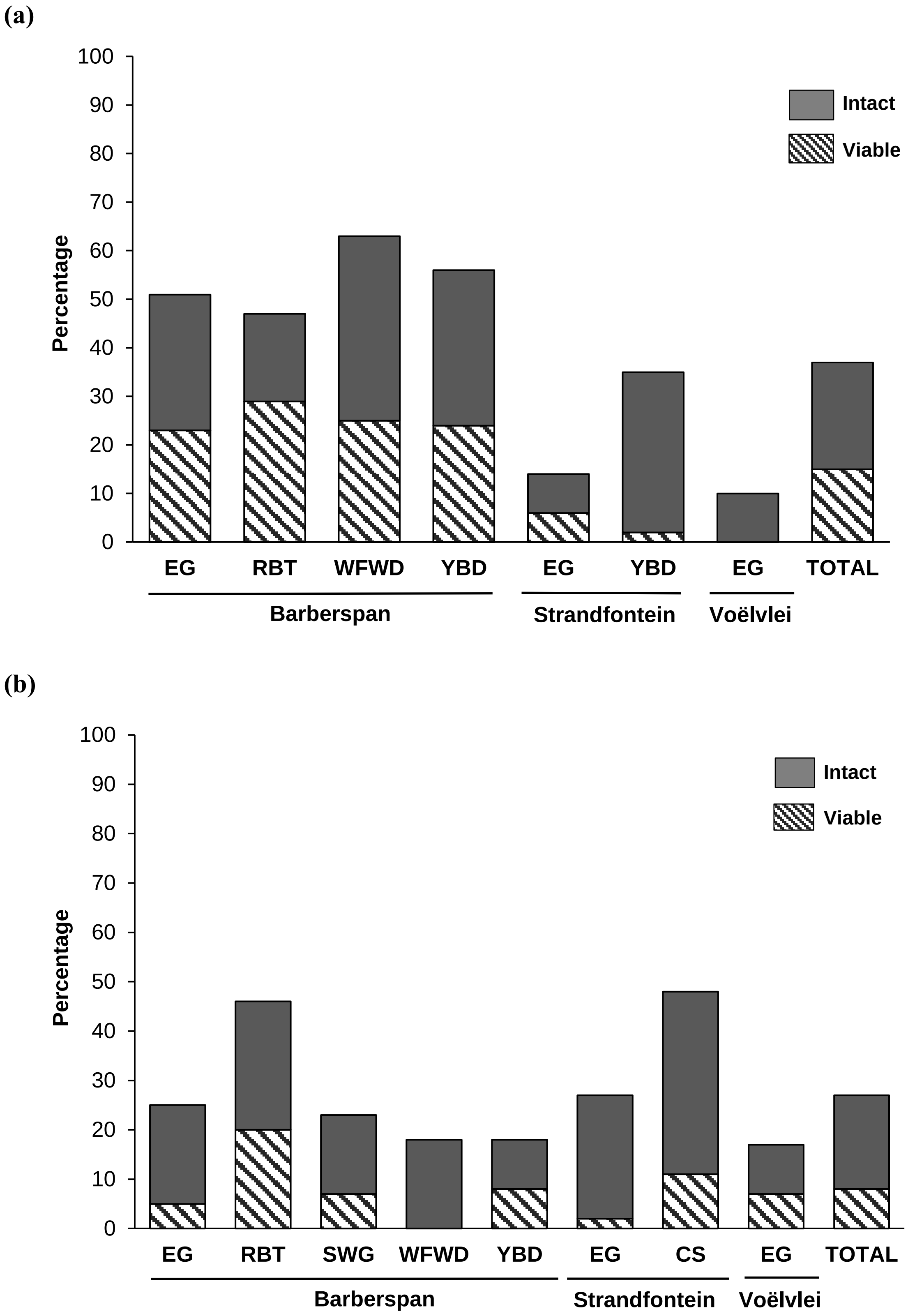


Figure 2 Percentage of samples that contained at least on intact propagule (bold) and at least one germination propagule (shaded): (a) Ectozoochory; (b) Endozoochory. CS = Cape Shoveler, EG = Egyptian Goose, RBT = Red-billed Teal, SWG = Spur-winged Goose, YBD = Yellow-billed Duck and WFWD = White-faced Whistling Duck.

Table 2 Results of model averaging based on alternative candidate GLMs (Appendix 3B). Parameter estimates (β), standard errors (SE), confidence intervals and significance of each factor influencing the presence of intact and germinating propagules, as well as the abundance of propagules are presented. The dependent variables are the (1) presence/absence and (2) abundance of intact propagules, and the (3) presence/absence of germinating propagules in the samples. In all models, Egyptian Goose (Bsp(EG)) and Barberspan (Site(BAR)) are the reference categories for the factors sampling location and bird species respectively. In the ectozoochory models, Method(mistnet) and Moult(no) are the reference categories for the factors of method and moult respectively. CS = Cape Shoveler, RBT = Red-billed Teal, SWG = Spur-winged Goose, YBD = Yellow-billed Duck and WFWD = White-faced Whistling Duck. STR = Strandfontein and VOE = Voëlvlei

Ectozoochory	**Presence/Absence Intact**				**Abundance Intact**				**Presence/Absence Germination**			
		Confidence Interval				**Confidence Interval**				**Confidence Interval**		
Predictors	**β ± SE**	**2.5%**	**97.5%**		**β ± SE**	**2.5%**	**97.5%**		**β ± SE**	**2.5%**	**97.5%**	
Intercept	1.34 ± 0.44	0.46	2.21	S	1.68 ± 0.33	1.05	2.33	S	-7.55 ± 1.07	-9.67	-5.43	S
Method(walk-in)	-1.28 ± 0.44	-2.16	-0.41	S	-2.10 ± 0.34	-2.78	-1.45	S	2.83 ± 1.07	0.71	4.94	S
Moult(yes)	0.36 ± 0.27	-0.17	0.89	NS	0.64 ± 0.19	0.28	1.01	S	0.06 ± 0.16	-0.28	0.67	NS
Site(STR)	-1.97± 0.32	-2.60	-1.34	S	-1.70 ± 0.26	-2.24	-1.21	S	1.35 ± 0.38	0.59	2.11	S
Site(VOE)	-2.39 ± 0.64	-3.65	-1.13	S	-2.43 ± 0.63	-3.91	-1.36	S	-	-	-	
Bsp	-	-	-		-	-			-	-	-	
Endozoochory	**Presence/Absence Intact**				**Abundance Intact**				**Presence/Absence Germination**			
		Confidence Interval				**Confidence Interval**				**Confidence Interval**		
Predictors	**β ± SE**	**2.5%**	**97.5%**		**β ± SE**	**2.5%**	**97.5%**		**β ± SE**	**2.5%**	**97.5%**	
Intercept	-1.02 ± 0.29	-1.60	-0.45	S	-0.11 ± 0.86	-1.79	1.58	NS	-3.68± 0.76	-5.54	-2.42	S
Sample mass	-0.03 ± 0.05	-0.12	0.06	NS	0.22 ± 0.07	-0.02	0.25	NS	-0.23 ± 0.04	-0.32	-0.14	S
Site(STR)	-	-	-		1.85 ± 0.65	0.57	3.15	S	2.55 ± 0.72	1.39	4.36	S
Site(VOE)	-	-	-		-2.01 ± 0.88	-3.74	-0.25	S	2.65 ± 1.02	0.49	4.80	S
Bsp(CS)	0.65 ± 0.41	-0.15	1.45	NS	-1.25 ± 0.73	-2.70	0.19	NS	-0.18 ± 0.29	-0.78	0.37	NS
Bsp (RBT)	1.00 ± 0.41	0.18	1.82	S	0.83 ± 0.91	-0.97	2.63	NS	-0.08 ± 0.83	-1.56	1.87	NS
Bsp(SWG)	-0.02 ± 0.48	-0.97	0.94	NS	1.66 ± 0.81	-3.25	-0.07	S	2.51 ± 1.02	0.35	4.66	S
Bsp(WFWD)	0.08 ± 0.85	-1.60	1.74	NS	0.88 ± 1.34	-1.78	3.51	NS	-	-	-	
Bsp(YBD)	-0.32 ± 0.39	-1.09	0.06	NS	-1.26 ± 0.73	-2.69	0.17	NS	1.68 ± 0.79	0.30	3.58	S

2.3.3 Comparison between ecto- and endozoochory

The presence of propagules transported externally was nearly double that of propagules found in the faecal samples (χ^2 = 11.01, df = 1, p < 0.001) (Fig. 2). The abundance of propagules was significantly higher in the faecal samples (χ^2 = 78.84, df = 1, p < 0.001). Finally, the presence of at least one germinating propagule was significantly higher in the faecal samples (χ^2 = 22.32, df = 1, p < 0.001). In all the models, the total presence, abundance and germination of propagules differed significantly by location (p-value < 0.001), but only the abundance of propagules differed significantly by bird species (χ^2 = 8.89, df = 2, p = 0.01).

The size range of propagules transported via ecto- and endozoochory were significantly different (Fisher exact test: p < 0.001), with higher than expected frequency of propagules for the external and faecal samples in the 2-4 mm and > 4 mm category, respectively. Of the 48 plant taxa recorded for the study a total of 18 species, just over a third were recorded in both the external and the faecal samples. A total of 14 and 16 species were thus unique to the external and faecal samples respectively. When comparing species composition at the Barberspan site using perMANOVA, I found that there was a significant difference between dispersal mode in the plant communities dispersed (F = 16.40, df = 1, p < 0.001), but not between bird species (F = 0.93, df = 2, p = 0.67) or the interaction between bird species and dispersal mode (F = 1.69, df = 2, p = 0.06).

2.4 DISCUSSION

Waterfowl in southern Africa demonstrate a high capacity for the dispersal of plant propagules through endo-and ectozoochory, with many germinating propagules transported in both cases. Germinating plant propagules were recovered from 15% of external samples and 8% of internal samples and included germination of 15 plant species in both cases. A relatively high diversity of transported propagules (48 plant species) was identified in this study. Many of these species were transported only via a specific dispersal mode. The results show that southern African waterfowl disperse the propagules of both aquatic and terrestrial plants, of both native and exotic status, in relatively high numbers.

As found by Brochet *et al.* (2010b), potential seed dispersal varied spatially with differences corresponding to variation in local plant community composition. I could not account for seasonality in the models and some variation in dispersed propagules was presumably due to temporal differences. Barberspan is in a different biome and climate zone to that of Voëlvlei and Strandfontein. However, at least for endozoochory propagule dispersal is decoupled from propagule production (Brochet *et al.* 2010b) and ducks are capable of accessing propagules throughout the year deep down in the sediments long after they have been shed by the plants (Green *et al.* 2002). Therefore, high rates of seed dispersal are not only linked to periods of high propagule production and seasonal effects might be difficult to detect using this methodology alone. In stochastic environments this decoupling may be a conservative bet-hedging strategy (Childs, Metcalf & Rees 2010) with seeds delaying germination in favour of potentially being dispersed later in the season when wetlands dry down. Differences in the feeding ecology of waterfowl species affect the number and germination of propagules (Green *et al.* 2002), and obvious feedbacks exist between plant community composition and propagule dispersal, creating further variation in both space and time in seed dispersal processes. For ectozoochory, it is likely that seasonal effects may be more pronounced. At least for terrestrial plants, for example grasses, the seeds may attach more readily to feathers if they are still on the plant or may remain on the ground only for a short time before being blown away.

2.4.1 Quantity and quality of waterbird-mediated dispersal

At least one intact propagule was found in 37% of the ectozoochory samples. This proportion was approximately double that found in other recent studies investigating ectozoochory (Brochet *et al.* 2010b; Raulings *et al.* 2011). External transport is usually a rare mode and is the dominant dispersal mode in only 5% of extant plant species (Sorensen 1986); the high proportion of "positive" ectozoochory samples was thus surprising. However, many of the plant species identified here lack the obvious adaptations that usually accompany ectozoochory and the dominant dispersal mode for most of these species is likely to be endozoochory. Furthermore, it is possible that the role of ectozoochory was inflated by the presence of khaki-weed *A. caracasana* in our samples. External samples from Barberspan were dominated by seeds of this species, which was common around the edges of the wetland. A total of 42% of waterfowl sampled were carrying at least one intact khaki-weed propagule on their feathers. Interestingly, I also found this propagule species in a few of the endozoochory samples (Appendix 2C: Table 2). The presence of propagules in the external samples thus differed greatly between Barberspan and the other two sampling sites (Table 2).

These results reflect the importance of considering ectozoochory as a significant seed dispersal mode as propagules that are well adapted to this mode of dispersal, such as the spiked seed of exotic *A. caracasana*, are capable of being dispersed in large numbers by waterbirds. Estimates of ectozoochory for the Strandfontein and Voëlvlei sites better reflected the findings of other studies (Brochet *et al.* 2010b; Raulings *et al.* 2011) (Fig. 2a).

Despite a higher presence and abundance of propagules found externally for the Barberspan site, total germination of transported propagules was highest for the Strandfontein site (Table 2), and demonstrates the need to investigate both quantity and quality aspects of seed dispersal. Effective seed dispersal encompasses both the number of seeds dispersed and the probability that seeds will survive handling by the dispersal agent to germinate and produce a new adult (Schupp *et al.* 2010). Therefore considering only the numbers of seeds transported may overestimate seed dispersal. It is also important to note that propagules that did not germinate under these experimental conditions may still be viable and I may have underestimated the dispersal of viable propagules (Brochet *et al.* 2010b).

Capture method (i.e., walk-in trap versus mist net) was influential in explaining the presence and abundance of propagules in the samples. Birds captured in mistnets had a greater probability of having propagules attached to their feathers, as well as carrying higher numbers of propagules. This result was unexpected and perhaps due to propagules becoming detached when birds became flustered upon collection from the traps. Birds caught with mistnets were perhaps more restrained by the nets and it is likely that fewer propagules were lost. The mechanism by which mistnets affect the germination of propagules is uncertain, but may be an artefact of different plant species found on birds captured in different ways. The germination protocol used in this field study was generalist and not all plant species will germinate equally as well under these specific conditions. Additionally, during flightless moult the abundance of propagules recovered externally was higher, most likely because the less vigorous transport modes of walking or swimming employed by moulting ducks cause fewer propagules to detach. Thus, the total number of propagules recovered may be slightly inflated, but it is important to note that the presence and germination of propagules was not significantly influenced by wing moult status. Additionally, as found by (Raulings *et al.* 2011), ectozoochory did not differ across sympatric bird species.

Duck species showed comparable dispersal potential via endozoochory, with 27% of all samples containing at least one intact propagule. Given that I could not reject the null model in this case, I conclude that none of the measured variables had an influence on the presence of propagules in the faecal samples. There were, however, notable differences in the abundance and germination of propagules retrieved from different bird species at different sampling sites. Other studies have also found differences in the abundance of propagules transported by different bird species (Figuerola, Green & Santamaría 2002; Green *et al.* 2008). These differences have been linked to body size, the density of lamellae on the interior edges of the culmen, diet, and foraging behaviour (Green *et al.* 2002; Guillemain *et al.* 2002). For example, Spur-winged Goose had the lowest abundance of propagules in the samples; which is unsurprising given that this species is primarily a grazing waterfowl species while others in our study (with the exception of Egyptian Geese) were primarily dabbling ducks (Table 2). Germination is also affected by other aspects of foraging ecology, morphology, and physiology, such as differing levels of damage to the seed coat resulting from variation in gizzard strength amongst bird species (Pollux, Santamaria & Ouborg 2005). García-Álvarez *et al.* (2015) also found higher germination in seeds ingested by Greylag Goose *Anser anser* in comparison to Mallard Duck *Anas platyrhynchos*, and suggested that this was due to the longer gut retention time of seeds eaten by mallards. One possible explanation proposed for the extended retention times was that seeds are likely to be retained for longer in the gizzard of the granivorous mallard than in that of the herbivorous greylag goose (García-Álvarez *et al.* 2015). Differences in the abundance of propagules dispersed between sites are again likely attributed to plant species composition at the sampling locations. Our sites varied substantially in the type of vegetation present, from open shorelines along a deep dam at Voëlvlei to shallow, well vegetated pans at Strandfontein (Fig. 1). Germination of propagules was lowest at the Barberspan site for both external and faecal samples. These propagules were sampled in early-winter at Barberspan in contrast to late-summer as at the other two sampling sites, hence a seasonal effect may be hindering germination.

In a few of the faecal samples, we recorded very high numbers of intact and germinating propagules (Table S2). Interestingly, nearly 71% of the 1330 propagules were recovered from only 10 samples. The recovery of large numbers of propagules from single samples is not unique to our study system; Green *et al.* (2008) recovered 116 intact plant propagules from a single pelican faecal sample in Australia and Brochet *et al.* (2010b) recovered 130 seeds from the sedge common spike-rush *Eleocharis palustris* from five teal rectum samples. Although the number of samples with high numbers of propagules is small (median of 1.00 intact propagule per sample), these occurrences may have significant implications for the plant community.

2.4.2 Relative contribution of ecto- and endozoochory

This is the most extensive study of ectozoochory by waterfowl to date. The large sample size permits a realistic re-evaluation of the relative importance of this dispersal mode in the field. Previous studies comparing ecto- and endozoochory in waterbirds had smaller sample sizes: 68 Green-winged Teal brushings in the Camargue, France (Brochet *et al.* 2010b) and samples from 3 Black Duck, 22 Chestnut Teal and 1 Grey Teal in the Gippsland Lakes, Western Australia (Raulings *et al.* 2011). In contrast to the above studies, I found that the presence of propagules was higher in the ectozoochory samples. However, a large number of the propagules recovered from the feathers were from one particular plant species at the Barberspan site. The abundance of propagules (mean of 15.83 versus 1.65 for internal and external respectively) and germination of propagules however was higher for faecal samples. Furthermore, it is likely that the role of endozoochory in southern Africa has been underestimated as I collected only one faecal sample per bird, which is a small portion of the daily faecal output for each bird (Green *et al.* 2008). Therefore, endozoochory appears to be the more important mechanism for both quantity and quality.

Our results suggest that both modes may be needed to provide the full dispersal function across a suite of plants. Whilst we cannot fully support the hypothesis that ecto- and endozoochory may be complementary dispersal modes, there was some evidence that the propagules dispersed via these two modes were different. Smaller propagules were dispersed externally, possibly because it may be easier for smaller propagules to become embedded in the feathers facilitating this process. I observed further differences between ecto- and endozoochory in terms of community composition. Of the 48 plant species recorded, 18 were shared between both dispersal modes, but the remainder (just below half) were unique to each mode. Additionally, the composition of species transported by each mode was significantly different. However, much more extensive sampling is needed to determine the extent to which certain plants species are "uniquely" dispersed via a particular mode.

Some propagule species dispersed externally (e.g., blackjack *Bidens pilosa* and cockelburr *Xanthium strumarium*) were barbed or spiked species that demonstrate apparent adaptations for ectozoochrous dispersal (Sorensen 1986). However, we also found many species lacking hooks and barbs that were generally recorded in higher abundance in the endozoochory samples. Additionally, many of the species with presumable adaptations to ectozoochory were also found in the faecal samples. For example, one of the internal samples contained 87 seeds of *B. pilosa*. This mismatch suggests that typical morphological indicators of dispersal syndromes (van der Pijl 1982) are not exclusive indicators of dispersal mode and again, that propagules transported by non-standard dispersal modes can often have important implications for communities (Higgins *et al.* 2003).

2.5 CONCLUSIONS

Southern African waterfowl are dispersers of multiple different plant species and both ecto- and endozoochory have valuable roles. Whilst the waterbirds in this study did demonstrate a high capacity for external transport, I agree with the perspective of previous research that ectozoochory is not the dominant mode of dispersal (van Leeuwen *et al.* 2012b). However, ectozoochory should not be discounted as it may facilitate the dispersal of opportunistic weeds and perhaps plays a complementary role to endozoochory. Importantly, the results point to a high capacity for the dispersal of exotic species by waterbirds via both ecto- and endozoochory. Furthermore, two plant species identified in this study are considered invasive species in South Africa, *Pinus sp*. and *Xanthium strumarium* and perhaps previous assumptions about their dispersal and spread need to be re-addressed. These data suggest that future studies on the dispersal potential of waterbirds to spread alien species would be an essential avenue of future enquiry (see Chapter 6).

This study extends our knowledge of the role waterbirds play in the dispersal of aquatic organisms and demonstrates, for the first time, the dispersal capacity of African waterfowl. Considering the large populations of waterfowl in southern Africa, most of which number in the millions (Hockey *et al.* 2005), the total number of propagules moved is likely to be very high. Inventories of the identity and quantity of propagules waterbirds may be dispersing in a landscape are important first steps in understanding the role these birds play in aquatic community connectivity.

Appendix 2A Sample sizes and specific collection dates for feather brushings and faecal samples. CS = Cape Shoveler, EG = Egyptian Goose, RBT = Red-billed Teal, SWG = Spur-winged Goose, WFWD = White-faced Whistling Duck and YBD = Yellow-billed Duck.

		Barberspan					**Strandfontein**			**Voèlvlei**	
Sampling Date		**EG**	**RBT**	**SWG**	**WFWD**	**YBD**	**CS**	**EG**	**YBD**	**EG**	**Total**
Brushing		**N=75**	**N=49**		**N=8**	**N=95**		**N=119**	**N=46**	**N=30**	**N=422**
2013	31/01 – 26/02	-	-	-	-	-	-	51	21	-	**72**
	11/04 – 17/04	-	-	-	-	-	-	-	-	30	**30**
	01/05 – 15/05	26	19	-	-	40	-	-	-	-	**85**
2014	03/02 – 25/02	-	-	-	-	-	-	68	25	-	**93**
	14/05 – 04/06	49	30	-	8	55	-	-	-	-	**142**
Faecal		**N=60**	**N=35**	**N=30**	**N=8**	**N=60**	**N=35**	**N=55**		**N=30**	**N=313**
2013	13/02 – 14/02	-	-	-	-	-	10	15	-	-	**25**
	20/04	-	-	-	-	-	-	-	-	30	**30**
	02/05 – 13/05	-	15	-	-	-	-	-	-	-	**15**
	27/05 – 29/05	30	-	30	-	30	-	-	-	-	**90**
2014	18/02 – 19/02	-	-	-	-	-	25	40	-	-	**65**
	20/05 – 04/06	-	20	-	8	-	-	-	-	-	**28**
	09/06 – 12/06	30	-	-	-	30	-	-	-	-	**60**

Appendix 2B A selection of candidate generalised linear models (GLMs) investigating the effects of location, bird species, capture method and moult status (ectozoochory only) and faecal sample mass (endozoochory only) on the presence/absence of 1) intact and 2) germinating propagules and on the abundance of propagules in the ectozoochory and endozoochory samples. Tables list only top candidate models totalling a cumulative Akaike's Information Criteria (AIC) weight Cum(wt) = 1.00. Models are ranked based on differences in the Akaike's Information Criteria (ΔAIC). K is the number of estimated parameters, AIC(wt) the weight of each model and LL the -2log-likelihood output for each model. The Null model with no predictor terms, only the constant, is also included for comparison.

1. Ectozoochory: Presence/Absence of intact propagules

Model	K	AIC	ΔAIC	AIC(wt)	Cum(wt)	LL
Site + Method	4	498.71	0.00	0.40	0.40	-245.35
Site + Method + Moult	5	498.89	0.18	0.36	0.76	-244.45
Site + Bird + Method + Moult	8	501.27	2.56	0.11	0.87	-242.65
Site + Bird + Moult	7	503.23	4.52	0.04	0.91	-244.62
Site + Bird + Method	7	503.26	4.55	0.04	0.95	-255.63
Site + Bird	6	504.77	6.06	0.02	0.97	-246.38
Site	3	504.79	6.08	0.02	0.99	-249.40
Site + Moult	4	506.78	8.07	0.01	1.00	-249.39
Null	1	556.93	58.22	0.00	1.00	-277.47

2. Ectozoochory: Abundance of intact propagules

Model	K	AIC	ΔAIC	AIC(wt)	Cum(wt)	LL
Site + Method + Moult	5	836.15	0.00	0.91	0.91	-413.07
Site + Method + Moult + Bird	8	840.82	4.67	0.09	0.99	-412.41
Method	4	846.35	10.20	0.01	1.00	-419.17
Null	1	899.61	63.47	0.00	1.00	-448.81

3. Ectozoochory: Presence/Absence of germinating propagules

Model	K	AIC	ΔAIC	AIC(wt)	Cum(wt)	LL
Site + Method	3	338.62	0.00	0.57	0.57	-166.31
Site + Method + Moult	4	339.95	1.33	0.29	0.87	-165.98
Site + Bird + Method	6	343.45	4.84	0.05	0.92	-165.73
Site + Bird + Method + Moult	7	344.20	5.58	0.04	0.95	-165.10
Method	2	346.01	7.40	0.01	0.97	-171.01
Method + Moult	3	346.37	7.76	0.01	0.98	-170.19
Moult	2	347.84	9.22	0.01	0.99	-171.92
Null	1	348.35	9.73	0.00	1.00	-173.17

4. Endozoochory: Presence/Absence of intact propagules

Model	K	AIC	ΔAIC	AIC(wt)	Cum(wt)	LL
Bird	6	362.61	0.00	0.28	0.28	-175.31
Null	1	363.46	0.85	0.18	0.47	-180.73
Sample	2	363.68	1.07	0.16	0.63	-179.84
Bird + Sample mass	7	364.61	2.00	0.10	0.73	-175.31
Site	3	364.85	2.24	0.09	0.83	-179.43
Site + Sample mass	4	365.21	2.60	0.08	0.90	-178.61
Site + Bird	8	365.35	2.74	0.07	0.97	-174.68
Site + Bird + Sample mass	9	367.35	4.74	0.03	1.00	-174.67

5. Endozoochory: Abundance of intact propagules

Model	K	AIC	ΔAIC	AIC(wt)	Cum(wt)	LL
Site + Bird + Sample mass	9	765.59	0.00	0.61	0.61	-373.80
Site + Bird	8	766.56	0.97	0.37	0.98	-375.28
Site	3	773.45	7.86	0.01	0.99	-383.72
Site + Sample mass	4	774.37	8.78	0.01	1.00	-383.19
Null	1	792.88	27.28	0.00	1.00	-395.44

6. Endozoochory: P/A of germinating propagules

Model	K	AIC	ΔAIC	AIC(wt)	Cum(wt)	LL
Site + Bird + Sample mass	8	818.50	0.00	0.98	0.98	-401.25
Site + Sample mass	4	826.02	7.53	0.02	1.00	-409.01
Null	1	874.22	55.72	0.00	1.00	-436.11

Appendix 2C

Table 1 List of plant family and plant taxa identified attached to the feet and feathers of sampled waterfowl in 2013 and 2014. Numbers indicate the total intact propagules recovered per taxa across site and bird species. (Numbers) indicate the total germinating propagules recovered per taxa across site and bird species. *Numbers* indicate the maximum number of propagules recovered per sample for each plant and bird species combination. Where the total recovery of propagules per plant species was one, maxima have not been indicated. Sample sizes (N) are indicated. EG = Egyptian Goose, RBT = Red-billed Teal, WFWD = White-faced Whistling Duck, YBD = Yellow-billed Duck.

Ectozoochory	**Barberspan**					**Strandfontein**			**Voèlvlei**		
	EG N=75	**RBT N=49**	**WFWD N=8**	**YBD N=95**	**Total N=227**	**EG N=119**	**YBD N=46**	**Total N=165**	**EG N=30**	**Total N=30**	**Grand Total N=422**
AMARANTHACEAE	**44 (18)**	**20 (10)**	**1 (1)**	**34 (15)**	**99 (44)**	**3 (2)**	**1 (1)**	**4 (3)**			**103 (47)**
Alternanthera caracasana	43 (18) *7*	19 (10) *3*	1 (1)	32 (13) *2*	95 (42)	2 (2) *2*	1 (1)	3 (3)			98 (45)
Amaranthus deflexus		1		2 (2) *2*	3 (2)	1		1			4 (2)
Amaranthus hybridus	1				1						1
ASTERACEAE		**1 (1)**	**1**	**6 (5)**	**8 (6)**	**3 (1)**	**1**	**4 (1)**	**1**	**1**	**13 (7)**
Bidens pilosa		1 (1)	1	4 (4) *1*	6 (5)	2 *1*		2			8 (8)
Helianthus annuus				2 (1) *1*	2 (1)		1	1	1	1	4 (1)
Xanthium strumarium						1 (1)		1 (1)			1 (1)
CERATOPHYLLACEAE		**1 (1)**			**1 (1)**						**1 (1)**
Ceratophyllum demersum		1 (1)			1 (1)						1 (1)
CHENOPODIACEAE	**1 (1)**	**1 (1)**			**2 (2)**	**2 (1)**		**2 (1)**			**4 (3)**
Atriplex sp.						1 (1)		1 (1)			1 (1)
Chenopodium sp.						1		1			1
Unknown3	1 (1)	1 (1)			2 (2)						2 (2)
CYPERACEAE	**5**				**5**	**2 (1)**		**2 (1)**	**1**	**1**	**8 (1)**
Eleocharis sp.	5 *2*				5	1		1			6

Ectozoochory	**Barberspan**					**Strandfontein**			**Voèlvlei**		
	EG N=75	**RBT N=49**	**WFWD N=8**	**YBD N=95**	**Total N=227**	**EG N=119**	**YBD N=46**	**Total N=165**	**EG N=30**	**Total N=30**	**Grand Total N=422**
Scirpus sp.						1 (1)		1 (1)			1 (1)
Unknown11									1	1	1
FABACEAE		**1 (1)**			**1 (1)**	**2 (1)**		**2 (1)**			**3 (2)**
Medicago arabica		1 (1)			1 (1)	2 (1) *2*		2 (1)			3 (2)
JUNCACEAE						**2**		**2**			**2**
Juncus sp.						2 *1*		2			2
LEMNACEAE**						**2**	**34**	**36**			**36**
Lemna gibba						2 *2*	34 *10*	36			36
PINACEAE	**1**				**1**				**1**	**1**	**2**
Pinus sp.	1				1				1	1	2
POACEAE	**18 (5)**	**7 (1)**	**4 (1)**	**15 (2)**	**44 (9)**						**44 (9)**
Cymbopogon caesius				1 (1)	1 (1)						1 (1)
Echinochloa sp.	1		1	1	3						3
Paspalum species			1		1						1
Themeda triandra	17 (5) *3*	5 *2*	2 (1)*1*	12 (1) *2*	36 (7)						36 (7)
Unknown7		1		1	2						2
Unknown9		1 (1)			1 (1)						1 (1)
POLYGONACEAE	**5 (1)**	**1 (1)**		**9 (3)**	**15 (5)**	**6 (1)**	**7**	**13 (1)**			**28 (6)**
Fallopia convolvulus							1	1			1
Persicaria lapathifolia	4 (1) *1*	1 (1)		9 (3) *2*	14 (5)	6 (1) *3*	6 *2*	12 (1)			26 (6)
Persicaria senegalensis	1				1						1
POTAMOGETONACEAE		**1**	**1**	**1**	**3**						**3**

Ectozoochory	**Barberspan**					**Strandfontein**			**Voèlvlei**		
	EG N=75	**RBT N=49**	**WFWD N=8**	**YBD N=95**	**Total N=227**	**EG N=119**	**YBD N=46**	**Total N=165**	**EG N=30**	**Total N=30**	**Grand Total N=422**
Potamogeton pectinatus		1	1	1	3						3
ROSACEAE		**1**			**1**						**1**
Rubus sp.		1			1						1
SOLANACEAE						**1 (1)**		**1 (1)**			**1 (1)**
Solanum nigrum						1 (1)		1 (1)			1 (1)
URTICACEAE							**2**	**2**			**2**
Urtica lobulata							2 *1*	2			2
Unidentified taxa	**1**	**1**	**1**	**1**	**4**						**4**
Unknown2		1		1	2						2
Unknown10	1		1		2						2
Grand Total	**75 (25)**	**35 (16)**	**8 (2)**	**66 (25)**	**184 (68)**	**23(8)**	**45 (1)**	**71 (9)**	**3**	**3**	**255 (77)**

**Live plants of *Lemna gibba* were collected from the captured birds, but could not be stored effectively in the field and the viability of these fronds could thus not be determined.

Table 2 List of plant family and plant taxa identified from faecal samples collected from waterfowl in 2013 and 2014. Numbers indicate the total intact propagules recovered per taxa across site and bird species. (Numbers) indicate the total germinating propagules recovered per taxa across site and bird species. *Numbers* indicate the maximum number of intact propagules recovered per sample for each plant and bird species combination. Where the total recovery of propagules per plant species was one, maxima have not been indicated. Sample sizes (N) are indicated. EG = Egyptian Goose, RBT = Red-billed Teal, SWG = Spur-winged Goose, WFWD = White-faced Duck, YBD = Yellow-billed Duck, CS = Cape Shoveler.

Endozoochory	**Barberspan**						**Strandfontein**			**Voë̀lvlei**		
	EG N=60	**RBT N=35**	**SWG N=30**	**WFWD N=8**	**YBD N=60**	**Total N=193**	**CS N=35**	**EG N=55**	**Total N=90**	**EG N=30**	**Total N=30**	**Grand Total N=313**
ALISMATACEAE	**1**					**1**		**18**	**18**			**19**
Alisma plantago-aquatica	1					1		18 *17*	18			19
AMARANTHACEAE		**2 (1)**			**1 (1)**	**3 (2)**	**1 (1)**		**2 (1)**	**1**	**1**	**5 (3)**
Alternanthera caracasana		2 (1) *1*				2 (1)						2 (1)
Amaranthus deflexus							1 (1)		1 (1)	1	1	2 (1)
Amaranthus hybridus					1 (1)	1 (1)						1 (1)
ASTERACEAE	**89 (1)**	**1 (1)**			**1**	**91 (2)**				**1 (1)**	**1 (1)**	**92 (3)**
Bidens pilosa	87 *87*				1	88						88
Helianthus annuus	2 (1) *1*	1 (1)				3 (2)						3 (2)
Xanthium strumarium										1 (1)	1 (1)	1 (1)
CARYOPHYLLACEAE								**61**	**61**			**61**
Unknown4								61 *59*	61			61
CHENOPODIACEAE								**34**	**34**			**34**
Chenopodium sp.								34 *34*	34			34
CYPERACEAE	**521 (6)**	**1**	**8 (1)**		**6**	**536 (7)**	1		1			**537 (7)**
Cyperus eragrostis	513 (6) *506*		2 *1*			515 (6)						515 (6)

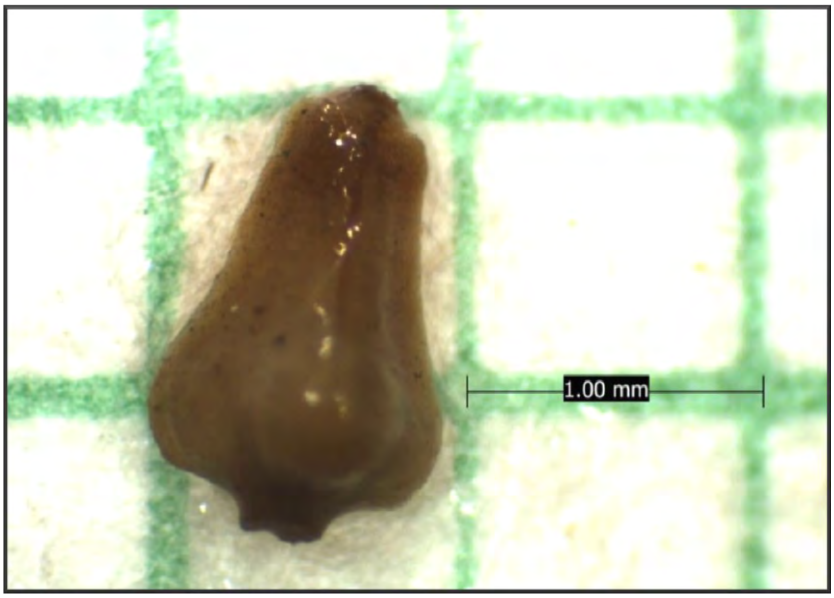
Endozoochory	**Barberspan**						**Strandfontein**			**Voèlvlei**		
	EG N=60	**RBT N=35**	**SWG N=30**	**WFWD N=8**	**YBD N=60**	**Total N=193**	**CS N=35**	**EG N=55**	**Total N=90**	**EG N=30**	**Total N=30**	**Grand Total N=313**
Eleocharis sp.	4 *4*	1				5						5
Scirpus sp.	4 *2*		6 (1) *4*		5 *3*	15 (1)						15 (1)
Unknown5					1	1						1
Unknown14							1		1			1
FABACEAE								**1**	**1**			**1**
Medicago arabica								1	1			1
MENYANTHACEAE							**6 (1)**		**6 (1)**			**6 (1)**
Nymphoides indica							6 (1) *4*		6 (1)			6 (1)
POACEAE		**6 (1)**			**1 (1)**	**7 (2)**		**276**	**276**			**283 (2)**
Panicum coloratum		1 (1)				1 (1)						1 (1)
Panicum sp.								274 *100*	274			274
Themeda triandra		5 *2*				5						5
Unknown8								1	1			1
Unknown9					1 (1)	1 (1)						1 (1)
Unknown15								1	1			1
POLYGONACEAE		**2 (1)**		**6**		**8 (1)**	**27**	**1**	**28**	**3 (1)**	**3 (1)**	**39 (2)**
Fallopia convolvulus				6 *6*		6				2 *2*	2	8
Persicaria lapathifolia		1 (1)				1 (1)	27 *11*	1	28	1 (1)	1 (1)	30 (2)
Rumex sp.		1				1						1
POTAMOGETONACEAE	**6 (3)**	**2 (2)**	**2 (1)**		**9 (5)**	**19 (11)**						**19 (11)**
Potamogeton nodosus			1			1						1
Potamogeton pectinatus	6 (3) *1*	2 (2) *1*	1 (1)		9 (5) *6*	18 (11)						18 (11)

Endozoochory	**Barberspan**						**Strandfontein**			**Voèlvlei**		
	EG N=60	**RBT N=35**	**SWG N=30**	**WFWD N=8**	**YBD N=60**	**Total N=193**	**CS N=35**	**EG N=55**	**Total N=90**	**EG N=30**	**Total N=30**	**Grand Total N=313**
ROSACEAE	**1**		**1**			**2**						**2**
Rubus sp.	1		1			2						2
SOLANACEAE							**32 (15)**	**108 (91)**	**140 (106)**			**140 (106)**
Solanum nigrum							32 (15) *31*	108 (91) *108*	140 (106)			140 (106)
ZANNICHELLIACEAE							**1**		**1**			**1**
Pseudalthenia aschersoniana							1		1			1
Unidentified taxa	**4**	**70 (1)**		**14**	**1**	**89 (1)**	**3 (1)**		**3 (1)**	**1**	**1**	**93 (2)**
Unknown1							1 (1)		1 (1)			1 (1)
Unknown10	4 *2*	70 (1) *34*		14 *14*	1	89 (1)						89 (1)
Unknown12										1	1	1
Unknown13							2 *1*		2			2
Grand Total	**618 (8)**	**84 (7)**	**11 (2)**	**20**	**22 (9)**	**755 (26)**	**70 (18)**	**499 (91)**	**569 (109)**	**6 (2)**	**6 (2)**	**1330 (137)**

Appendix 2D Photographic inventory of selected unidentified propagules from specific found at the specified location. The family has been indicated in several instances.

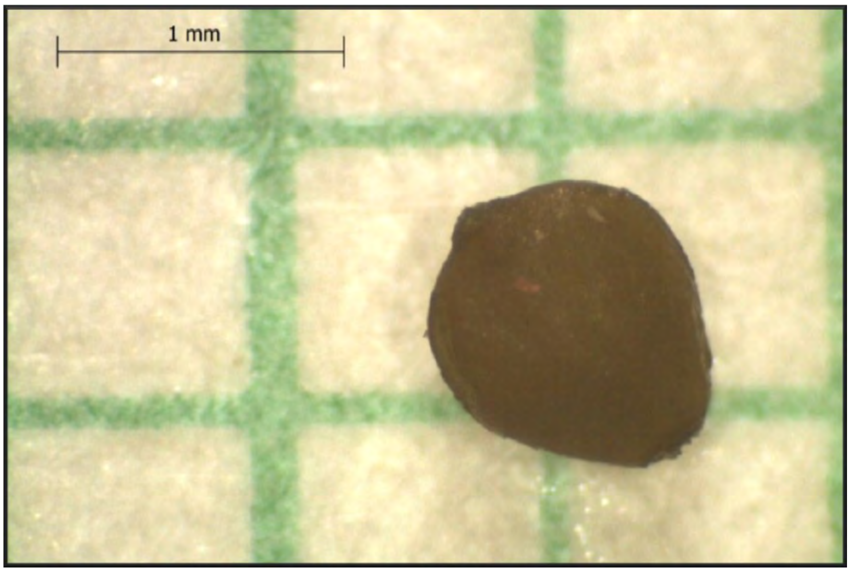
Unknown 2

Location: Barberspan, North West Province, South Africa



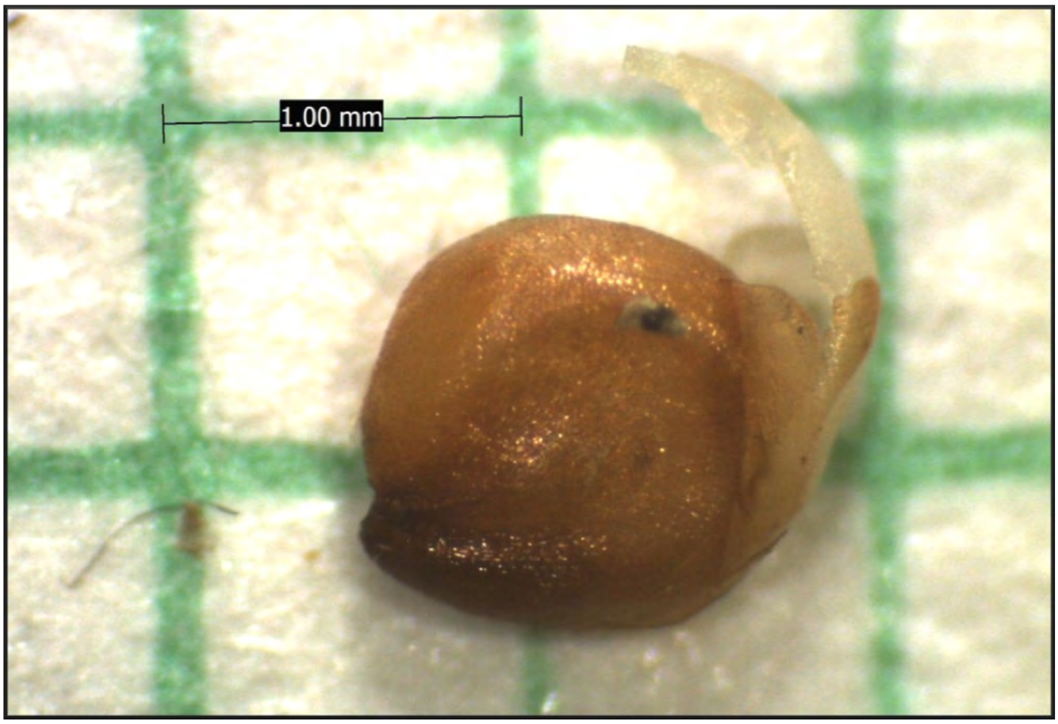
Unknown5 – Cyperaceae

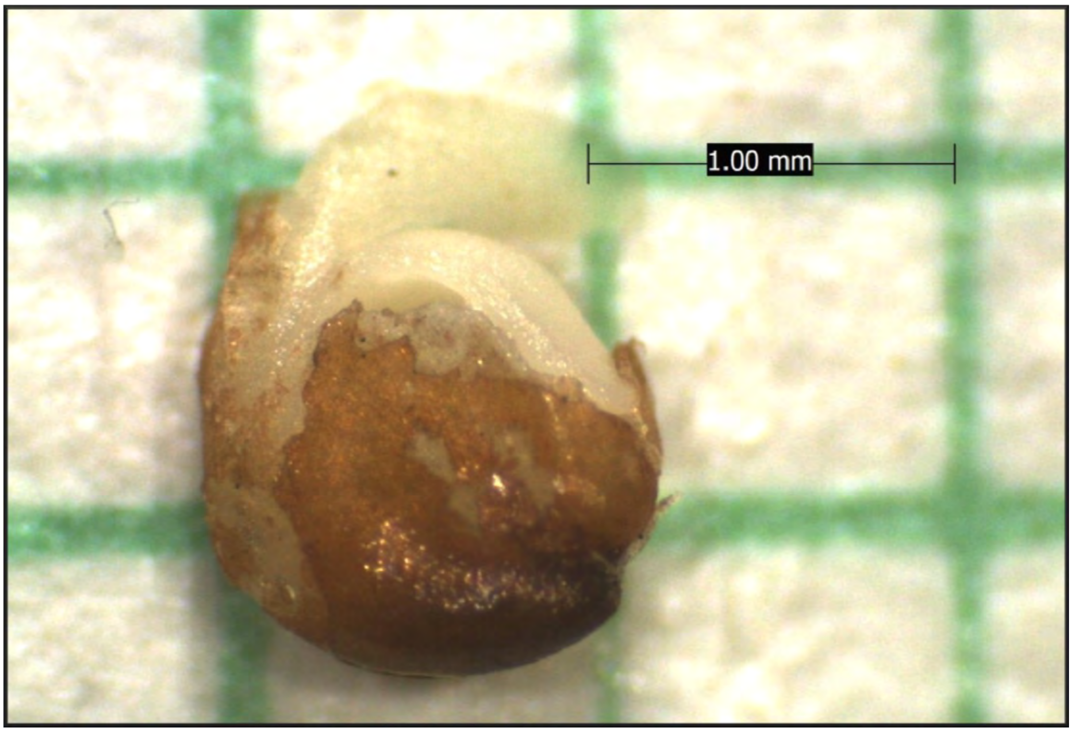
Location: False Bay, Western Cape Province, South Africa



Unknown 3 – Chenopodiaceae

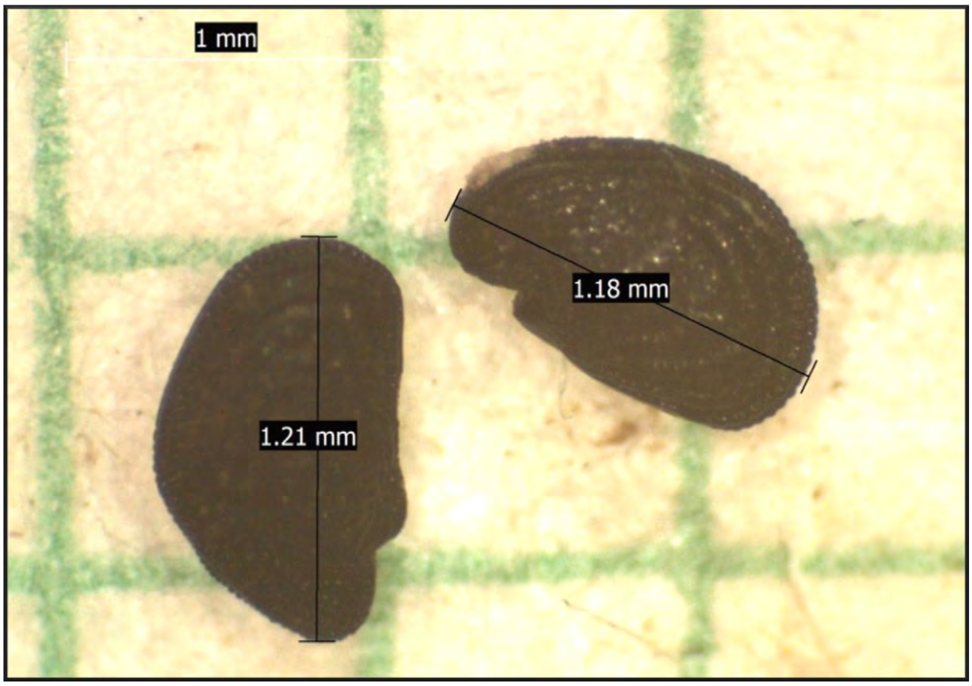
Location: Barberspan, North West Province, South Africa

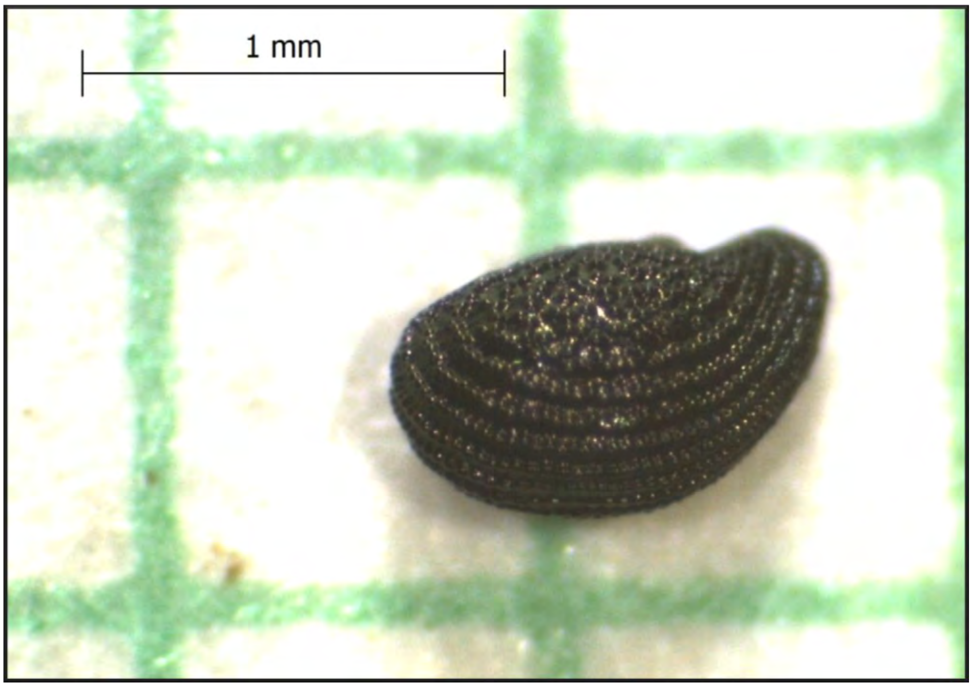




Unknown4 – Caryophyllaceae

Location: False Bay, Western Cape Province, South Africa



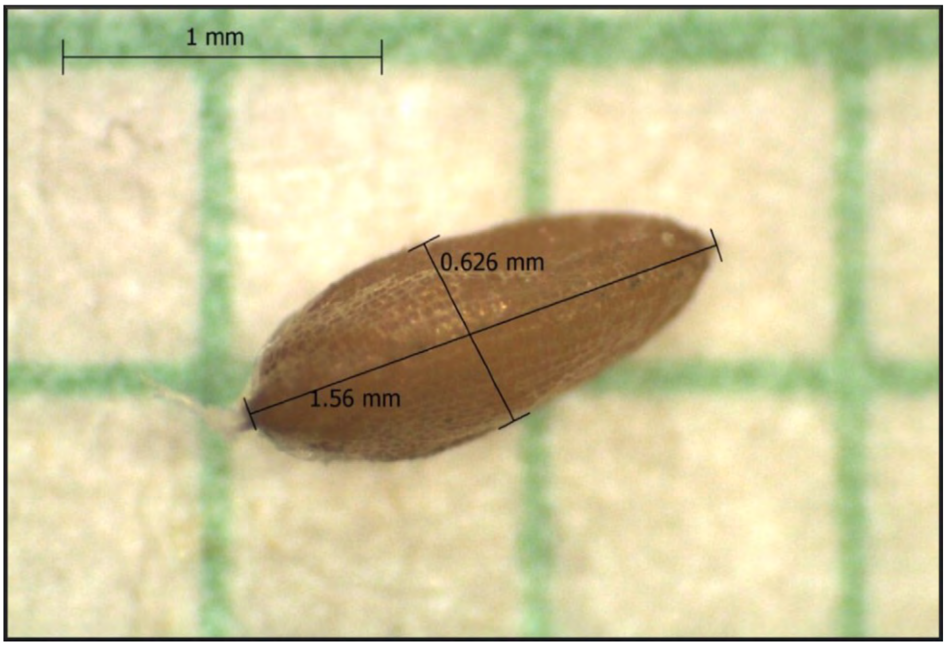


Unknown 9 – Poaceae

Location: Barberspan, North West Province, South Africa

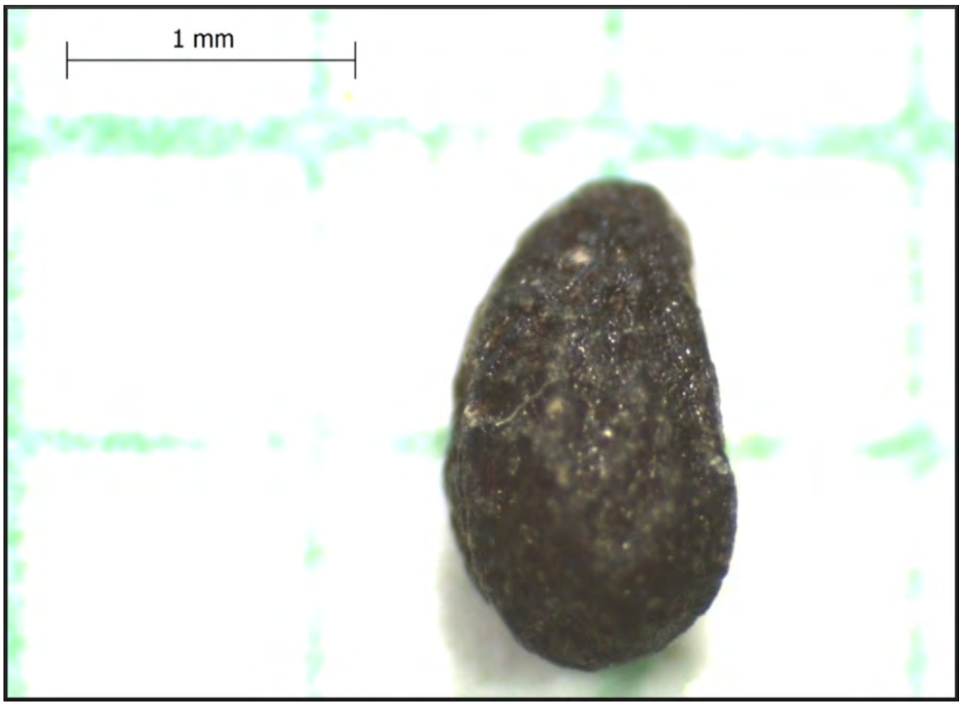
Unknown 11 - Cyperaceae

Location: Voëlvlei Dam, Western Cape Province, South Africa



Unknown 10

Location: Barberspan, North West Province, South Africa



Unknown 12

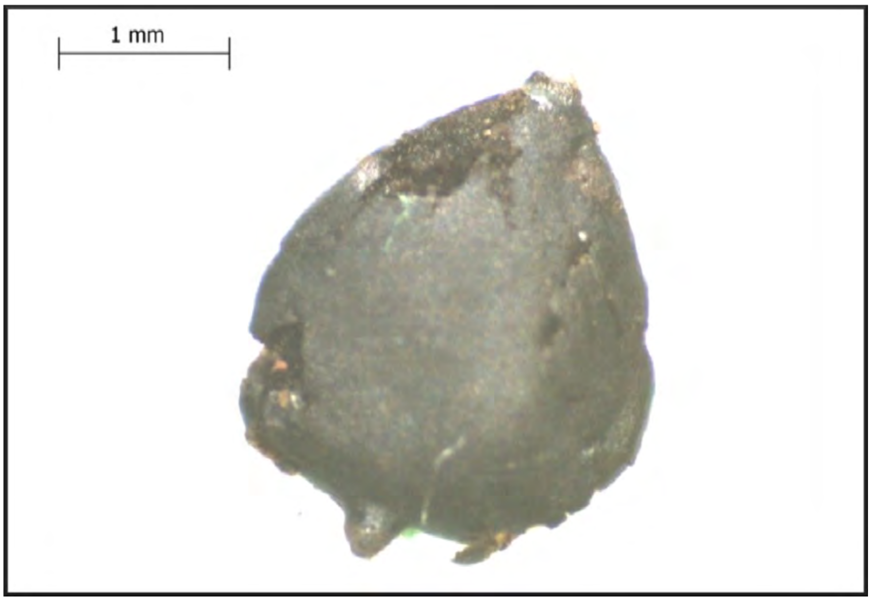
Location: Voëlvlei Dam, Western Cape Province, South Africa

Unknown 13

Location: False Bay, Western Cape Province, South Africa

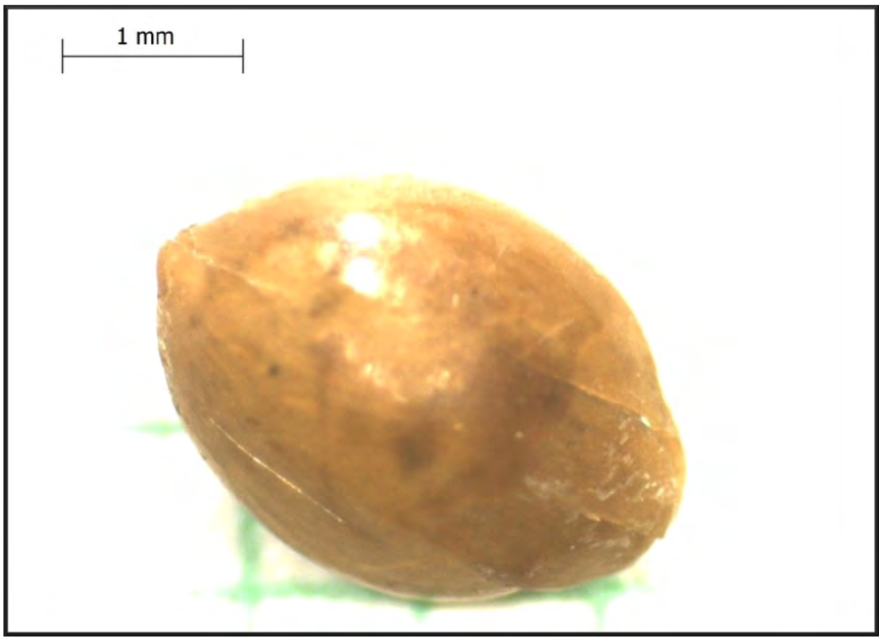
Unknown 14 - Cyperaceae

Location: False Bay, Western Cape Province, South Africa



Unknown 15 - Poaceae

Location: False Bay, Western Cape Province, South Africa



CHAPTER 3

THE ROLE OF WATERBIRDS IN THE DISPERSAL OF FRESHWATER CLADOCERA AND BRYOZOA IN SOUTHERN AFRICA

Published: African Zoology

ABSTRACT

It has long been presumed that waterbirds disperse the propagules of aquatic organisms. However, it is only in recent years that this claim has been empirically explored and little is known about waterbird-mediated dispersal in southern Africa. Aquatic invertebrates are thought to be well adapted to dispersal by waterbirds because of their ability to produce hardy resting eggs. I explored the capacity of waterbirds to disperse the eggs of both cladocera and bryozoans via endo- and ectozoochory. I examined 283 faecal samples and 394 feather brushings from six waterbird species and two wetland sites in South Africa for the presence of diapausing eggs. A total of 108 intact diaspores were recovered, with intact eggs present in 16% and 7% of the faecal samples and feather brushings respectively. The results indicate that southern African waterbirds do take up the resting eggs of aquatic invertebrates and that these eggs can survive intact through the gut or remain attached to the feathers. These results provide evidence that waterbirds may be important vectors for aquatic invertebrates in southern Africa and imply that waterbirds may play a vital role in maintaining connectivity between invertebrate populations in isolated wetland patches.

3.1 INTRODUCTION

Scientists have been curious about how organisms reach isolated habitats for over a century (Darwin 1859). The capacity of highly mobile waterbirds to disperse aquatic invertebrates between isolated freshwater wetlands has recently received much attention in the dispersal literature (Green & Figuerola 2005a; van Leeuwen *et al.* 2012b, 2013). Genetic analysis and mechanistic modelling have demonstrated the continental scales at which waterbirds can affect the distribution of aquatic invertebrates (Figuerola, Green & Michot 2005; Viana *et al.* 2013b). Despite these advances, our knowledge of the transport of aquatic invertebrates is limited both spatially and taxonomically as the majority of studies have been conducted in western Europe and the taxonomic range of propagules dispersed by waterbirds is therefore possibly much larger than currently recognised (van Leeuwen *et al.* 2012b; Green & Elmberg 2014). Given the potential for invasive aquatic invertebrates to rapidly displace native species (Mergeay, Verschuren & De Meester 2006; Sánchez *et al.* 2012) a sound knowledge of species dispersed is vital to protecting our freshwater heritage.

Waterbirds can disperse the propagules of aquatic invertebrates in two ways: intact passage through the gut (endozoochory) or by attachment to the feet and feathers (ectozoochory) (Figuerola & Green 2002a). To date waterbirds have been implicated in the dispersal of over 39 invertebrate species (van Leeuwen *et al.* 2012b) from a broad range of taxonomic groups including bryozoans, crustaceans (branchiopods, cladocerans, copepods, ostracods), nematodes, molluscs and rotifers (Charalambidou, Ketelaars & Santamaria 2003a; Charalambidou *et al.* 2005; Green & Figuerola 2005a; Frisch *et al.* 2007; Sánchez *et al.* 2012; van Leeuwen *et al.* 2013).

The diapausing or resting eggs of many aquatic invertebrates are well suited to passive dispersal by waterbirds due to their resistance to drought and cold (Panov *et al.* 2004). Recent studies have shown the remarkable ability of these resting stages to pass through the digestive tract of waterbirds while remaining viable and producing adults (Brochet *et al.* 2010a; van Leeuwen *et al.* 2012a). Thus, it is possible that the same mechanism by which these organisms survive the variable and uncertain conditions of freshwater environments also provides an opportunity to move between these environments (Snyder 2006).

Freshwater cladocerans (water fleas) and bryozoans (moss animals) are well known for the production of resting eggs in the form of chitinous ephippia and statoblasts respectively (Castellini *et al.* 1991). I evaluated the capacity of southern African waterbirds to transport resistant ephippia and statoblasts. Given the variable hydroperiods that characterise freshwater wetlands in arid zones, it is expected that the dispersal capacity might be high in order to spread risk in this stochastic environment (Levin *et al.* 1984). I determined the presence and abundance of resting eggs transported via both endo- and ectozoochory through an examination of fresh faecal samples and feather brushings**,** and tested for differences in frequency and amount between the two dispersal modes and across bird species and sampling location.

3.2 MATERIALS AND METHODS

During 2013 and 2014 field samples were collected from two permanent wetlands in South Africa: Barberspan Nature Reserve (BAR), North West Province (26°35’ S 25°34’ E) in May/June and False Bay Ecology Park (Strandfontein - STR), Western Cape (34°04’ S 18°30’ E) in January/February. These dates correspond with peak wing feather moult in southern African waterfowl and where chosen to facilitate the capture of good numbers of ducks. Approximately one third of all captured ducks (predominantly Egyptian Goose

Alopochen aegyptiaca) were undergoing wing feather moult and could not fly. This sampling formed part of a larger study investigating the role of waterbirds in seed dispersal (Chapter 2) Data on invertebrate presence and abundance were collected opportunistically from the same samples. Both ephippia and statoblasts are readily identifiable and collectable, and were thus ideal for this purpose.

Faecal samples (*N* = 283) were collected from six different waterfowl species including Red-billed Teal *Anas erythrorhyncha* (N = 35), Cape Shoveler *A. smithii* (*N* = 35), Yellow-billed Duck *A. undulata* (*N* = 60), White-faced Whistling Duck *Dendrocygna viduata* (*N* = 8), Egyptian Goose (*N* = 115) and Spur-winged Goose *Plectropterus gambensis* (*N* = 30) (Table 1). Fresh faecal samples were collected from monospecific roosting sites, with the exception of Red-billed Teal and White-faced Whistling Duck where samples were collected directly from captured birds. Large numbers of ducks were present at the study site and care was taken to collect samples at least 2 m apart so one could be confident that samples represented independent replicates. Faecal samples were collected in individual plastic vials and stored at 4 °C to prevent bacterial growth.

Ectozoochory samples (*N* = 394) were collected from live ducks captured in baited funnel traps or mistnets and included samples from Red-billed Teal (*N* = 49), Yellow-billed Duck (*N* = 141), White-faced Whistling Duck (*N* = 8), Egyptian Goose (*N* = 194) and Spur-winged Goose (*N* = 2) (Table 1). Captured ducks were brushed over a plastic tray with a fine-toothed comb for three minutes, following which their feet and bill were scrubbed with a toothbrush and rinsed with water into the same collection tray (Figuerola & Green 2002b; Brochet *et al.* 2010b). This residue was rinsed onto filter paper, lightly air-dried and stored in a sealed envelope at 4 °C.

Samples were processed in the August/September of the collection year. Individual faecal samples and feather brushing samples were washed through a set of stacked sieves (1 mm, 250 µm and 63 µm mesh sizes) and the residue on each sieve was examined under a binocular microscope (Nikon SMZ-10, Japan). The presence of intact propagules in each fraction was not determined, although it was noted that the ephippia and statoblasts were largely confined to the 1 mm sieve. Sieving was used to partition the larger biological specimens from the generally finer sand grains, however each fraction of the sample was still examined. All intact ephippia and statoblasts were removed, counted and stored in distilled water in 2 ml Eppendorf^{TM} tubes at 4 °C for later identification if possible.

Table 1 Abundance of resting eggs per invertebrate taxon recovered from each waterbird species at Barberspan and Strandfontein. Sample size (*n*) for both faecal and feather samples are given below each duck species. The sample size for the faecal samples is presented first, followed by feather samples in parentheses.

Sample Site	**Bird Species**	**Sample Size**	**Invertebrate taxon**	
		Endo- & (Ectozoochory)	*Daphnia spp.*	*Lophopodella capensis*
Barberspan (BAR)	Egyptian Goose	60 (75)	12	14 (1)
	Red-billed Teal	35 (49)	-	-
	Spur-winged Goose	30	1	1
	Yellow-billed Duck	60 (95)	15 (5)	10
	White-faced Whistling Duck	8 (8)	4	1 (3)
Strandfontein (STR)	Egyptian Goose	55 (119)	5 (18)	(1)
	Cape Shoveler	35	7	1
	Yellow-billed Duck	(46)	(7)	-
	Spur-winged Goose	(2)	(2)	-

To investigate differences between endo- (faecal) and ectozoochory (feather) I used general linear models (GLMs). Samples containing one or more intact resting eggs were categorised as having eggs present. The effect of dispersal mode (i.e. endo- and ectozoochory) on the presence of resting eggs in the samples was modelled using a GLM with binomial error distribution and logit link function and included sampling location and bird species as additional covariates. Red-billed Teal samples were excluded from the analysis because no eggs were recovered leading to zero variance in this group and large parameter estimates and standard errors. Feather brushings from Spur-winged Goose were also excluded from the analysis as I only had two samples. To test for a difference in the abundance of intact eggs between the dispersal modes I used a GLM with Poisson error distribution and log link function, and once again included sampling location and bird species as additional fixed effects. Only samples with eggs present were included in this analysis. In both models, the significance of effects was assessed by means of likelihood ratio tests (LRT) between the full model and the nested model lacking the tested independent term. Where bird species was found to have a significant effect I tested for significant difference between species pairs using post-hoc tests with sequential Bonferroni adjustment to account for the multiple comparisons. All statistical analyses were conducted with R version 3.2.2 (R Core Team 2015).

3.3 RESULTS

A total of 108 intact resting eggs were collected (Table 1), of which 76 were cladoceran ephippia belonging to the genus *Daphnia* (Fig. 1) (Mergeay, Verschuren & Meester 2005; Korosi & Smol 2012) and 32 were statoblasts identified as a species of bryozoan endemic to South Africa, *Lophopodella capensis* (Okamura pers. comm.). Resting eggs of both *Daphnia spp.* and *L. capensis* were recovered from both sampling sites and only one waterbird species, the Red-billed Teal, sampled at Barberspan was not carrying any eggs in either the faecal or feather samples (Table 1).

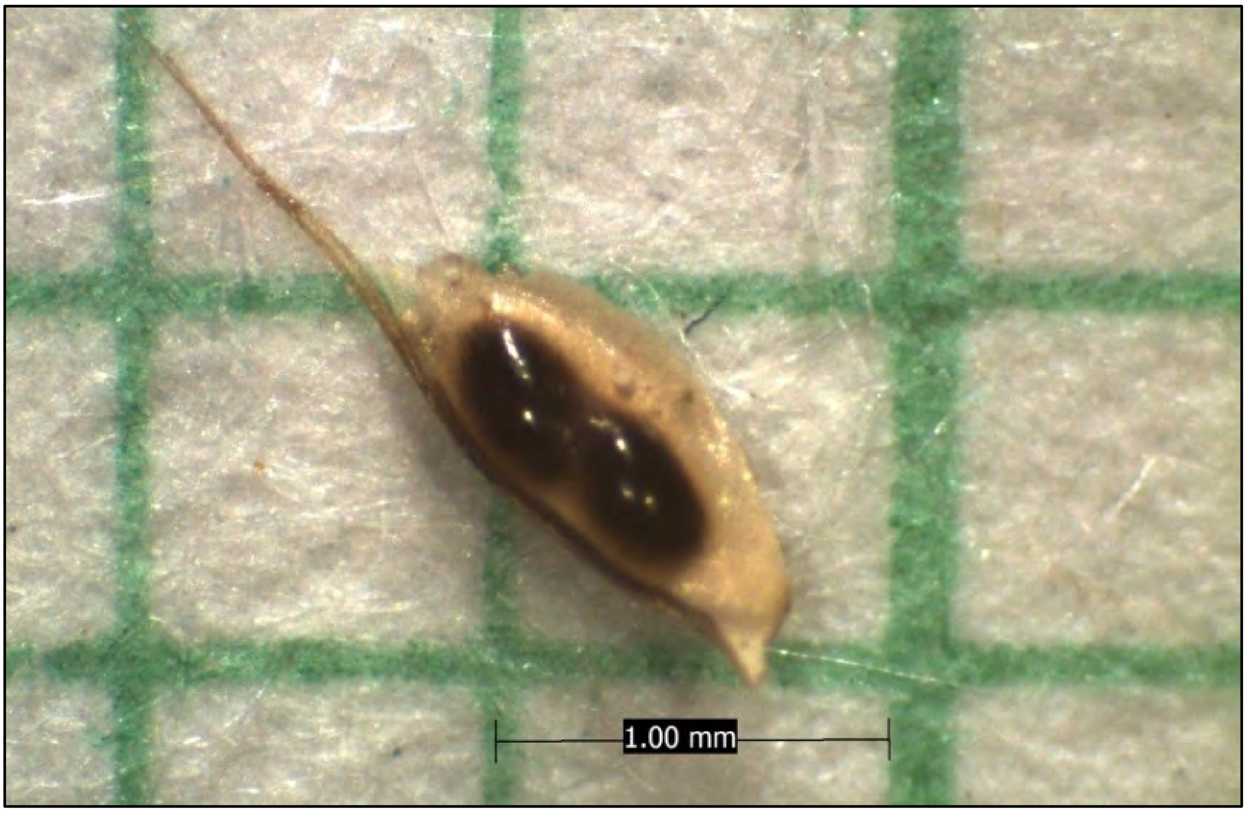


Figure 1 Ephippium of *Daphnia sp.* recovered from Barberspan Nature Reserve.

Approximately 11% of all samples collected contained at least one intact resting egg, with eggs present in 16% and 7% of faecal and feather samples respectively. Endozoochory samples had a significantly higher presence of intact eggs (χ^2 = 7.76, df = 1, *p* = 0.005). The presence of eggs in samples also differed significantly across the bird species (χ^2 = 10.69, df

= 4, p = 0.030), but not between sampling locations (χ^2 = 1.18, df = 1, p = 0.278). White-faced Whistling Duck have a significantly higher presence of eggs in both the faecal and feather samples in comparison to Egyptian Goose (z = 3.13, p = 0.018) and Yellow-billed Duck (z = 2.89, p = 0.048) (Fig. 2), but no other significant differences were found for the pairwise comparisons. The mean (±SE) number of eggs found per "positive" sample was 1.58 ± 1.57 (median = 1.00; maximum = 9) and 1.32 ± 0.98 (median = 1.00; maximum = 6) for endo- and ectozoochory respectively. The abundance of eggs present in the samples was not significantly different between dispersal mode (χ^2 = 0.32, df = 1, p = 0.571), across bird species (χ^2 = 1.79, df = 4, p = 0.774) or between sampling location (χ^2 = 0.15, df = 1, p = 0.701).

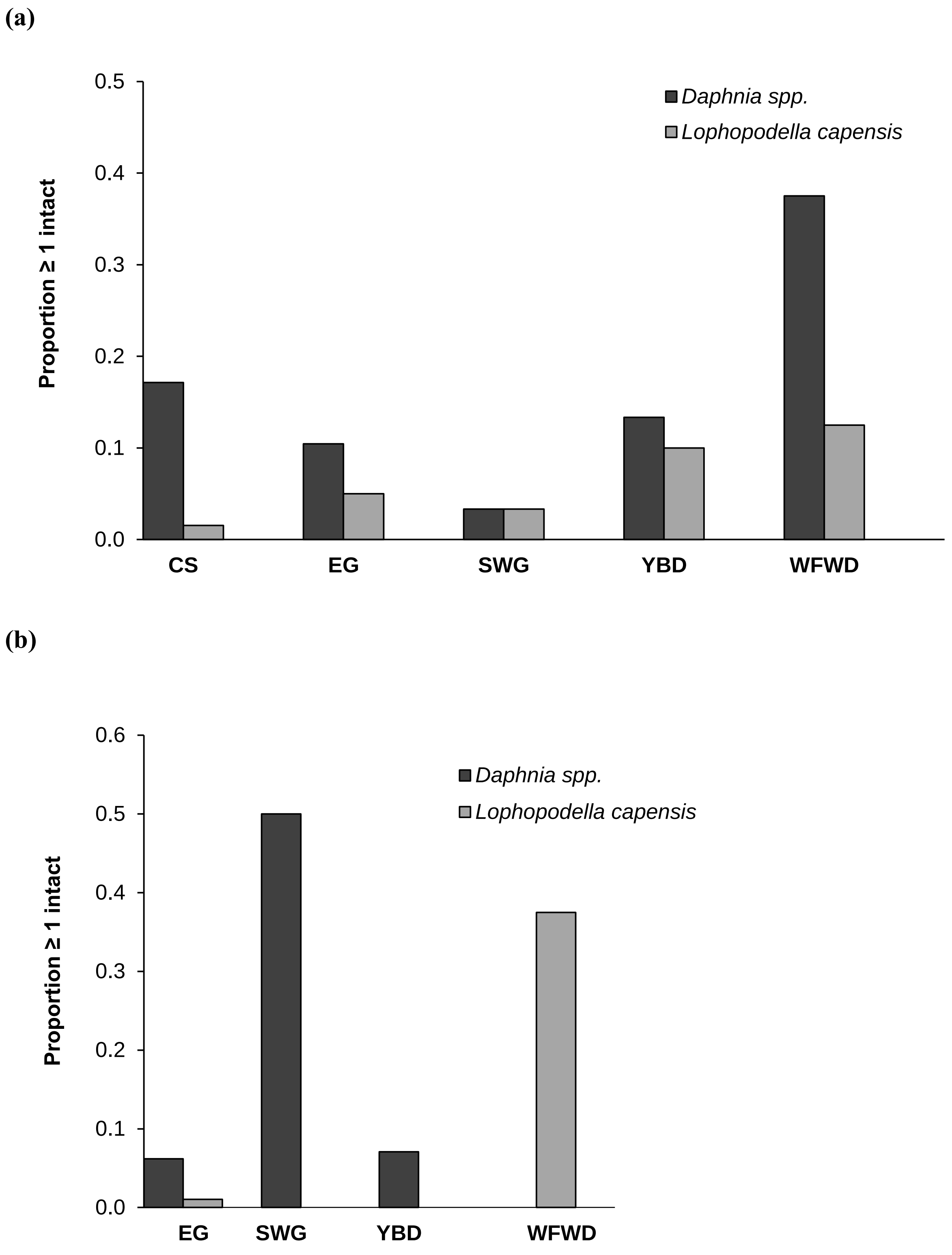


Figure 2 The proportion of samples that contained at least one intact ephippium (dark grey) or statoblast (light grey); (a) endozoochory, (b) ectozoochory. CS = Cape Shoveler, EG = Egyptian Goose, SWG = Spur-winged Goose, YBD = Yellow-billed Duck and WFWD = White-faced Whistling Duck.

3.4 DISCUSSION

To the best of my knowledge this study is the first in Africa to explore the capacity of waterbirds to disperse aquatic invertebrates. The results show that waterbirds in southern Africa take up the propagules of aquatic invertebrates and that these propagules are capable of surviving ingestion intact or can remain attached to the feet and feathers. The viability of the resting eggs was not determined and so I cannot be certain of effective dispersal, but from similar studies it seems likely that a significant proportion will remain viable and will produce adults (Frisch *et al.* 2007; Brochet *et al.* 2010a). A recent meta-analysis for example found that 30% of macroinvertebrate propagules recovered from faecal samples were viable (van Leeuwen *et al.* 2012b)

These results closely matched the outcomes of other studies, for example, Charalambidou and Santamaría (2005) recorded diapausing eggs in 14% of faecal samples and Brochet *et al.* (2010a) had invertebrates emerge from 10% of feather brushings. It is possible that my results do however, underestimate the presence of invertebrate eggs as I only counted large, obvious ephippia and statoblasts and did not use whole sample emergence tests which commonly yield high numbers of ciliates and nematodes (e.g. Green *et al.* 2008).

The presence of intact eggs was significantly higher (approximately double) for the faecal samples. This result was surprising as based on diet preference of the sampled waterbird species, only Cape Shoveler is considered largely insectivorous (although also feeding on crustaceans) (Hockey *et al.* 2005). The prevalence of invertebrate propagules in the diet is perhaps due to accidental ingestion of eggs as birds forage for plant matter in the water column (Green *et al.* 2002), particularly given the prevalence of seeds within the same samples (Chapter 2). Seemingly, large numbers of eggs are not purposefully ingested as a food source and the lack of a significant difference between the abundance of eggs in the faecal samples and feather brushings further supports this idea. In both waterbirds (Brochet *et al.* 2010b) and landbirds (Costa *et al.* 2014) endozoochory is proposed as the dominant dispersal mode for seeds and it seems likely that this too is the case for invertebrate propagules.

Foraging mode may be an important determinant of the number of propagules ingested. For example, White-faced Whistling Duck, which regularly dive to reach aquatic vegetation near the sediments, had a high presence of ephippia in the samples despite the small sample size. Propagule banks in the sediment are consistent sources of resting eggs

(Bilton *et al.* 2001) and suggests that diving ducks may have an important role to play in dispersing these diapausing eggs. Propagule banks mean that the presence of eggs in the wetland is decoupled from actual egg production and may explain why I did not observe a difference between sampling locations despite sampling at different times of year. The spatial and temporal distribution of invertebrate eggs in the water column and sediment and how these are accessed by different waterbird species would be an interesting next step in determining the vectoring capacity of the waterbird community.

Without having quantified the viability of diapausing eggs it is difficult to draw generalities about the relative contribution of endo- and ectozoochory in the field. The probability of transport via the gut is higher in this study (16% versus 7%), but the viability of the propagules may be affected such that the number effectively dispersed is the same or lower. Other resting eggs are well adapted to with stand periods of desiccation (Bilton *et al.* 2001) and are perhaps transported better externally, especially as they may not require the same scarification that aquatic seeds require to break dormancy (Santamaría *et al.* 2002).

Perhaps the most interesting finding was not that waterbirds disperse aquatic invertebrates, but which invertebrate species were potentially dispersed. Resting eggs of both endemic (*L. capensis*) and cosmopolitan (*Daphnia spp.* - possibly *D. purex* or *D. magna*) invertebrates can be transported in this way, suggesting that changes in waterbird communities and movement patterns, as well as introductions of non-native invertebrates, may have important consequences for freshwater diversity (Chapter 6). For example, in Africa, a diverse assemblage of *D. pulex* genotypes has been greatly replaced by a single alien American *Daphnia* clone (hybrid *Daphnia pulex* x *Daphnia pulicaria*) which is thought to have been spread throughout the continent by waterbirds (Mergeay *et al.* 2006).

In conclusion, southern African waterbirds have a high capacity for the dispersal of freshwater aquatic invertebrates, but much more in-depth field and experimental studies are needed to properly quantify this role. This study has shown that both endo- and ectozoochory are possible means of transport, but the relative roles are difficult to evaluate. Finally, acknowledgement of waterbird community and movement dynamics is paramount if we are to understand the capacity of aquatic invertebrates to move. The dispersal landscape is continually changing as freshwater resources become increasingly fragmented and impoundments emerge in previously water scarce areas (Morita & Yamamoto 2002; Fagan

2002). How these processes enhance or hinder dispersal of aquatic invertebrate species are essential avenues for future research.

CHAPTER 4

SEED TRAITS AND BIRD SPECIES INFLUENCE THE DISPERSAL PARAMETERS OF WETLAND PLANTS

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ABSTRACT

Patterns of seed dispersal are strongly influenced by disperser and propagule traits. However, the relative importance of these characteristics for dispersal outcomes is unclear. I investigated differences in the potential dispersal of wetland plants between Egyptian Goose *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha*, two southern African duck species. The seeds of seven wetland plants with varying traits were fed to the ducks and the dispersal parameters of gut passage time, recoverability and germinability of ingested seed were determined. I tested the effect of disperser species and seed traits on the dispersal parameters. In addition, I determined if increased retention times lead to lower recovery and germination of ingested seed. It was predicted that the seed traits of small size and increased hardness would be better at mediating the trade-off between retention time and recoverability and germination, but that this might differ between vectors. The dispersal parameters varied significantly between Egyptian Goose and Red-billed Teal. In particular, Egyptian Goose had longer average and maximum retention times of seeds, but also higher recoverability. Furthermore, short seeds had significantly longer average retention times and were also recovered in the highest numbers. Small seed length potentially facilitates endozoochory by two complementary mechanisms. First short seeds are less digestible, leading to higher recoverability. Second, due to lower digestibility, short seeds are able to survive at longer retention times to be dispersed further, similarly to hard seeds (with hardness positively correlated to seed mass). These results suggest that small seed length and hardness are optimal seed traits facilitating endozoochory in wetland plants. Dispersal parameters were also influenced by the bird species and indicate that differences in vector morphology and digestive physiology may likely have important consequences for seed dispersal. Hence, vector characteristics should be given more explicit considerations in future studies of seed dispersal in aquatic systems.

4.1 INTRODUCTION

Animal mediated dispersal of seeds through the gut (endozoochory) is a widely employed dispersal mechanism (Janzen 1984; Jordano 1995). Highly mobile vertebrates, particularly birds, mammals and fish, have the ability to disperse large numbers of ingested seeds over distances up to hundreds of kilometres (Pollux *et al.* 2005; Jordano *et al.* 2007;

Bruun *et al.* 2008). However it is difficult to measure the final positions of these seeds relative to the parent plants. The problem of tracking animal dispersed seeds can be overcome to a certain degree by developing mechanistic models that describe patterns of seed dispersal based on animal movement behaviour and seed retention times (Cousens *et al.* 2010).

Mechanistic models of endozoochory typically estimate the probability distribution of seed dispersal distances by combining the probability of seed passage over time with the distance away from the propagule source that an animal moves (Kays, Jansen & Knecht 2011; Viana *et al.* 2013b). Such models rely on information about seed passage through the gut and animal movement within a landscape (Cousens *et al.* 2010). Developing a mechanistic dispersal model requires data on dispersal parameters of seeds such as (1) the time taken for seeds to pass through the vector's gut (retention time); (2) the quantities of seeds consumed and the proportion that survive (recoverability); and (3) the numbers of seeds that germinate (germinability). It also requires (4) empirical data on the movement path of the animal vector and (5) information on the frequency with which seeds are deposited in suitable habitat.

Experimental feeding trials are a convenient method of determining the dispersal parameters of seeds. These trials provide essential information on the time taken for seeds to pass through the digestive tract, and are used to quantify the proportion of seeds that survive gut passage and remain viable (Soons *et al.* 2008). In addition, feeding trails can be used to determine how variation in seed traits amongst plant species can affect the dispersal parameters (Soons *et al.* 2008; Kleyheeg *et al.* 2014), providing further insights into the mechanisms underpinning successful endozoochorous dispersal. Recently, feeding trials have been used to quantitatively compare the potential for waterbird mediated dispersal amongst a variety of wetland plants (Charalambidou *et al.* 2005; Soons *et al.* 2008; Brochet *et al.* 2010c).

The passive dispersal of wetland plant seeds by waterbirds has long been implicated in the cosmopolitan distribution of wetland plants (Darwin 1859). Despite its distinguished beginning, only in recent years has this hypothesis gained empirical support, and both field studies and experimental research have highlighted the major role that waterbirds play in the dispersal of these plants (see van Leeuwen *et al.* 2012). However, it is difficult to generalise the role waterbirds play in the dispersal of wetland plants, as there is little information on variation in the dispersal parameters of seeds, particularly outside the genus Anas and outside examples from Western Europe. Therefore, to further develop our mechanistic understanding of wetland plant dispersal we need to quantify the dispersal parameters of different wetland plant species in different waterbird vectors from different geographical regions.

For animal-mediated seed dispersal systems, effective dispersal depends on the traits that influence retention time in the animal vector, as well as recoverability and germinability of the seeds (Figuerola & Green 2002; Jordano *et al*. 2007; Cousens *et al*. 2010). Typically, there is a trade-off between increasing retention time in the gut and the quality of dispersal i.e. recoverability and germinability, which I hypothesise is mediated by specific seed traits. Determining how seed traits influence the dispersal parameters is important as this trade-off plays a vital role in shaping the dispersal kernels of wetland plants. For example in highly variable environments, such as wetlands, theory predicts the emergence of "fat-tailed" dispersal kernels where most seeds settle close to the parent plant, but a few seeds are spread over large distances (Snyder 2011; Burgess *et al.* 2015). Therefore, seed traits (e.g. seed coat thickness and seed size) which on occasion facilitate recovery at long retention times, whilst still ensuring high recovery and germination in general, may be considered optimal for effective dispersal in wetland systems. These traits, however, may also have differing effects depending on the vector under consideration (Cousens *et al*. 2010).

Here, I investigate how variation in seed traits affects the dispersal parameters – retention time, recoverability and germinability – of wetland plants dispersed by two different waterfowl vectors in southern Africa. Previous research has suggested that seed size and hardness are important traits that can produce variation in dispersal (Soons *et al*. 2008; Kleyheeg *et al*. 2014). Furthermore, differences between vectors in body size and digestive physiology for example, can also have important consequences for the dispersal of wetland plants (Viana *et al.* 2013a; García-Álvarez *et al.* 2015).

Seven wetland plant species were selected with varying seed traits and fed to Egyptian Goose *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha* (Anatidae), two common southern African waterbird species. These two waterfowl species have similar diets (Chapter 7) and habitats (Hockey *et al.* 2005), but differ markedly in size (Egyptian Goose: mean ± SD 2.1 ± 0.20 kg; Red-billed Teal: 0.6 ± 0.03 kg). It was expected that the dispersal parameters would be strongly influenced by both disperser and propagule characteristics. The following predictions were tested:

1. Plant species with smaller seeds (mass and/or length) have shorter retention times in the gut and are less readily digestible, leading to higher recoverability and germinability.
2. Harder seeds are more resistant to digestion leading to higher recoverability and germination, and particularly facilitating recovery at longer retention times.
3. Gut retention time, recoverability and germination differ between the two vectors.
4. The passage of wetland seeds through the gut of waterfowl may enhance the germination of seeds.
5. Within a given seed species an increase in retention time results in lower recoverability and germinability.

4.2 MATERIALS AND METHODS

The seeds of four wetland plant species (*Amaranthus hybridus*, *Persicaria lapathifolia*, *Potamogeton pectinatus* and *Ruppia maritima*), were collected in early April 2014 from False Bay Ecology Park/Strandfontein (34°04’124 S 18°30’ E), a Ramsar wetland in the Western Cape province of South Africa. An additional three wetland plant species (*Elegia capensis*, *Panicum schinzii* and *Prionium serratum*) were purchased from a supplier of whole seed (Silverhill Seeds, Cape Town). Seeds collected from the field were removed from their stalks and stored in the dark at 4 °C along with purchased seed until the start of the feeding experiment in June 2014. The seeds together represented seven different wetland plant families and were chosen to reflect differences in the seed traits of size, both mass and length and hardness (Table 1). Furthermore, *E. capensis* and *P. serratum* are plant species endemic to South Africa, and represent the first attempt at describing waterbird-assisted dispersal in the Restionaceae and Prioniaceae plant families.

Table 1 Mean seed traits (± SE) of each plant species in the feeding experiment

Seed taxon	**Family**	**Length/SL (mm)**	**Mass/SM (mg)**	**Hardness/SH (N)**
Amaranthus hybridus (*A. hyb*)	AMARANTHACEAE	0.22 ± 0.02	0.97 ± 0.00	0.17 ± 0.01
Elegia capensis (*E. cap*)	RESTIONACEAE	0.55 ± 0.05	2.71 ± 0.03	0.29 ± 0.05
Panicum schinzii (*P. sch*)	POACEAE	0.68 ± 0.03	2.64 ± 0.01	8.27 ± 0.37
Persicaria lapathifolia (*P. lap*)	POLYGONACEAE	1.10 ± 0.04	2.13 ± 0.07	48.31 ± 4.61
Potamogeton pectinatus (*P. pec*)	POTAMOGETONACEAE	1.54 ± 0.04	2.69 ± 0.05	15.57 ± 1.63
Prionium serratum (*P. ser*)	PRIONIACEAE	0.05 ± 0.02	0.89 ± 0.00	0.01 ± 0.00
Ruppia maritima (*R. mar*)	RUPPIACEAE	1.03 ± 0.05	2.51 ± 0.05	16.26 ± 0.91

4.2.1 Seed measurement

A small proportion of the seeds of each plant species were placed into a drying oven at 60 °C for 2 days prior to measurement of seed length, mass and hardness (Table 1) (Brochet *et al*. 2010c). Care was taken to only include seeds with an intact endosperm. The length of 20 randomly selected seeds per plant species was measured to the nearest 0.01 mm under a binocular stereoscope (Leica EZ4, Germany). Individual seed mass of 20 seeds per species was measured on a precision weighing analytical balance (Shimadzu, Japan) to 0.01 mg. For two species with very small seeds (*A. hybridus* and *P. serratum*), 10 groups of 20 seeds were used to calculate individual seed mass. Seed hardness was measured on a device intended to determine the compression of metals (Instron 3365, USA) and was set to apply increasing force at 1 mm.minute-1. Five seeds from each species were selected for the compression test and seed hardness was quantified as the force in newton (N) taken to crack the seed coat.

4.2.2 Feeding trial and processing

To compare the effects of disperser species, seed traits and retention times on dispersal parameters, I fed the seeds of seven wetland plant species to Egyptian Goose and Red-billed Teal. With the exception of *E. capensis* and *P. serratum* the plant species selected for this experiment are commonly recorded in the diets of these two waterfowl species (Chapter 2 & 7).

Twenty waterfowl (10 Egyptian Goose and 10 Red-billed Teal) were captured in May 2014 from Barberspan Nature Reserve, South Africa (26°35’ S 25°34’ E) using baited funnel walk-in traps. Previous ingestion studies have generally used captive waterfowl, which have the advantage of habituation to people. However, waterfowl in captivity have shorter intestines (Clench & Mathias 1995), which can affect the recovery and passage time of seeds. Thus, use of wild waterfowl may offer a more realistic estimate of the effects of disperser species and seed traits on dispersal. However, it should be noted that the waterfowl digestive tract is highly plastic and changes can occur within a couple of weeks in response to diet (Charalambidou *et al*. 2005). Wild-caught waterfowl were housed in an outdoor aviary (20 x 3 x 2.5 m) at Barberspan for the duration of the 8 week experiment and fed on a diet of mixed grains (maize and sunflower seeds) with free access to grit and water. The birds were free to supplement feeding with grass *Themeda triandra*, which was the only plant species growing in the aviary. A two week habituation period was observed prior to the start of the six week feeding experiment. The mass of each duck was recorded every week as an indicator of adjustment to captivity as weight loss is a good indicator of chronic stress (Konkle *et al.* 2003). Individual Red-billed Teal showed a small, but insignificant increase in body mass over the course of the experiment (repeated measures ANOVA: $F_{7,63} = 2.09$, $p = 0.058$) (start mass ± SD: 0.55 ± 0.06 kg; end mass: 0.59 ± 0.04 kg). Conversely, Egyptian Goose demonstrated a significant decrease in body mass and may have suffered some stress during the experiment (repeated measures ANOVA: $F_{7,63} = 2.38$, $p = 0.032$) (start mass ± SD: 2.22 ± 0.4 kg; end mass: 2.07 ± 0.2 kg). Egyptian Goose and Red-billed Teal do not display sexual dimorphism and were not sexed in the field. On completion of the experiment, the captured waterfowl were returned to the wild.

Feeding trials were conducted on a weekly basis from 10 June through 23 July 2014. During the 6 weeks, all 20 captive waterfowl were each force-fed 100 seeds of a single plant species per week. Each plant species was fed seven times to both of the waterfowl species, resulting in 14 replicates of 100 seeds per plant species (7 replicates each for goose and teal) and 9800 ingested seeds. The seeds were randomly assigned to the individual ducks making sure that the same plant species were never fed to the same individual twice over the entire experiment. Each plant species was fed at least once each week.

Each replicate began by placing each individual duck into a separate cage (Egyptian Goose 100 x 60 x 60 cm; Red-billed Teal 50 x 50 x 50 cm) with plastic mesh flooring (1 cm mesh size) and removable plastic sheeting below on the eve prior to force-feeding in order to habituate the ducks to the new environment. Early the following morning each duck was force-fed its designated 100 seeds, which were embedded in a soft maize-porridge pellet to ensure that all seeds were easily ingested. A very small number of seeds (~1%) were regurgitated, and were counted to later correct for exact numbers of ingested seeds. The cages were housed in a second outdoor aviary, allowing the captive waterfowl exposure to natural light conditions during the experiment. Maize and water were available ad libitum throughout the experiment. Following force-feeding, faecal samples were collected from the waterfowl for 36 hours before being released back into the aviary for 5 days until the start of the next trial.

Faecal matter fell through the mesh floor onto a removable plastic mat below and was collected at 2-hour intervals for the first 12 hours, at 4-hour intervals for the next 12 hours and at 6-hour intervals for the last 12 hours. At each collection time, the cages were visually inspected to recover any faecal matter that had not been dislodged. The faecal samples were immediately sieved through a 63 µm sieve and all seeds with an intact endosperm at each time interval were counted, collected and stored in 1 ml Eppendorf™ tubes at 4 °C until the start of the germination trial.

4.2.3 Germination trials

For each plant species, 7 replicates of 20 seeds each were counted out during the third week of the experimental feeding trail and stored again at 4 °C as the non-ingested controls. Intact seeds recovered from the feeding trials, as well as the controls were set into a germination trial in September 2014. Individual samples from each collection time, as well as the controls, were placed in 2 ml plastic vials half-filled with distilled water and a maximum limit of 10 seeds per vial. Sample vials were placed into a phytotron unit set at a light:dark cycle of 16:8 h and respective temperatures of 24:16 °C. Germination was checked every 3 days for 21 days and then once a week until the end of the 6 week trial. Germinated seeds were counted and removed and water was replenished on each check. Seeds that failed to germinate were returned to the fridge at 4 °C for one month, before being set to germinate under the same conditions for a further 6 weeks. Fynbos species, such as *E. capensis* typically germinate better following a fire. Therefore for the second germination trial seeds of *E. capensis* were soaked for a day in "Instant Smoke Plus Seed Primer" to stimulate germination (Lange & Boucher 1990).

4.2.4 Statistical analysis

The measured seed traits were suspected to be highly inter-correlated and were tested for correlation prior to inclusion in further analysis. Seed mass and hardness were significantly correlated (Spearman's correlation: rs 0.89, $p = 0.01$), but seed length was not correlated with either hardness (rs 0.50, $p = 0.23$) or mass (rs 0.32, $p = 0.48$). Consequently only seed length and hardness were included in the subsequent analyses.

The typical data output from the experiment was the number of intact and germinating seeds per time interval for each waterfowl and plant species (Fig. 1) (Table 2). From the retrieval and germination data we calculated four seed dispersal parameters for each replicate; (1) the average retention time (TAVE); (2) the maximum retention time (TMAX); (3) the total number of recovered seeds (recovered); and (4) the total number of germinating seeds (germinated). Generalised linear mixed models (GLMMs) were used to explore the effect of disperser species (BS) and seed traits i.e. length (SL) and hardness (SH) on each of the four dispersal parameters. As the body mass of Egyptian Goose changed significantly throughout the experiment, and Red-billed Teal body mass changes could be considered meaningful at an alpha = 0.1, I included an index of change in body mass (BMC) as an additional covariate in the models to account for any physiological changes within the ducks that may affect the dispersal parameters. For each of the four cases all numerical covariates were centred and individual bird was included as a random effect to account for differences amongst individuals. Seed species was also included as a random effect to avoid pseudo-replication due to multiple observations for equal seed sizes (see Kleyheeg *et al*. 2014).

Table 2 Average retention time (Mean ± SE), median retention time, maximum retention time (Max) and maximum retention time at which germination occurred for recovered seeds (GMax) and the percentages of recovered seeds (± SE) and germinated seed (± SE) from the Egyptian Goose, Red-billed Teal and control samples. Germination is the % recovered seeds that germinated.

	Retention Time (hours)								**Recovered Seeds (%)**		**Germination (%)**		
	Mean	**Median**	**Max**	**GMax**	**Mean**	**Median**	**Max**	**GMax**					
Seed taxon		**Egyptian Goose**				**Red-billed Teal**			**Egyptian Goose**	**Red-billed Teal**	**Egyptian Goose**	**Red-billed Teal**	**Control**
Amaranthus hybridus	5.14 ± 0.51	5	30	30	3.57 ± 0.19	4	10	10	68 ± 11	39 ± 9	86 ± 5	81 ± 5	79 ± 9
Elegia capensis	4.57 ± 0.19	5	12	0	1.71 ± 0.60	2	30	4	13 ± 2	3 ± 1	0	4 ± 2	1 ± 1
Panicum schinzii	4.86 ± 0.60	4	24	12	3.14 ± 0.59	4	20	6	23 ± 5	15 ± 5	21 ± 4	25 ± 5	9 ± 2
Persicaria lapathifolia	5.10 ± 0.29	5	36	30	5.17 ± 0.56	5	36	36	42 ± 6	27 ± 6	24 ± 3	41 ± 4	43 ± 4
Potamogeton pectinatus	4.14 ± 0.47	4	20	20	1.86 ± 0.77	2	30	30	13 ± 4	3 ± 2	44 ± 9	37 ± 8	22 ± 3
Prionium serratum	4.57 ± 0.19	4	30	30	3.43 ± 0.19	3	20	12	72 ± 10	71 ± 10	5 ± 2	3 ± 2	2 ± 1
Ruppia maritima	5.14 ± 0.38	5	30	24	2.43 ± 0.19	2	20	20	29 ± 5	5 ± 1	13 ± 3	21 ± 7	4 ± 1

For each of the four seed dispersal parameters all possible combinations of the independent predictors were modelled, as well as all the two-way interactions between bird species, seed length and seed hardness. The candidate set of 28 possible subsets of the four predictor variables were compared using Akaike's Information Criteria corrected for small sample sizes (AICc) (Burnham & Anderson 2002). The strongest model has the smallest AICc, however if the difference between two AICc values (ΔAICc) was < 2, models were considered equivalent. In most cases several models fell below ΔAICc = 2, and a model-averaging approach of all candidate models within Δ2 AICc was used to obtain the final parameter estimates, standard errors, and confidence intervals (Table 3) (Burnham & Anderson 2002). The model averaged parameters were considered significant if the 95% confidence interval surrounding the parameter estimate did not include zero. The p-values are included to ease interpretation of the level of significance of the model averaged parameters, however, I am aware that this is not promoted under the Burnham and Anderson (2002) paradigm. See Appendix 4A for model rankings. Multicollinearity, especially between seed length and hardness, was not considered an issue in the models as indicated by variance inflation factors < 3 for all variables. The R^2GLMM of the top model was used as an overall measure of fit and can be categorized into two types: marginal and conditional (Nakagawa & Schielzeth 2013). The marginal R^2 (mR^2) represents the variance explained only by the fixed factors, whilst the conditional R^2 (cR^2) is interpreted as variance explained by both fixed and random factors.

The average retention time (TAVE) and log transformed maximum retention time (TMAX) were both normally distributed. The effect of bird species, seed traits and change in body mass on both TAVE and TMAX were analysed in two separate linear mixed effects models, GLMM1a and GLMM1b. The total number of recovered seeds (recovered) was modelled using a binomial error distribution and logit link function and included the total number of seeds fed as a denominator (GLMM2). Similarly, the total number of germinating seeds (germinated) was modelled with a binomial error distribution and logit link function, but included the total number of intact seeds recovered as a denominator (GLMM3a). However, the null model fell within a Δ2 AICc of the top model, and I thus reformulated the candidate set, substituting seed traits (SL and SH) with seed species (SS) as a predictor (GLMM3b).

In GLMM4 I tested the effect of ingestion by the waterfowl species versus the non-ingested controls. The proportion of germinated seeds was modelled using a binomial error distribution and logit link function. A candidate set of five models was considered composed of all possible combinations and interactions between the predictors seed species (SS) and treatment (TT) (Table 3). Individual bird (or individual control) was included as a random effect.

In GLMM5 and GLMM6 I modelled the effect of increasing retention time on seed recoverability and germinability, respectively. To preserve information about the pattern of seed retrieval over time the proportion of seeds recovered at each 2-hour time interval was used as the dependent variable. Similarly, for germination the proportion of intact seeds at each time interval that later germinated was used as the dependent variable. The relationship between proportion of recovered (or germinating) seeds and retention time was analysed using repeated-measures GLMMs with a binomial error distribution and log link function. Observations on retrieval over time were not independent and it was necessary to include the random effect of individual bird nested within each time interval. The analysis was restricted to data from the first 12 hours as 96% of all seeds were recovered within this time (Fig. 1), and high numbers of zeros at longer time intervals affected model convergence. The time interval (retention time – RT) was included as a centred linear, as well as squared covariate (RT2), to test for both linear and curvilinear patterns in retrieval and germination. All possible combinations and interactions between bird species and retention time (both RT and RT2) were considered in the candidate models (Table 3). The effect of seed species could not be investigated as GLMMs containing all three predictors (BS, RT and SS) would not converge on a solution. Model selection using AICc and model-averaging as described above were used to obtain final parameter estimates and confidence intervals in GLMMs4-6 (Table 3).

All statistical analyses were performed in R version 3.2.2 (R Core Team 2015) with packages *lme4* (Bates *et al*. 2014) for GLMMs and *AICcmodavg* (Mozerolle 2015) for model selection and averaging.

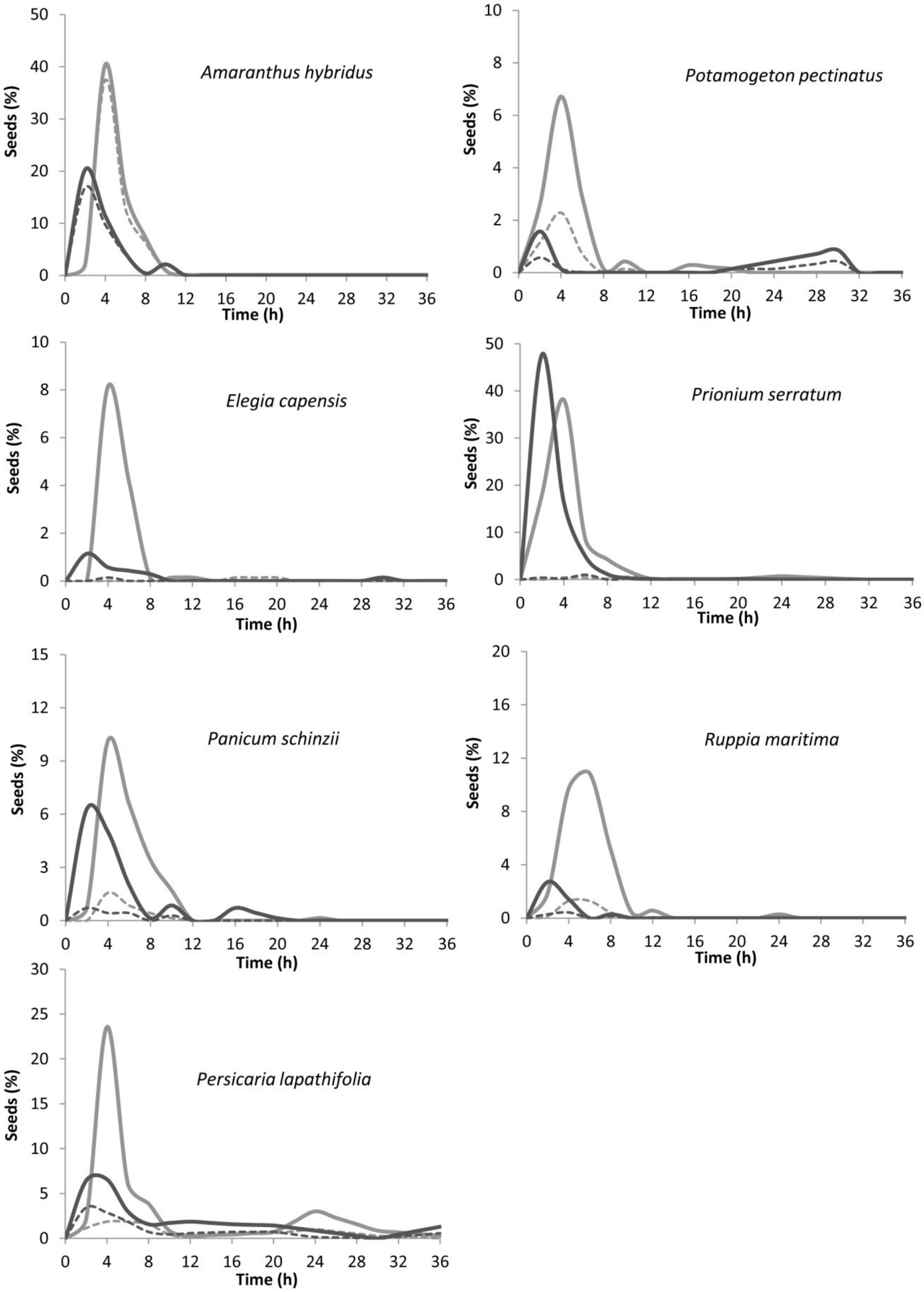

Figure 1 Average number of seeds recovered (solid line) and germinated (dashed line) in each time interval over the 36 hours for which faecal matter was collected. Germination is expressed as the total number of seeds that germinated from the total number ingested in each replicate. ▬ = Red-billed Teal; ▬ = Egyptian Goose.

4.3 RESULTS

Nearly 30% of all fed seeds were recovered intact from the faecal samples (2938 seeds). Seeds of all plant taxa were recovered and percentages ranged from 3% to 72% depending on the bird or seed species (Table 2). Of the intact seeds, 936 successfully germinated i.e. 32% of all recovered seeds and 10% of all seeds ingested. The percentage of intact seeds that germinated varied from 0% to 86% across the seed species (Table 2). The average retention times for seeds ingested by Egyptian Goose were longer than for Red-billed Teal, with the exception of *P. lapathifolia* seeds (Table 2). Overall, 96% of all recovered seeds were evacuated within 12 hours, but 85 seeds (3%) were recovered after 12 hours and 27 seeds (1%) after 24 hours (Fig. 1). However 65% of all seeds passing after 12 hours were represented by one seed species, *P. lapathifolia*. The maximum retention time for any one seed was well above 12 hours for most seed species. Additionally 36 seeds (4%) and 11 seeds (1%) germinated after 12 hours and 24 hours respectively. The maximum retention time at which at least one seed germinated was also over 12 hours for most taxa with the exception of *E. capensis* (Table 2).

4.3.1 Effect of disperser and seed traits

Seed species differed significantly in size (ANOVA: $F_{6,133} = 128.1$; $p < 0.001$) and hardness (ANOVA: $F_{6,28} = 65.11$; $p < 0.001$) (Table 1). Most seed species pairs differed significantly in length (Tukey contrasts for 15 of 21 combinations, $p < 0.05$), but exceptions such as *R. maritima* and *P. lapathifolia* showed overlap. Similarly, for hardness, many pairs differed (Tukey contrasts for 12 of 21 combinations, $p < 0.05$), but for example *A. hybridus* overlapped with *E. capensis*.

Four candidate models fell within a Δ2 AICc of the top model investigating the effects of disperser species (BS), body mass change (BMC) and seed traits (SL and SH) on average retention time (Appendix 4A: GLMM1a). The average retention time of all seeds was significantly lower in red-billed teal (GLMM1a: Table 3). Seed length was significantly negatively correlated with average retention time, whilst seed hardness significantly positively affected average retention time (Table 3). No significant effect of changes in body mass or an interaction between disperser species and/or seed traits was found. The variance explained by the fixed effects was 36%, indicating a good fit of the data; an additional 5% variance was explained by the inclusion of bird individual and plant species as random effects. Five candidate models fell within a Δ2 AICc of the top model investigating the effects of the predictors on maximum retention time (Appendix 4A: GLMM1b). The maximum retention time of seeds was significantly lower in red-billed teal and significantly increased with seed hardness (GLMM1b: Table 3). No effect of changing body mass, seed length or an interaction of disperser species with seed traits was detected. The variance explained by the fixed effects was 21%, and an additional 8% of the variance was explained by the inclusion of bird individual and plant species as random effects.

Six candidate models fell within a Δ2 AICc of the top model investigating the total recovery of seeds (Appendix 4A: GLMM2). The number of seeds recovered intact was significantly lower in red-billed teal (GLMM2: Table 3). Seed length had a significant effect on the total number of recovered seeds, with shorter seeds recovered in higher quantities (Table 3). There was no effect of body mass change, seed hardness or any interactions. In this model the fixed effects explained 33% of the variance, and random effects an extra 4% of the variance.

The candidate models fitted to the number of germinating seeds were no better than a null model and indicated that disperser species and seed traits were poor predictors of the total number of germinating seeds (results not shown). A second set of candidate models with disperser species and seed species (SS) as fixed effects was run (Appendix 4A: GLMM3b). Two candidate models fell within Δ2 AICc of the top model, and seed species was found to be the only significant predictor of differences in the number of germinating seeds (GLMM3b: Table 3). *A. hybridus* had the highest number of germinating seeds, whilst *P. serratum* had the lowest. There was no difference in the number of germinating seeds between the two bird species, and no effect of body mass. The top model explained 49% of the variance, and no variance was explained by the random effects.

Table 3 Final parameter estimates (β), standard errors (SE) and confidence intervals of model averaging based on alternative GLMMs (see Supplementary Material Appendix 4A). Significant parameters i.e. where confidence intervals do not overlap zero, are indicated in bold. The p-values are included for ease of interpretation of the level of significance for each parameter. The R^2_{GLMM} (m) and R^2_{GLMM} (c) for the top models are presented as a measure of fit. Egyptian Goose (BS(EG)) is the reference category for all models containing disperser species (BS) as a predictor, with the exception of model 4 where the control (TT (control)) is set as the reference category. RBT = Red-billed Teal. *Persicaria lapathifolia* (SS(PER)) is the reference category for all models containing seed species (SS). Seed species codes *A. hyb* = *Amaranthus hybridus*, *E. cap* = *Elegia Capensis*, *P. sch* = *Panicum schinzii*, *P. pec* = *Potamogeton pectinatus*, *P. ser* = *Prionium serratum* and *R. mar* = *Ruppia maritima.* Continuous predictors include seed length (SL), seed hardness (SH), index of body mass change (BMC), retention time (RT) and retention time squared (RT^2). Note: Only parameters of model averaged alternative GLMMs are shown and the results of GLMM3a and GLMM6 are not shown.

GLMM1a	**T_{AVE}**					**GLMM1b**	**T_{MAX}**				
		Confidence Interval						**Confidence Interval**			
Predictors	**β ± SE**	**2.5%**	**97.5%**	***p-value***		**Predictors**	**β ± SE**	**2.5%**	**97.5%**	***p-value***	
Intercept	4.82 ± 0.26	**4.32**	**5.33**	<0.001	**$R^2_{GLMM(m)}$**	**Intercept**	2.46 ± 0.16	**2.14**	**2.77**	<0.001	**$R^2_{GLMM(m)}$**
BS(RBT)	-1.74 ± 0.31	**-2.36**	**-1.13**	<0.001	35.52	**BS(RBT)**	-0.49 ± 0.14	**-0.77**	**-0.20**	0.001	20.87
SL	-0.68 ± 0.31	**-1.29**	**-0.08**	0.027	**$R^2_{GLMM(c)}$**	**SL**	-0.69 ± 0.30	-0.81	0.03	0.070	**$R^2_{GLMM(c)}$**
SH	0.62 ± 0.22	**0.18**	**1.06**	0.006	40.70	**SH**	0.21 ± 0.22	**0.04**	**0.68**	0.026	28.93
BS(RBT)*SL	-0.46 ± 0.28	-1.01	0.09	0.100		**BS(RBT)*SL**	-0.02 ± 0.09	-0.55	0.20	0.364	
SL*SH	-0.30 ± 0.25	-0.81	0.20	0.241		**SL*SH**	-0.01 ± 0.06	-0.18	0.38	0.488	
BMC	0.10 ±0.15	-0.20	0.41	0.503							

GLMM2	**Recovered**					**GLMM5**	**Recovered/time**				
		Confidence Interval						**Confidence Interval**			
Predictors	**β ± SE**	**2.5%**	**97.5%**	***p-value***		**Predictors**	**β ± SE**	**2.5%**	**97.5%**	***p-value***	
Intercept	-0.69 ± 0.24	**-1.17**	**-0.19**	0.006	**$R^2_{GLMM(m)}$**	**Intercept**	-4.09 ± 0.17	**-4.42**	**-3.76**	<0.001	**$R^2_{GLMM(m)}$**
BS(RBT)	-1.34 ± 0.28	**-1.86**	**-0.78**	<0.001	33.33	**BS(RBT)**	0.04 ± 0.07	0.15	0.16	0.600	37.55
SL	-1.37 ± 0.27	**-1.90**	**-0.85**	<0.001	**$R^2_{GLMM(c)}$**	**RT^2**	-2.48 ± 0.24	**-3.00**	**-2.01**	<0.001	**$R^2_{GLMM(c)}$**
SH	0.27 ± 0.28	-0.28	0.81	0.343	36.49						42.58
BS(RBT)*SL	-0.37 ± 0.25	-0.86	0.12	0.138							
BMC	0.15 ± 0.14	-0.13	0.42	0.293							
GLMM3b	**Germinated**					**GLMM4**	**Treatment**				
		Confidence Interval						**Confidence Interval**			
Predictors	**β ± SE**	**2.5%**	**97.5%**	***p-value***		**Predictors**	**β ± SE**	**2.5%**	**97.5%**	***p-value***	
Intercept	-0.86 ± 0.21	**-1.29**	**-0.43**	<0.001	**$R^2_{GLMM(m)}$**	**Intercept**	-0.88 ± 0.30	**-1.46**	**-0.29**	0.003	**$R^2_{GLMM(m)}$**
PS(*A. hyb*)	2.91 ± 0.30	**2.31**	**3.51**	<0.001	49.03	**PS(*A. hyb*)**	2.57 ± 0.34	**2.05**	**3.10**	<0.001	50.75
PS(*E. cap*)	-2.87 ± 0.67	**-4.20**	**-1.55**	<0.001	**$R^2_{GLMM(c)}$**	**PS(*E. cap*)**	-3.54 ± 0.57	**-4.67**	**-2.42**	<0.001	**$R^2_{GLMM(c)}$**
PS(*P. sch*)	-0.64 ± 0.34	-1.31	0.04	0.065	49.03	**PS(*P. sch*)**	-1.12 ± 0.29	**-1.69**	**-0.54**	<0.001	50.75
PS(*P. pec*)	0.34 ± 0.37	-0.39	1.07	0.365		**PS(*P. pec*)**	-0.15 ± 0.30	-0.74	0.43	0.608	
PS(*P. ser*)	-2.86 ± 0.34	**-3.53**	**-2.19**	<0.001		**PS(*P. ser*)**	-3.16 ± 0.31	**-3.79**	**-2.54**	<0.001	
PS(*R. mar*)	-1.04 ± 0.35	**-1.74**	**-0.34**	0.004		**PS(*R. mar*)**	-1.67 ± 0.31	**-2.29**	**-1.05**	<0.001	
BS(RBT)	0.07 ± 0.16	-0.20	0.63	0.307		**BS(RBT)**	0.40 ± 0.34	**0.15**	**1.06**	0.010	
						BS(EG)	0.31 ± 0.28	**0.04**	**0.87**	0.030	

4.3.2 Effect of ingestion on germination

Two candidate models (< Δ2 AICc) were considered equivalent when investigating the effect of gut passage on germination (Appendix 4A: GLMM4). The proportion of germinating seeds was significantly higher in both Egyptian Goose and Red-billed Teal in comparison to the non-ingested control (GLMM4: Table 3) (Fig. 2). Plant species was again also a significant predictor of the differences in the number of seeds germinating. The top model explained 51% of the variance, with no variance attributed to the random effects. The 95% confidence intervals for the total number of germinating seeds were calculated to determine significant differences between the pairs of ingested and control seeds. Significant differences between ingested and non-ingested controls were detected for *P. lapathifolia, P. schinzii* and *R. martima* (Fig. 2).

4.3.3 Effect of retention time

Two candidate models (< Δ2 AICc) were considered equivalent when investigating the effect of retention time on the number of recovered seeds (Appendix 4A: GLMM5). Retention time squared (RT^2) had a significant and negative effect on the number of seeds recovered such that the number of seeds recovered decreased non-linearly with time, and indicates there may be an optimum (GLMM5: Table 3). There was no effect of disperser species or an interaction between disperser and time on the number of recovered seeds. Thirty-eight percent of the variance was explained by the fixed effects, with an additional 5% of variance attributed to the random effects. Finally I checked for an effect of retention time on the number of germinating seeds (GLMM6). The top model selected was the null model, indicating that neither retention time nor disperser species had an effect on seed germination within a particular time interval (results not shown). I also tested if the presence/absence of germination was affected by retention time, and again the top model selected was the null model (results not shown).

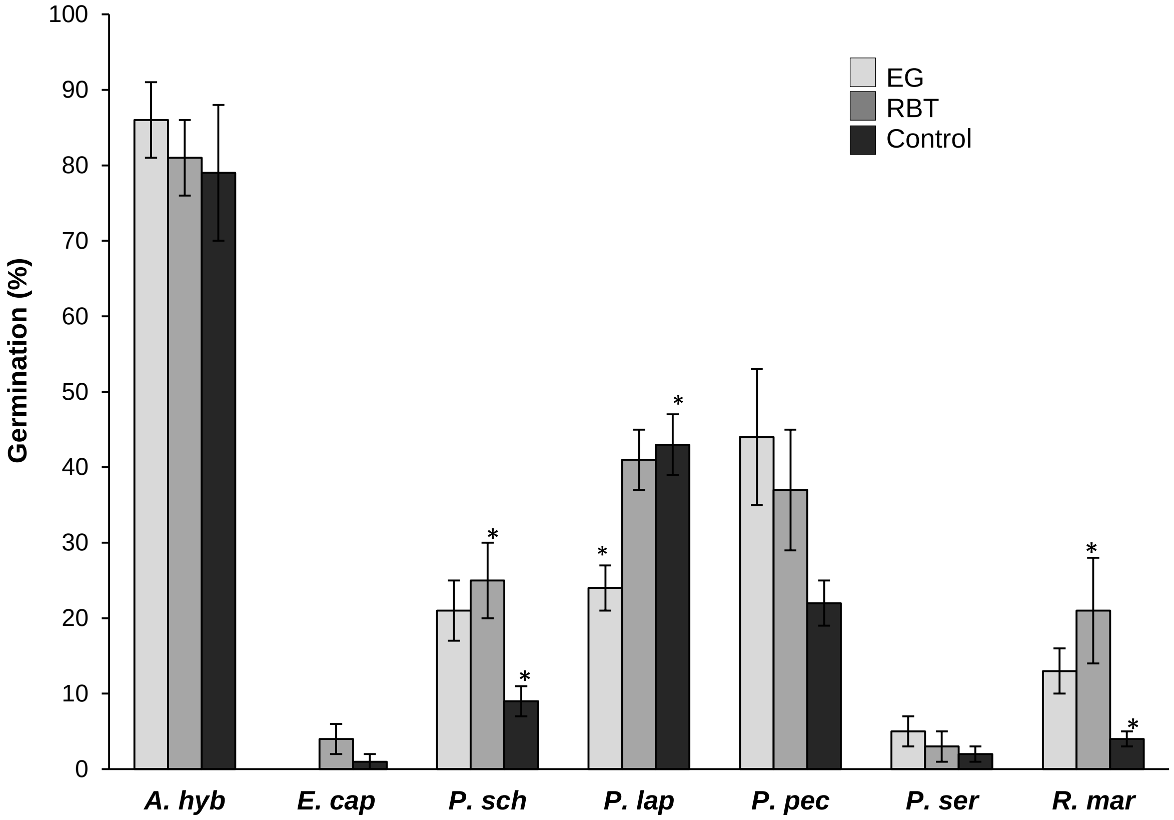

Figure 2 Proportion of seeds germinating (± SE) from non-ingested controls versus ingested by Egyptian Goose and Red-billed Teal. *Indicates a significant difference in germination between a pair. EG = Egyptian Goose, RBT = Red-billed Teal. *A. hyb* = *Amaranthus hybridus*, *E. cap* = *Elegia Capensis*, *P. sch* = *Panicum schinzii*, *P. lap* = *Persicaria lapathifolia*, *P. pec* = *Potamogeton pectinatus*, *P. ser* = *Prionium serratum* and *R. mar* = *Ruppia maritima.*

4.4 DISCUSSION

Egyptian Goose and Red-billed Teal are important endozoochorous dispersers of the seeds of wetland plants in southern Africa. At least some seeds of all plant species fed to the waterfowl passed through the gut intact and later germinated. However, there is an increased risk of seeds being digested at increased retention times; therefore, not all wetland plant species are equally well suited to endozoochorous dispersal. The results of this study support the hypothesis that certain seed traits are better able to facilitate endozoochory by meditating the trade-off between retention time and recoverability. This experimental approach has elucidated the role of seed length, and to a certain degree, seed hardness in facilitating endozoochory at both local and potentially long-distance scales. In addition, the dispersal parameters varied between Egyptian Goose and Red-billed Teal. These results suggest that in addition to seed traits, the characteristics of the waterbird vector are important considerations when explaining patterns of dispersal in wetland ecosystems.

4.4.1 General

The observed range of seed retrieval, 3-72%, was similar to other studies; 0-54% in Soons *et al*. (2008), 2-51% in Wongsriphuek *et al*. (2008) and 2-63% Brochet *et al*. (2010c). The proportion of retrieved seeds that germinated, 0-86% was also similar to the 3-83% found by Brochet *et al*. (2010c). However, comparison of retrieval and germination of *P. lapathifolia*, *P. pectinatus* and *R. maritima* with results from these same plant species in other published feeding trials were less consistent (Charalambidou, Santamaria & Langevoord 2003c; Wongsriphuek *et al.* 2008; Soons *et al.* 2008; Figuerola *et al.* 2010; Brochet *et al.* 2010c). For example, *P. lapathifolia* showed much higher recoverability (61%) when fed to Common Teal *A. crecca* (Brochet *et al*. 2010c) than the Red-billed Teal in our study (27%), but showed nearly 10 times better germinability in Red-billed Teal (41%) when compared to Mallard Duck *A. platyrhynchos* (4.7%) (Wongsriphuek *et al*. 2008). These discrepancies reiterate that differences between vectors in body size, diet and physiology, for example, may be very important in determining the capacity for dispersal amongst a waterbird community. Differences in experimental protocols between the various feeding trials must also be acknowledged.

Retention times of seeds were difficult to compare with the published literature. The average retention time across the experiments does not yield comparative values as this measure is sensitive to late emerging seeds and therefore, dependent on the duration of each trial. A better measure is perhaps the median retention time. Red-billed Teal had highly variable median retention times, but were comparable with results from the Common Teal (3 hours) (Brochet *et al.* 2010c). Despite the common name, the Egyptian Goose is taxonomically a shelduck, and I therefore interpreted the median retention times relative to the largest considered duck species in the literature, the Mallard Duck. Egyptian Goose and the Mallard Duck had comparable median retention times of 4-5 hours (Wongsriphuek *et al.* 2008; García-Álvarez *et al.* 2015). Maximum retention times for both recovered and germinating seeds in Red-billed Teal and Egyptian Goose closely matched the literature with intact and viable seeds of most wetland plant species recovered well after 24 hours (for example Soons *et al*. 2008). However, it must be noted that maximum retention times in this study may be underestimated due to the 36 hour duration of the experiment as seeds have been recorded intact after gut passage times of 96 hours (García-Álvarez *et al*. 2015).

4.4.2 Effect of bird species on dispersal parameters

Both the average and maximum retention time of seeds were significantly shorter in Red-billed Teal than in Egyptian Goose (Table 3). This result could potentially be explained by differences in body size as diet and habitat do not vary considerably between the two vectors (Hockey *et al.* 2005; Chapter 7). Body mass is correlated with the length of the intestines (Demment & Soest 1985; Jackson 1992), and longer intestines increase the time it takes for seeds to pass (Mayhew & Houston 1993), thus we would expect seeds to be retained for longer in larger birds. The average retention time scales with (body mass)^0.25 in birds, and thus with a near fourfold increase in mass between Egyptian Goose and Red-billed Teal one could expect that the former would on average retain seeds 1.4 times longer (Karasov 1990). The estimated average retention time matched this prediction and across all seed species was slightly higher, at 1.8 times longer in Egyptian Goose. Interestingly, the relationship was not constant across the different seed species (Table 2). There was considerable variation in this ratio, from equal retention times recorded for *P. lapathifolia* to a 2.5 times increase in retention time for *E. capensis* between the two waterfowl species. This variation can at least in part be explained by two factors that are not accounted for in the average retention time ~ mass relationship: (1) digestibility of a seed species is not the same for both bird species; and (2) digestion is not constant relative to retention time (Demment & Soest 1985).

Physiology and feeding behaviour, and not only body size, may also be important contributing factors to observed differences between the vectors in retention time and recoverability. That is, seeds are not necessarily retained for longer in Egyptian Goose, but seeds are more readily destroyed at longer retention times in the Red-billed Teal and thus seed are only observed at earlier time intervals. Additionally, low variation in average retention times between seed species ingested by Egyptian goose suggests that there may be an absolute value of gut retention and that at high intake rates seed traits may have less influence on retention times (Karasov 1990). During the experiment both bird species were given free access to food and water, but the geese were observed to more readily feed on the food provided within the cage. Studies in mammalian herbivores have shown that digestibility can be reduced with high intake rates (Demment & Soest 1985). Given access to abundant food Egyptian Goose may trade-off digestive efficiency against consuming a greater overall volume (van Leeuwen *et al.* 2012) and this may also explain why despite the longer retention times, the number of seeds recovered was significantly higher for Egyptian Goose. This would in turn mean that the role of Egyptian Goose in seed dispersal in the natural environment might differ between periods of plenty or scarcity, with greater dispersal potential during periods of plenty. In Red-billed Teal, by contrast, differences in the retention rates and seed recoverability more likely reflect the influence of seed traits. This study provides valuable data on two species that can be used in future analyses on the effect of disperser characteristics on dispersal parameters.

There was no difference between the two bird species in the proportion of seeds that germinated. Furthermore, the germination of seeds significantly increased after ingestion. It has been shown that despite the risks of digestion, gut passage may also increase germinability (Traveset & Verdú 2002). Increased germination following gut passage has been recorded in waterfowl (DeVlaming & Proctor 1968; Brochet *et al.* 2010c), and both mechanical scarring of the seed coat and exposure to digestive enzymes have been identified as important for stimulating germination (Santamaría *et al*. 2002; Kleyheeg 2015). However not all studies have recorded increased germination rates following seed ingestion by waterfowl (Wongsriphuek *et al*. 2008; Soons *et al*. 2008). Further study of adaptations of wetland plant seeds for dispersal should provide important insights into the evolutionary processes underlying bird-mediated dispersal and the variation within these systems (van Leeuwen *et al.* 2012b).

4.4.3 Effect of seed traits and plant species on dispersal parameters

Seed length was a significant predictor of both average retention time and recoverability. Shorter seeds were not only excreted in larger numbers, but also appeared to have longer retention times (Table 3). These results may seem counterintuitive at first, but if one considers that perhaps only short seeds survive at longer time intervals, then the longer retention times for shorter seeds can be more readily interpreted. Thus, short seed length may facilitate endozoochory through two complementary mechanisms. Firstly, shorter seeds are less digestible, leading to higher recoverability; and secondly, lower digestibility suggests shorter seeds can be retained longer in the gut and potentially be dispersed further. Producing large numbers of small seeds is one possible way in which wetland plants can circumvent the negative effects of high retention times needed for long-distance dispersal (Figuerola *et al.* 2010). However, this also represents a trade-off between investment in seed size and number of seeds and ultimately in competitive ability within the new environment and dispersal distance (Jakobsson & Eriksson 2000). I also detected an effect of seed hardness on both average and maximum retention time. This result can be interpreted similarly to the above discussion, with harder seeds being more resistant to digestion and hence more likely to survive at longer retention times. Harder-seeded species however, were not recovered in higher numbers and is again suggestive that retention time is the factor influencing recoverability, but this can be moderated by seed traits such as size and hardness. Small, hard seeded species are perhaps best suited to endozoochory. Small seeds are recovered in high numbers and hard seeds are best able to survive at longer retention times. Thus, whilst seed size is definitely an important determinant of endozoochorous dispersal as noted in many studies (Soons *et al.* 2008; Figuerola *et al.* 2010; Brochet *et al.* 2010c), it is not the only determinant and these results suggest that seed hardness also has a role to play. It is also likely that other seed traits do play important roles in explaining variability amongst plant species in dispersal parameters, but the interrelated nature of these traits makes them difficult to measure.

There was no effect of seed traits on germination. Plant taxon better explained these differences, suggesting that plant species have differing capacity for germination following gut passage and that germination requirements may differ. Seeds that germinated in high numbers in this study were the exotic weed species *A. hybridus* and *P. lapathifolia*, which as fast-growing pioneer species are stimulated to germinate rapidly once favourable conditions return (Barrat-Segretain 1996; Galatowitsch, Anderson & Ascher 1999). However, it must be noted that not all wetland plant species will germinate equally well under these specific experimental conditions, and I may have underestimated viability in this study.

4.4.4 Retention times and implications for dispersal

To test for an effect of retention time on seed dispersal parameters I looked specifically at patterns of retrieval and germination over time. The number of seeds recovered was significantly higher at lower retention times, and is consistent with an increasing risk of digestion at longer retention times (Kleyheeg *et al.* 2014). These results however, suggest that this trade-off between increased retention time and recoverability can be mediated by seed length and hardness. There was no effect of retention time on the number of seeds that germinated in each time interval. This finding was consistent with the idea that if seeds remain intact at longer time intervals germination may actually be enhanced due to increased mechanical or chemical digestion of the seed coat (Brochet *et al*. 2010c).

Retention time is a key factor affecting the survival of seeds through the gut, but it is also a determinant in the eventual distance a seed may be dispersed. Similarly to previous studies, the majority of seeds (96%) were recovered fairly quickly, within 12 hours of ingestion. This result suggests that local dispersal likely occurs more frequently than long-distance dispersal. However, as most wetland plant species investigated here had retention times of greater than 24 hours, some long-distance dispersal is also expected. Therefore, variation in seed traits plays a vital role in determining the shape of the dispersal kernel of wetland plants through their influence on retention time and recovery.

The average and maximum retention times were generally longer in the larger Egyptian Goose and implies that seeds may be dispersed further by this species. Furthermore, Egyptian Goose has a higher mean maximum daily movement rate suggesting seeds can be moved further over a given unit of time, as well as a larger home range (Cumming, Gaidet & Ndlovu 2012). Egyptian Goose would appear to be the better dispersal agent for almost all the seeds species in this study as they retained seeds for longer, had significantly higher recoverability of seeds and move further. However, moving long distances may not be the only relevant factor and key behaviours, such as appropriate habitat selection or preferential seed selection, may also affect seed deposition and establishment (Cousens *et al*. 2010). Furthermore, the different capacities for movement within our chosen waterbird species will likely have important implications for aquatic connectivity such that different vectors facilitate dispersal at different spatial scales (Robledo-Arnuncio *et al*. 2014). The incorporation of movement behaviour and vector feeding ecology into plant dispersal ecology is key to further development in the field (Cousens *et al*. 2010).

4.5 CONCLUSIONS

To my knowledge this is the first experimental feeding trial to investigate rates of gut passage in African duck species. The comparison of these results with other published studies demonstrates that there is still a large amount of variation, especially on the part of differences between vectors, which needs to be investigated further. However, some trends were consistent and it appears that the general role of seed size in moderating recoverability and retention may hold across the different regions. We have made good progress in unravelling the mechanisms by which seed traits may affect dispersal patterns, and future research must turn its attention to the role of the vector. The next key step in developing our mechanistic understanding of dispersal is to fully incorporate vector movement and behaviour. Integrating these feeding trial data with movement data from waterbirds in different landscapes will now enable us to better quantify endozoochorous dispersal and how it may differ in space and time.

Appendix 4A A selection of candidate generalised linear mixed effects models (GLMMs) investigating the effects of bird species, seed characteristics, seed species and retention time on the dispersal parameters of retention time, recoverability and germinability of seeds. Tables list only top candidate models totalling a cumulative corrected Akaike's Information Criteria (AIC$_c$) weight Cum(wt) = 1.00. Models are ranked based on differences in the corrected Akaike's Information Criteria (ΔAIC$_c$). K is the number of estimated parameters, AIC(wt) the weight of each model and LL the -2log-likelihood output for each model. The Null model with no predictor terms, only the constant and random effects, is also included for comparison. The R^2 GLMM (m) or variance explained by only the fixed effects; and R^2 GLMM (c) or variance explained by both fixed and random effects are presented for each model as a measure of fit. **Note:** * indicates an interaction, and describes a model which includes both main effects and the interaction

Fixed Effects	**Fixed Effects**	**Random Effects**
BS = Bird species	SS = Seed species	(1|ID) = Bird individual
BMC = Body mass change index	TT = Treatment	(1|SS) = Seed species
SL = Seed size (length)	RT = Retention time	(T|ID) = Bird individual within time interval
SH = Seed hardness	RT^2 = Retention time squared	

GLMM1a: Average retention time (T$_{AVE}$); Random effects = (1|ID) + (1|SS)

Model (FE)	K	AIC$_c$	ΔAIC$_c$	AIC$_c$(wt)	Cum(wt)	LL	R$^2_{GLMM(m)}$	R$^2_{GLMM(c)}$
BS*SL + SH	8	362.52	0.00	0.20	0.20	-172.45	35.52	40.70
BS + SL + SH	7	362.71	0.23	0.18	0.39	-173.75	33.88	36.92
BS + SL*SH	8	363.78	1.26	0.11	0.49	-173.08	34.82	36.35
BS*SL + SH + BMC	9	364.51	1.99	0.08	0.57	-172.23	35.80	42.15
BS + SL + SH + BMC	8	364.84	2.32	0.06	0.64	-173.61	34.06	38.07
BS	5	364.97	2.45	0.06	0.70	-177.16	24.74	39.17
BS*SL + SH	8	365.07	2.56	0.06	0.75	-173.73	33.91	36.82
BS*SL	7	365.30	2.78	0.05	0.80	-175.03	29.27	42.13
BS + SL	6	365.71	3.20	0.04	0.85	-176.39	27.65	38.53
BS + SL*SH + BMC	9	365.83	3.32	0.04	0.88	-172.89	35.07	37.30
BS + BMC	6	366.84	4.32	0.04	0.91	-176.96	25.00	40.28
BS + SH	6	367.12	4.61	0.02	0.93	-177.10	25.00	39.23
BS*SL + BMC	8	367.17	4.66	0.02	0.95	-174.78	29.54	43.46
BS*SH + SL + BMC	9	367.23	4.71	0.02	0.97	-173.59	34.09	37.96
SL + SL + BMC	7	367.68	5.16	0.02	0.98	-176.22	9.11	41.21
BS + SH + BMC	7	369.03	6.52	0.01	0.99	-176.89	25.25	40.36
BS*SH	7	369.41	6.89	0.01	1.00	-177.08	25.01	39.16
Null	4	380.63	18.11	0.00	1.00	-186.10	0.00	41.20

GLMM1b: Maximum retention time (T_{MAX}); Random effects = (1|ID) + (1|SS)

Model (FE)	K	AIC$_c$	ΔAIC$_c$	AIC$_c$(wt)	Cum(wt)	LL	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
BS + SL + SH	7	206.39	0.00	0.18	0.18	-95.52	20.87	28.93
BS	5	206.56	0.17	0.16	0.34	-97.93	9.10	30.21
BS + SL	6	207.93	1.54	0.08	0.43	-97.46	11.90	30.00
BS + SL*SH	8	207.98	1.59	0.08	0.51	-95.11	22.68	29.43
BS*SL + SH	8	208.30	1.91	0.07	0.58	-95.27	21.25	29.29
BS + SL + SH + BMC	8	208.65	2.26	0.06	0.63	-95.45	20.96	29.13
BS + SH	6	208.67	2.28	0.06	0.69	-97.83	9.91	30.23
BS + BMC	6	208.70	2.31	0.06	0.75	-97.85	9.21	30.51
BS*SH + SL	8	208.79	2.41	0.05	0.80	-95.52	20.87	28.94
BS*SL	7	209.73	3.34	0.03	0.83	-97.19	12.32	30.18
BS + SL + BMC	7	210.12	3.74	0.03	0.86	-97.39	12.01	30.25
BS + SL*SH + BMC	9	210.25	3.86	0.03	0.89	-95.02	22.83	29.61
BS*SL + SH + BMC	9	210.66	4.27	0.02	0.91	-95.22	21.32	29.46
BS + SH + BMC	7	210.87	4.48	0.02	0.93	-97.76	9.96	30.52
BS*SH	7	211.01	4.62	0.02	0.95	-97.83	9.86	30.25
BS*SH + SL + BMC	9	211.12	4.73	0.02	0.96	-95.45	20.96	29.14
BS*SL + BMC	8	212.02	5.63	0.01	0.97	-97.13	12.40	30.41
BS*SH + BMC	8	213.26	6.87	0.01	0.98	-97.75	9.97	30.54
Null	4	213.40	7.01	0.01	0.99	-102.47	0.00	28.88

GLMM2: Recovered; Random effects = (1|ID) + (1|SS)

Model (FE)	K	AIC$_c$	ΔAIC$_c$	AIC$_c$(wt)	Cum(wt)	LL	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
BS + SL	6	768.58	0.00	0.19	0.19	-377.83	33.33	36.49
BS *SL	7	768.69	0.11	0.18	0.38	-376.72	33.94	37.18
BS + SL + BMC	7	769.81	1.24	0.11	0.48	-377.28	33.58	36.90
BS*SL + BMC	8	769.83	1.25	0.10	0.59	-376.11	34.24	37.64
BS + SL + SH	7	770.05	1.47	0.09	0.68	-377.40	33.81	36.46
BS*SL + SH	8	770.19	1.61	0.09	0.77	-376.28	34.45	37.16
BS + SL + SH + BMC	8	771.32	2.74	0.05	0.82	-376.85	34.06	36.87
BS*SL + SH + BMC	9	771.37	2.79	0.05	0.87	-375.66	34.74	37.63
BS*SH + SL	8	771.48	2.90	0.05	0.91	-376.93	34.01	36.46
BS + SH*SL	8	771.66	3.08	0.04	0.95	-377.02	34.17	36.58
BS*SH + SL + BMC	9	772.80	4.22	0.02	0.98	-376.38	34.27	36.87
BS + SL*SH + BMC	9	773.11	4.54	0.02	1.00	-376.53	34.39	37.00
SL*SH + BMC	8	777.35	8.78	0.00	1.00	-379.87	32.43	36.73
Null	4	793.59	25.01	0.00	1.00	-392.58	0.00	37.04

GLMM3b: Germinated; Random effects = (1|ID)

Model (FE)	K	AIC_c	ΔAIC_c	AIC_c(wt)	Cum(wt)	LL	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
SS	9	378.21	0.00	0.61	0.61	-179.00	49.03	49.03
BS + SS	10	379.69	1.47	0.29	0.91	-178.47	49.07	49.07
BS + SS + BMC	11	382.18	4.02	0.08	0.99	-178.44	49.11	49.11
BS*SS	16	386.91	8.70	0.01	1.00	-173.78	49.60	49.61
Null	3	508.49	130.28	0.00	1.00	-251.11	0.00	0.00

GLMM4: Treatment (TT); Random effects = (1|ID)

Model (FE)	K	AIC_c	ΔAIC_c	AIC_c(wt)	Cum(wt)	LL	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
TT + SS	11	558.27	0.00	0.66	0.66	-267.11	50.75	50.75
SS	9	559.64	1.37	0.33	0.99	-270.13	50.07	50.62
TT*SS	23	566.31	8.04	0.01	1.00	-255.40	52.49	52.49
Null	3	758.81	200.53	0.00	1.00	-376.32	0.00	0.00

GLMM5: Recovered/time; Random effects = (T|ID)

Model (FE)	K	AIC_c	ΔAIC_c	AIC_c(wt)	Cum(wt)	LL	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
RT^2	6	1977.97	0.00	0.64	0.64	-982.91	37.55	42.58
$BS + RT^2$	7	1979.79	1.82	0.26	0.90	-982.79	37.71	42.62
$BS*RT^2$	8	1981.72	3.75	0.10	1.00	-982.72	37.49	42.11
Null	5	2033.05	55.08	0.00	1.00	-1011.47	0.00	34.43

CHAPTER 5

TAILS OF TRAVELLING SEEDS: INCORPORATING TAXONOMIC AND SPATIAL VARIATION INTO PATTERNS OF SEED DISPERSAL BY WATERBIRDS

ABSTRACT

The spatial distribution of dispersed seeds has significant consequences for plant population structure and dynamics. For many plant species, animal-mediated dispersal is a vital mechanism by which seeds are moved to new habitat. Patterns of animal movement represent a key component of plant dispersal patterns and the effect of spatiotemporal variation in animal movement on seed dispersal distances is of particular interest. In aquatic systems, waterbirds play a pivotal role in the dispersal of aquatic plant seeds. However, little is known about the spatial distribution of waterbird-dispersed seeds and how it varies with dispersal vectors and across different landscapes. I developed a simple mechanistic model combining feeding trial data with high-resolution GPS telemetry data to investigate the seed dispersal distances of two southern African waterfowl species Egyptian Goose *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha* across five study populations in southern Africa. Potential local scale dispersal was strongly favoured, with mean dispersal distances below 5 km in all instances. However, both waterfowl species also demonstrated a high potential capacity for long-distance dispersal (LDD), with seeds capable of being moved up to 500 km from the source. Red-billed Teal typically had shorter mean dispersal distances, as expected from their smaller home ranges, but showed similar LDD distances to Egyptian Goose. Furthermore, there was high variation between the study populations in dispersal distances (both local and LDD). These results demonstrate that southern African waterfowl may play an important role in connecting aquatic habitats at both local and landscape scales. However, different waterbird vectors provide different dispersal functions, and these differ greatly across landscapes. Integrating taxonomic and spatio-temporal variation into spatial patterns of dispersal is central to our understanding of the fates of animal dispersed seeds.

5.1 INTRODUCTION

Seed dispersal is an essential process for plant species with consequences that influence gene flow, adaptation and connectivity, and facilitate the shifting or expansion of geographic ranges (Robledo-Arnuncio *et al.* 2014). The spatial distribution of dispersed seeds sets the template for future demographic processes, such as predation, germination, growth and reproduction (Nathan & Muller-Landau 2000), yet knowledge of factors affecting the spatial distribution of seeds and their consequences for dispersal outcomes remains limited (Campos-Arceiz *et al.* 2008). In most ecosystems a large proportion of the plant community is reliant on vertebrates for the dispersal of seeds (Howe & Smallwood 1982). However, despite the critical role animal-mediated dispersal plays in organising plant communities our ability to predict dispersal by animals remains elusive (Cousens *et al.* 2010). This is in part because patterns of seed dispersal emerge from complex interactions between the characteristics of the dispersed seeds and vector movement behaviour (Côrtes & Uriarte 2013).

It is useful to be able to quantify the spatial distribution of dispersed seeds because seed dispersal can have significant consequences for a plant population's spatial structure and dynamics (Russo, Portnoy & Augspurger 2006). The determination of seed dispersal distances constitutes the most basic spatial descriptor of dispersal (Nathan *et al.* 2012). The statistical distribution of dispersal distances in a population, the dispersal kernel, is the probability density function (PDF) describing the distribution of post-dispersal locations relative to a source point (Nathan & Muller-Landau 2000). Dispersal kernels provide basic information about the scale of dispersal (Nathan *et al.* 2012), demonstrating the scale(s) at which seeds are dispersed as well as the frequency and extent of long-distance dispersal (LDD) events.

Patterns of animal movement are an important component of passive dispersal and are therefore a key influence on dispersal kernels. The effect of spatio-temporal variation in animal movement on seed dispersal distances deserves further attention (Côrtes & Uriarte 2013), as differences in animal movement patterns between seasons and in different habitats can alter the shape and scale of the dispersal kernels. For example, Mueller *et al.* (2014) demonstrated that the dispersal service provided by Trumpeter Hornbills *Bycanistes bucinator* in fragmented forests differed between the breeding and non-breeding seasons, with inter-patch connectivity decreasing during the breeding season. Furthermore, it is now acknowledged that for most plant species multiple vectors contribute to dispersal (Robledo-Arnuncio *et al.* 2014), with each vector dispersing seeds at different scales and contributing differentially to the overall dispersal kernel of a given plant species (*sensu* Jordano *et al.* 2007; Spiegel & Nathan 2007). Improvements in determining the fates of animal dispersed seeds therefore requires integration of spatio-temporal and taxonomic variation in animal movements into estimates of dispersal distances (Côrtes & Uriarte 2013; Robledo-Arnuncio *et al.* 2014).

In aquatic ecosystems, waterbirds are important dispersal vectors for wetland plants via both endozoochory and ectozoochory (Brochet *et al.* 2010b; Raulings *et al.* 2011; van Leeuwen *et al.* 2012b) and undertake frequent and directed movements between wetlands (Figuerola & Green 2002a). Waterbirds in this way provide connectivity between hydrologically isolated catchments. However, seed dispersal by waterbirds is not constant between vector species and is also subject to spatio-temporal variation, for example between geographical regions and seasons (Brochet *et al.* 2009; Viana *et al.* 2013b). Several previous studies that investigated the dispersal distances of aquatic organisms by waterbirds make unrealistic estimates of the scale of dispersal as they fail to accurately account for waterbird movement (Charalambidou *et al.* 2003c; Soons *et al.* 2008). These studies provided approximations of dispersal distances by combining gut retention times with maximum sustained flight speeds of dispersal vectors. More recent attempts at modelling dispersal by waterbirds use ringing recovery data, and proved useful in describing how the scale of long-distance dispersal (LDD) varied during migration between North America and Europe (Viana *et al.* 2013b). Moreover, these data demonstrate that differences in dispersal distances also arise due to differences in the movement capacity of the waterbird vectors (Viana *et al.* 2013a).

Whilst some progress has been made in determining the spatial patterns of seeds dispersed by waterbirds, the number of studies is still very limited and even fewer studies have acknowledged the influence of spatio-temporal or taxonomic differences on dispersal distances (but see Viana *et al.* 2013b; Kleyheeg 2015 for examples). I used a simple mechanistic model to describe and compare the dispersal distances of wetland plants dispersed by two waterfowl species in southern Africa. The dispersal kernels were derived by incorporating two key processes affecting endozoochorous dispersal into the model; vector movement and gut retention time (Cousens *et al.* 2010). Movement data were available in the form of high-resolution GPS satellite data from the tracking of two Afrotropical waterfowl species, Egyptian Goose *Alopochen aegyptiaca* and Red-billed Teal *Anas erythrorhyncha* across five study populations in southern Africa. The gut retention data are described in Chapter 4; the seeds of five common wetland plant species were fed to Egyptian Goose and Red-billed Teal and gut passage of the seeds was monitored through time.

To investigate the effects of taxonomic and spatial variation on dispersal distances, I firstly tested whether the dispersal distances and characteristics of the dispersal kernels differed between the two vector species, as well as intra-specifically for different plant species. I predicted that dispersal distances would be further for Egyptian Goose than Red-billed Teal, due to the goose's higher daily movement distances and faster flight speeds (Cumming *et al.* 2012). Thus, Egyptian Goose and Red-billed Teal might contribute differentially, but complementarily to the total dispersal kernels of wetland plants. Secondly, for each vector, I tested for differences in the dispersal kernels across the five study populations (three for Red-billed Teal). Cumming et al. (2012) showed that different populations of Egyptain Goose and Red-billed Teal have varying movement patterns in accordance with the population from which they were tagged. Thus, I expected that dispersal distances would differ by site due to differences in the movement strategies of the vectors across the different populations (Cumming *et al.* 2012; Ndlovu 2012). These kernels provide the first estimates of the dispersal distances of wetland plants brought about by seed dispersing waterfowl anywhere in Africa.

5.2 MATERIALS AND METHODS

5.2.1 Study sites and study populations

Egyptian Geese and Red-billed Teal were fitted with satellite GPS platform transmitter terminals (PTTs; Microwave Telemetry Inc., Columbia, MD, USA) at several wetland sites in southern Africa; (1) False Bay Ecology Park (Strandfontein – STR) (34°04' S 18°30' E), (2) Barberspan Nature Reserve (BAR) (26°35' S 25°34' E) and (3) Lake Manyame (MAN) (17°49' S 30°36' E), and included (4) Jozini Dam (JOZ) (27°20' S 31°54' E) and (5) Voëlvlei Dam (VOE) (33°21' S 19°02' E) as additional tagging sites for Egyptian Geese (Fig. 1) (Appendix 5A).

The tagging locations span approximately 17 and 14 degrees of latitude and longitude respectively and are situated in different biomes and agricultural regions (Cumming *et al.* 2012) (Fig. 1). Rainfall seasonality also differs between the sites. The Strandfontein and Voëlvlei sites are situated within the Fynbos biome and experience a Mediterranean climate with hot, dry summers and mild, wet winters. Barberspan, Jozini and Lake Manyame typically receive summer rainfall (Appendix 5B). The populations of Egyptian Goose and Red-billed Teal at each of the tagging sites can be considered independent from each other as overlap between the bird populations appears to be rare, as suggested from both ringing recoveries (Oatley & Prys-Jones 1986; Underhill *et al.* 1999; Ndlovu *et al.* 2013) and telemetry data (Cumming *et al.* 2012) (Fig. 1). Furthermore, there is asynchrony within each population in the peak timing of breeding and moulting (Ndlovu 2012; Ndlovu *et al.* 2013). Egyptian Geese from Strandfontein and Voëlvlei do however show some overlap in trajectories (Fig. 1a), but based on a three month difference i.e. January versus April respectively, in the peak numbers of moulting individuals between the two sites, I continued to treat them as separate populations (Appendix 6B).

5.2.2 Feeding trial

The gut retention time (GRT) data, as well as data on recoverability and germinability of the seeds of different wetland plants, was obtained from my previous research in Chapter 4. Briefly, seeds of five widespread and common wetland plants (*Amaranthus hybridus, Persicaria lapathifolia, Potamogeton pectinatus, Panicum schinzii* and *Ruppia maritima*) were experimentally fed to captive Red-billed Teal and Egyptian Geese. For each experimental replicate 100 seeds per plant species were force fed to different individuals, with each plant species fed seven times to each bird species. The droppings were collected over increasing time intervals starting 2 hours after force feeding and ending after 36 hours. The droppings were processed by washing through a set of stacked sieves and all intact propagules removed, counted and later set into germination trials under controlled conditions. The proportion of seeds that passed through the birds intact and the proportion of these intact seeds that later germinated were multiplied to calculate the probability of germination for each time interval (Fig. 2). These five plant species are common in the diet of Egyptian Goose and Red-billed Teal (Chapter 7), and many were also noted to be dispersed by these bird species via endozoochory (Chapter 2). I used only the GRT of germinating seeds in the dispersal kernels as only germinating seeds will lead to successful dispersal events. However, it is important to note that this may underestimate effective dispersal as not all species germinated equally well under the experimental conditions. Additionally the original experiment included GRT estimates for *Elegia capensis* and *Prionium serratum*; however, both were excluded from this analysis as these species are confined to the Cape Floristic Region and had very poor germination success in the experiment.

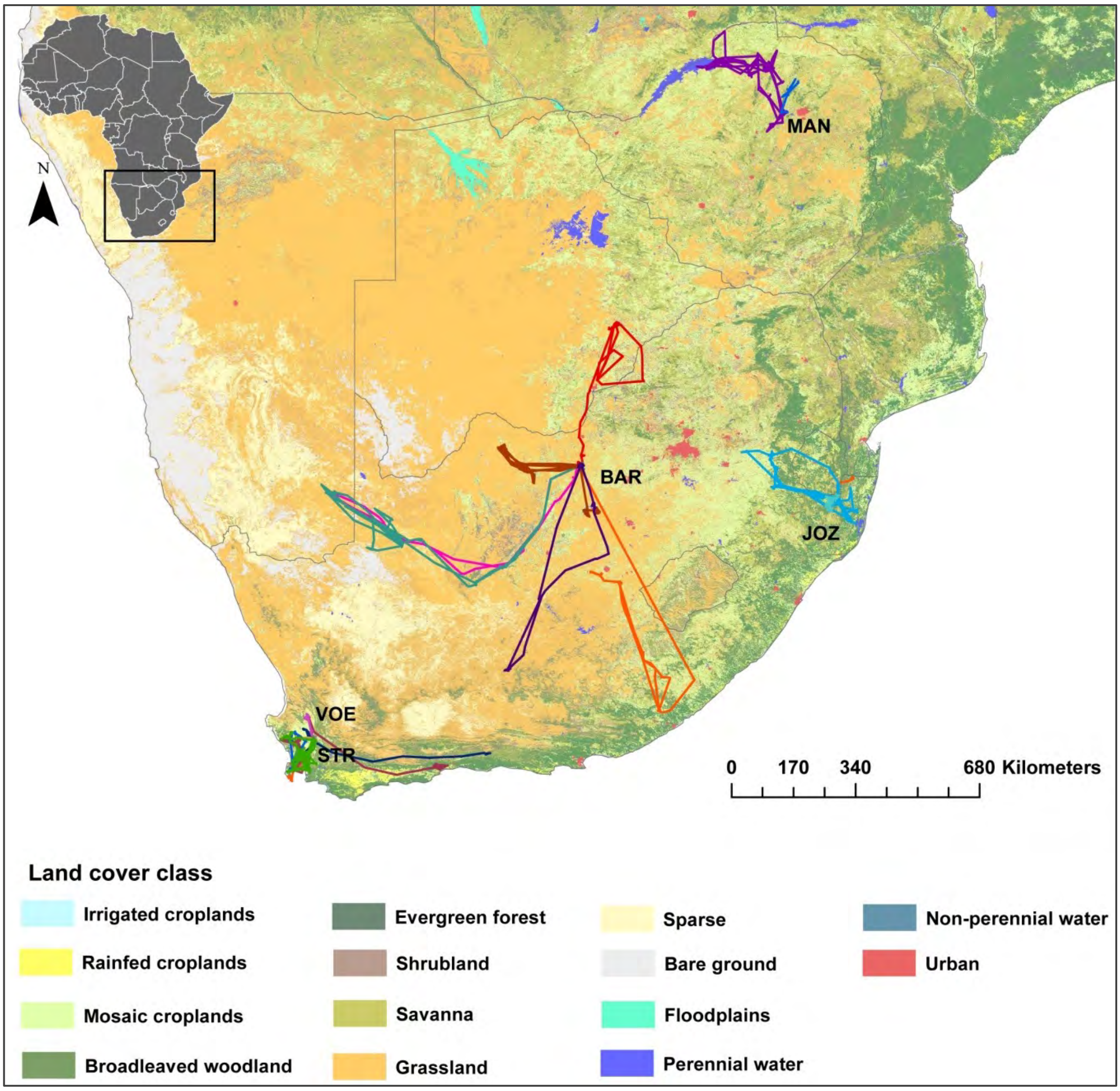

Figure 1a Satellite telemetry movement paths of Egyptian Goose tagged at five locations in southern Africa. Land cover data derived from the GlobCover dataset available at 300 m resolution (Arino *et al*. 2012). BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = False Bay Ecology Park/Strandfontein and VOE = Voëlvlei Dam.

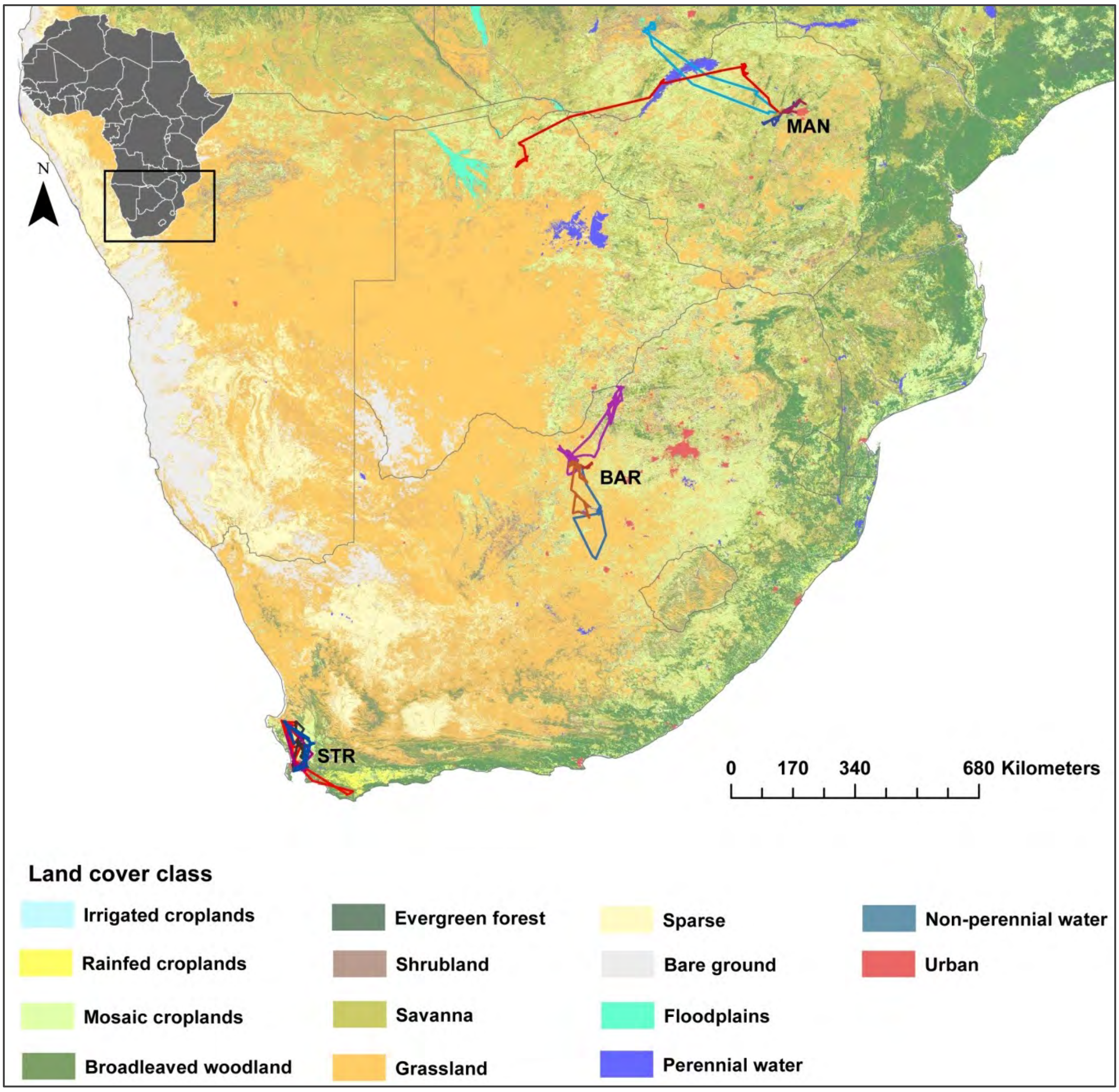

Figure 1b Satellite telemetry movement paths of Red-billed Teal tagged at three locations in southern Africa. Land cover data derived from the GlobCover dataset available at 300 m resolution (Arino *et al*. 2012). BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = False Bay Ecology Park/Strandfontein and VOE = Voëlvlei Dam.

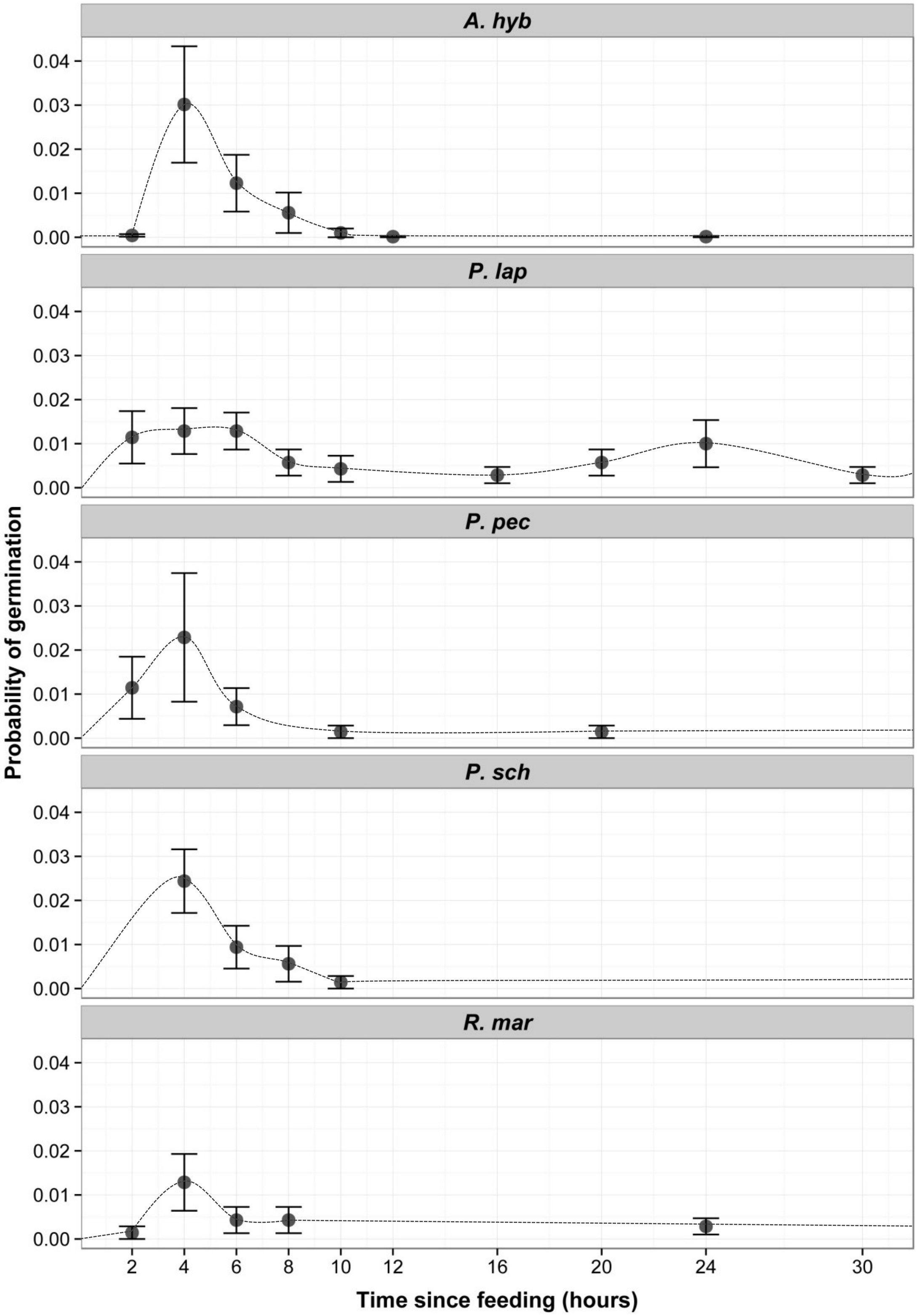

Figure 2a Gut retention times of germinating seeds force fed to Egyptian Goose *A. hyb* = *Amaranthus hybridus, P. lap = Persicaria lapathifolia, P. pec = Potamogeton pectinatus, P. sch = Panicum schinzii* and *R. mar = Ruppia maritima*. Probability of germination in *A. hyb* is under represented as it was rescaled by a factor of 10 for both bird species to fit on the same axis as the other four plant species. Dashed line indicates trend over time.

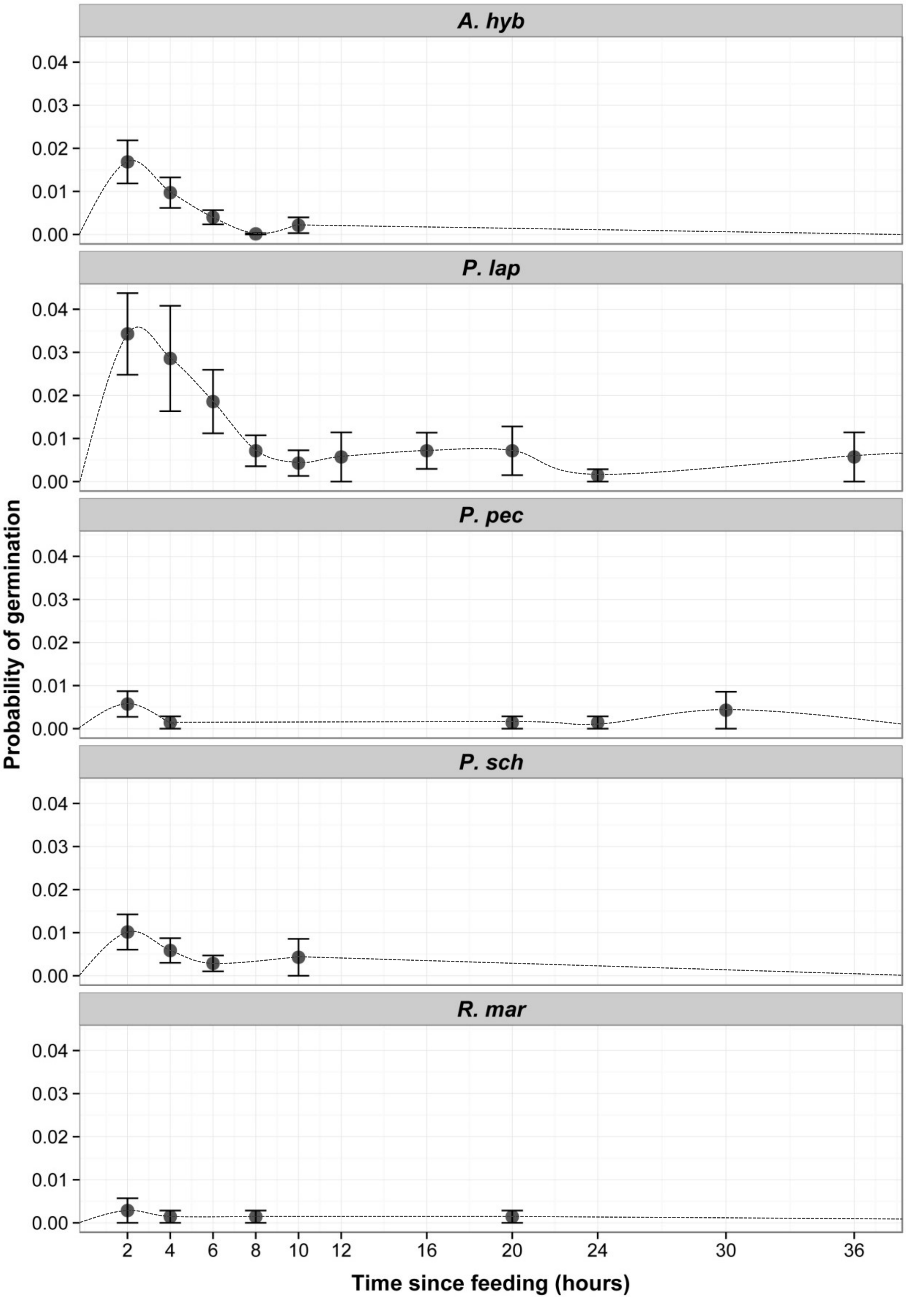

Figure 2b Gut retention times of germinating seeds force fed to Red-billed Teal. *A. hyb = Amaranthus hybridus, P. lap = Persicaria lapathifolia, P. pec = Potamogeton pectinatus, P. sch = Panicum schinzii* and *R. mar = Ruppia maritima*. Probability of germination in *A.* was rescaled by a factor of 10 for both bird species to fit on the same axis as the other four plant species, real range 0 – 0.4. Dashed line indicates trend over time.

5.2.3 Telemetry and analysis movement data

Birds were captured using either maize-baited walk-in traps or mist nets and transmitters were attached using a backpack harness made from Teflon ribbon; 30-g PTT for Egyptian Geese; 22-g PTT for Red-billed Teal. Transmitters were set to capture a GPS location every 2 h (30-g PTTs) or every 4 h (22-g PTTs) and transmit data to the Argos satellite every 3 to 5 days (see Cumming & Ndlovu 2011 for details). The majority of tracked individuals were tagged in 2008 as part of a study on waterbird movement and avian influenza (Cumming *et al.* 2011). Additional tracking sites were added in 2012 and 2013, hence the difference in tracking periods for Voëlvlei and Jozini Dams (Appendix 5A)

All individuals with at least 30 full days of tracking data were included in the subsequent analyses and resulted in sample sizes of $N = 23$ for Egyptian Geese and $N = 15$ for Red-billed Teal (Appendix 5A). In total, all sites had greater than 15 full days of continuous tracking data per month, with the exception of Voëlvlei for which there was no data in February and March. In total 7292 days (ca. 20 years in total) of GPS tracking data were used to create the eventual dispersal kernels

Movement trajectories were analysed using the R package *adehabitatLT* (Calenge 2006). Missing fixes were common in the data and I used the package's *cutltraj* function to segment the trajectories into continuous tracks. For each individual bird, the data thus comprised a set of trajectories each listing successive relocation co-ordinates, a straight-line distance moved between successive time steps and a displacement from the start of each trajectory.

5.2.4 Data analysis

5.2.4.1 Estimation of dispersal kernels

The dispersal kernels were estimated using similar methods to Westcott & Graham 2000; Westcott *et al.* 2005; Kays, Jansen & Knecht 2011; Lenz *et al.* 2011; Breitbach *et al.* 2012. The displacement distributions for each Egyptian Goose and Red-billed Teal were calculated first. Typically studies select a number of random starting points across the entire trajectory and calculate the Euclidean distance to the end point based on a distribution of gut retention times (Westcott & Graham 2000). However, we know that animal behaviour, and particularly the time of day when animals forage has a significant effect on the dispersal kernels produced (Westcott *et al.* 2005; Kays *et al.* 2011). Therefore feeding events were inferred from the daily movement patterns of the birds, from which I determined the start times for the model (Fig. 3). To do this the average distance moved in each 2-hour interval (4-hour interval for the Red-billed Teal) was plotted over a 24-hour period across all the sites. The daily movement patterns for each bird species are highly conserved across the sites and demonstrate a strong diurnal signal. For Egyptian Geese the pattern was interpreted as early morning transit to the foraging grounds, followed by a late morning return to the roost site, followed again by late afternoon forage and subsequent return to roost site. These assumptions are supported by data from intensive field counts, from the same study sites, which show increases in numbers of loafing birds around the middle of the day (Ndlovu, Cumming & Hockey 2014). Start times for the model were therefore selected as representing foraging at 4 am, 6 am, 8 am, 2 pm, 4 pm and 6 pm. For Red-billed Teal, the pattern was more difficult to interpret as the time intervals between successive relocations were much longer. However, the data suggest birds fly out to foraging grounds and spend the majority of the day foraging, before finally flying back to a roost site in the late afternoon. I thus selected 6 am, 10 am and 2 pm as starting times.

To produce the displacement distributions, random start points were drawn from the movement trajectory of each individual bird based only on the selected forage times above. The number of random start points drawn was constrained by the available data per tracked individual and was ten times the number of full days tracked: i.e., random start points (*n*) = (days tracked x 10), which gave between 310 and 4720 points. The displacement distribution data were thus weighted, with individuals that were tracked for a longer duration contributing more to the eventual dispersal kernels. For each randomly selected start point the displacement from a starting co-ordinate to the location each individual had 2, 4, 6, 8, 10, 12, 16, 20, 24, 30 and 36-hours later was determined, following established methods (Westcott & Graham 2000; Westcott *et al.* 2005; Kays *et al.* 2011; Raulings *et al.* 2011; Lenz *et al.* 2011; Breitbach *et al.* 2012). The time intervals coincide with the time intervals in the GRT experiment and resulted in a set of 11 full displacement distributions per tracked individual. Unfortunately, GPS positions for Red-billed Teal were captured every four hours and therefore only eight displacement distributions at 4, 8, 12, 16, 20, 24 and 36-hour time intervals could be produced.

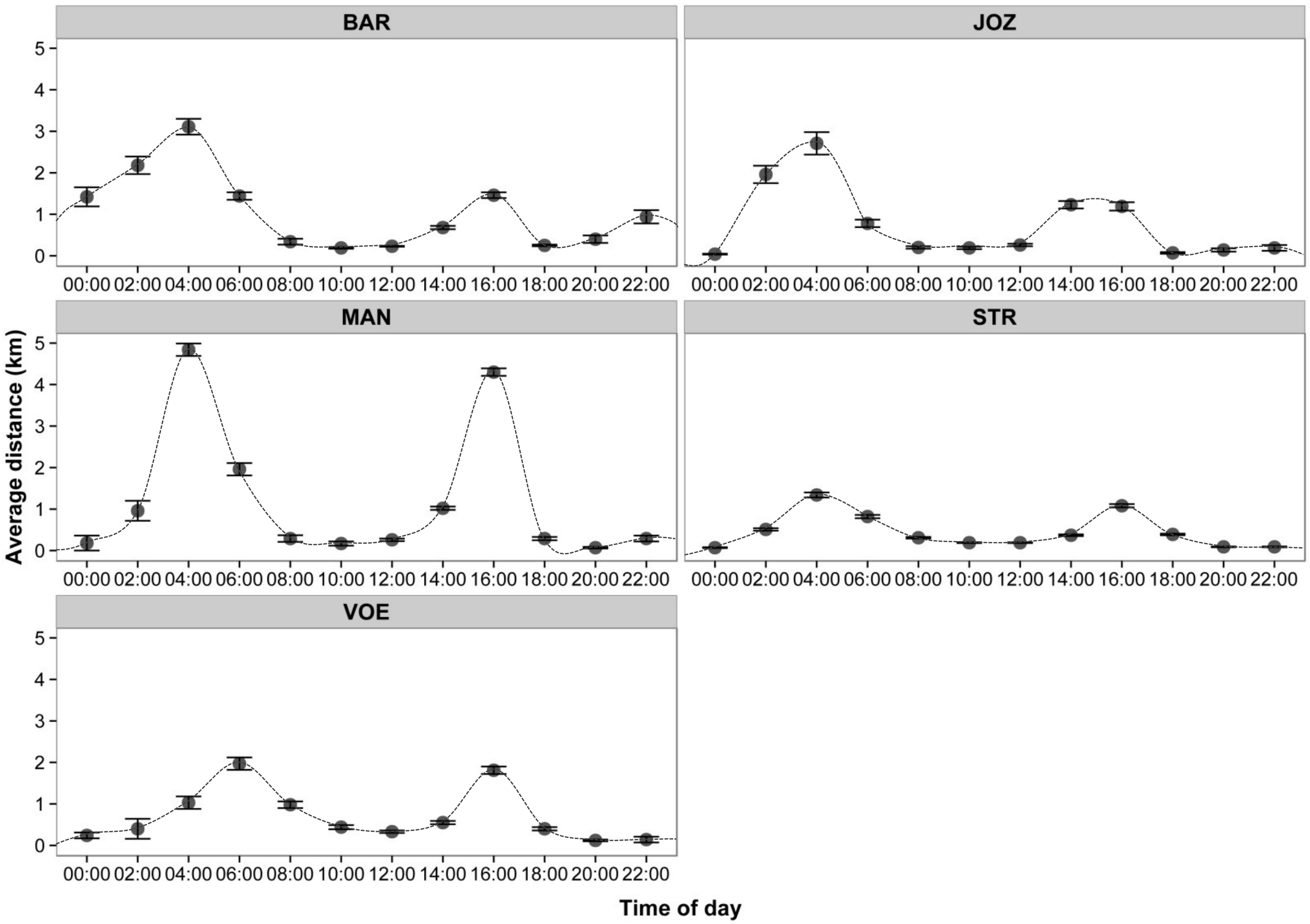

Figure 3a Daily movement patterns for Egyptian Goose tagged at five locations in southern Africa. BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = Strandfontein and VOE = Voëlvlei Dam. Dashed line indicates trend over time

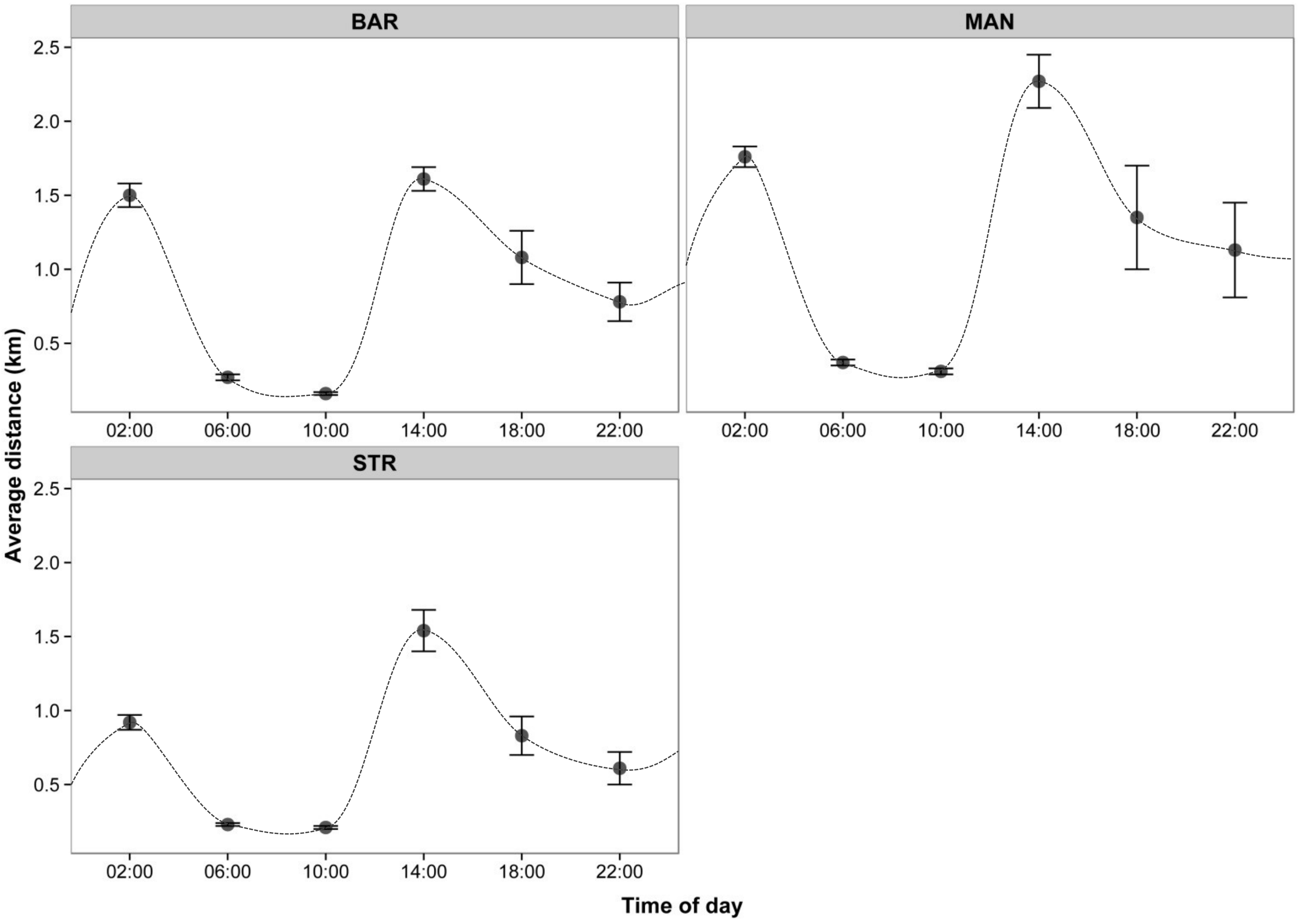

Figure 3b Daily movement patterns for Red-billed Teal tagged at three locations in southern Africa. BAR = Barberspan Nature Reserve, MAN = Lake Manyame and STR = Strandfontein. Dashed line indicates trend over time.

The individual displacement distributions of each individual were then combined with the GRT data at each matched time interval. For each seed species and at each time interval I produced a list of germination probabilities of equivalent length to the *n* random start times above through bootstrapping the raw GRT data (Fig. 2). Therefore, for each displacement distribution at each time interval there was a randomly sampled germination probability. To create the final dispersal kernel the displacement distributions and germination probabilities were combined based on matched times. All instances where a germination probability was zero resulted in a null dispersal event and were removed from the data. This procedure weights the eventual dispersal kernel by the GRT distribution and only allows dispersal events at distances where seeds pass through the gut and germinate. For both Egyptian Geese and Red-billed Teal, the dispersal kernels were calculated separately for each individual bird and then later combined to produce a realised dispersal kernel for each of the five plant species (Fig. 4). It is recognised that there is significant variability across individual level dispersal kernels. I therefore also undertook a nonparametric bootstrap of the individual kernels to find confidence bands and estimate dispersal parameters for each vector and plant species combination. These dispersal parameters are very similar to the parameters of the full kernel (Appendix 5D Table 1). To explore differences between study populations similar methods were used, but the displacement distributions were now determined for separately each study site. Dispersal kernels for each study population were determined for only one seed species, *P. lapathifolia* (Fig. 5). However, the dispersal parameters for all other seed species and study population combinations are listed in Appendix 5D (Table 2).

5.2.4.2 Statistical analysis

To describe the dispersal kernels mathematically the dispersal distances were log transformed to reduce skew and each distance distribution was fitted to five different continuous probability density functions (PDF: normal, lognormal, Weibull, gamma and Cauchy) using maximum likelihood estimates (Lenz *et al.* 2011). The AIC for each fitted distribution was calculated with the R package *fitdistrplus* (Delignette-Muller, Dutang & Pouillot 2015) and the best fitting density function was selected based on the lowest AIC value (Appendix 5C). The skew and the 95% confidence intervals of the shape and scale parameters of the selected PDF were calculated to describe the distribution (Table 1 & 2).

To test for differences between the relevant dispersal kernels I used two approaches. Firstly, a Kolmogorov-Smirnov two-sample test (KS-test) was used to determine whether the distributions of dispersal distances were statistically different to each other. Secondly, I described and compared differences in the mean, median and maximum dispersal distances, as well as the frequency of long distance dispersal (LDD) events > 100 km (Table 1 & 2). Comparisons were conducted only between different levels of each single factor; i.e. (1) between waterfowl species for the same plant species, (2) among plant species within the same waterfowl species, and (3) among different study populations for the same plant species and waterfowl species.

All modelling and statistical analysis were conducted in R statistical software version 3.2.2 (R Core Team 2015).

Table 1 Dispersal kernel parameters for five wetland plants dispersed by Egyptian Goose and Red-billed Teal. The mean, median and maximum dispersal distances for each of the kernels are shown, along with the percentage of all dispersal events that are further than 100 kilometres from the source. The parameters of the Wiebull distribution characterising each dispersal kernel are described by the 95% confidence intervals for the shape and scale parameters as well as a measure of skew. A negative skew indicates left skewed kernels and positive skew indicates right skewed kernels. *A. hyb = Amaranthus hybridus, P. lap = Persicaria lapathifolia, P. pec = Potamogeton pectinatus, P. sch = Panicum schinzii* and *R. mar = Ruppia maritima*.

Goose **Plant**	**Mean ± se (km)**	**Median (km)**	**Max (km)**	**> 100km (%)**	**Shape 2.5%**	**Shape 97.5%**	**Scale 2.5%**	**Scale 97%**	**Skew**
A. hyb	2.98 ± 0.03	0.67	472	0.26	4.02	4.06	3.07	3.09	-0.03
P. lap	3.55 ± 0.03	0.70	470	0.47	3.92	3.96	3.10	3.11	0.04
P. pec	2.72 ± 0.04	0.61	373	0.21	3.93	3.99	3.03	3.05	-0.01
P. sch	2.75 ± 0.04	0.63	461	0.18	4.01	4.06	3.06	3.08	-0.04
R. mar	2.91 ± 0.03	0.66	442	0.30	3.92	3.98	3.06	3.07	0.04
Teal									
A. hyb	1.46 ± 0.03	0.38	222	0.05	3.88	3.95	2.81	2.83	0.06
P. lap	2.75 ± 0.05	0.50	426	0.23	3.71	3.76	2.94	2.96	0.13
*P. pec**	2.51 ± 0.13	0.39	425	0.24	3.59	3.70	2.89	2.92	0.27
P. sch	2.09 ± 0.06	0.42	416	0.15	3.85	3.96	2.79	2.81	-0.04
R. mar	2.36 ± 0.06	0.41	226	0.11	3.73	3.85	2.93	2.97	0.04

*Shape and scale are for a fitted gamma distribution

Table 2 Dispersal kernel parameters for *P. lapathifolia* dispersed by Egyptian Goose and Red-billed Teal across different locations in southern Africa. The mean, median and maximum dispersal distances for each of the kernels are shown, along with the percentage of all dispersal events that are further than 100 kilometres from the source. The parameters of the Wiebull distribution characterising each dispersal kernel are described by the 95% confidence intervals for the shape and scale parameters as well as a measure of skew. BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = False Bay Ecology Park/Strandfontein and VOE = Voëlvlei Dam.

Site	Mean ± se (km)	Median (km)	Max (km)	> 100km (%)	Shape 2.5%	Shape 97.5%	Scale 2.5%	Scale 97.5%	Skew
Goose									
ALL	3.55 ±0.03	0.70	470	0.47	3.92	3.96	3.10	3.11	0.04
BAR*	5.03 ±0.16	0.51	373	1.50	9.14	9.51	3.35	3.49	0.32
JOZ*	3.27 ±0.08	0.35	219	0.41	9.94	10.31	3.77	3.91	0.82
MAN	4.01 ±0.07	1.12	123	0.07	4.44	4.45	3.31	3.33	-0.16
STR	1.63 ±0.02	0.44	64	0.00	4.03	4.09	2.91	2.93	0.73
VOE	4.65 ±0.12	1.68	346	0.57	5.58	5.69	3.44	3.46	-0.42
Teal									
ALL	2.75 ±0.05	0.50	426	0.23	3.71	3.76	2.94	2.96	0.13
BAR	2.33 ±0.06	0.34	204	0.11	3.28	3.36	2.86	2.89	0.20
MAN	3.32 ±0.15	0.85	426	0.26	4.40	4.51	3.14	3.17	-0.08
STR	2.10 ±0.07	0.34	223	0.26	3.69	3.77	2.84	2.86	0.32

*Shape and scale are for a fitted gamma distribution

5.3 RESULTS

5.3.1 Differences between vectors

The dispersal kernels were leptokurtic, favouring local dispersal (median < 1 km; mean < 5 km) and in most cases with a long tail to the right (Table 1 & Fig. 4). The mean value is much larger than the median value due to the long-tailed nature of the dispersal distributions (Fig. 4 & 5). The fat-tailed Weibull distribution was the best fit to the kernels, with the exception of the dispersal distribution of *P. pectinatus* by Red-billed Teal that was best fitted by a gamma distribution (Appendix 5C).

Pairwise KS-tests of the dispersal distributions for each plant species between Egyptian Goose and Red-billed Teal were highly statistically significant (all $D > 0.07$; all $p < 0.001$). For all plant species both the median and mean dispersal distances were significantly longer for Egyptian Geese than Red-billed Teal (Mann-Whitney *U* test: W=25, $p = 0.008$ & W=23.5, $p = 0.03$ respectively). The maximum dispersal distances between the two bird species were not significantly different (Mann-Whitney *U* test: W=22, $p = 0.06$) and in one instance, *P. pectinatus*, Red-billed Teal were projected to disperse seeds nearly 50 km further than the Egyptian Goose. The proportion of LDD over 100 km was relatively high (1 in every 200 to 2000 dispersal events, depending on the plant species) and again was not significantly different between the bird species (Mann-Whitney *U* test: W=21, $p = 0.10$), which may be expected due to the rarity of these events.

For Egyptian Goose, all pairwise KS-tests between the dispersal distributions of the different plant species were significantly different (all $D > 0.09$; all $p < 0.005$). The plant species *P. lapathifolia* had the longest mean and median dispersal distances and was a close second to *A. hybridus* for the longest dispersal distance. For Red-billed Teal only the dispersal kernels for *P. lapathifolia* and *R. maritima* could be considered equivalent ($D = 0.008$; $p = 0.584$), whilst the remainder of the kernels were significantly different (all $D > 0.02$; all $p < 0.009$). Again, *P. lapathifolia* had the longest mean, median and in this instance maximum dispersal distance.

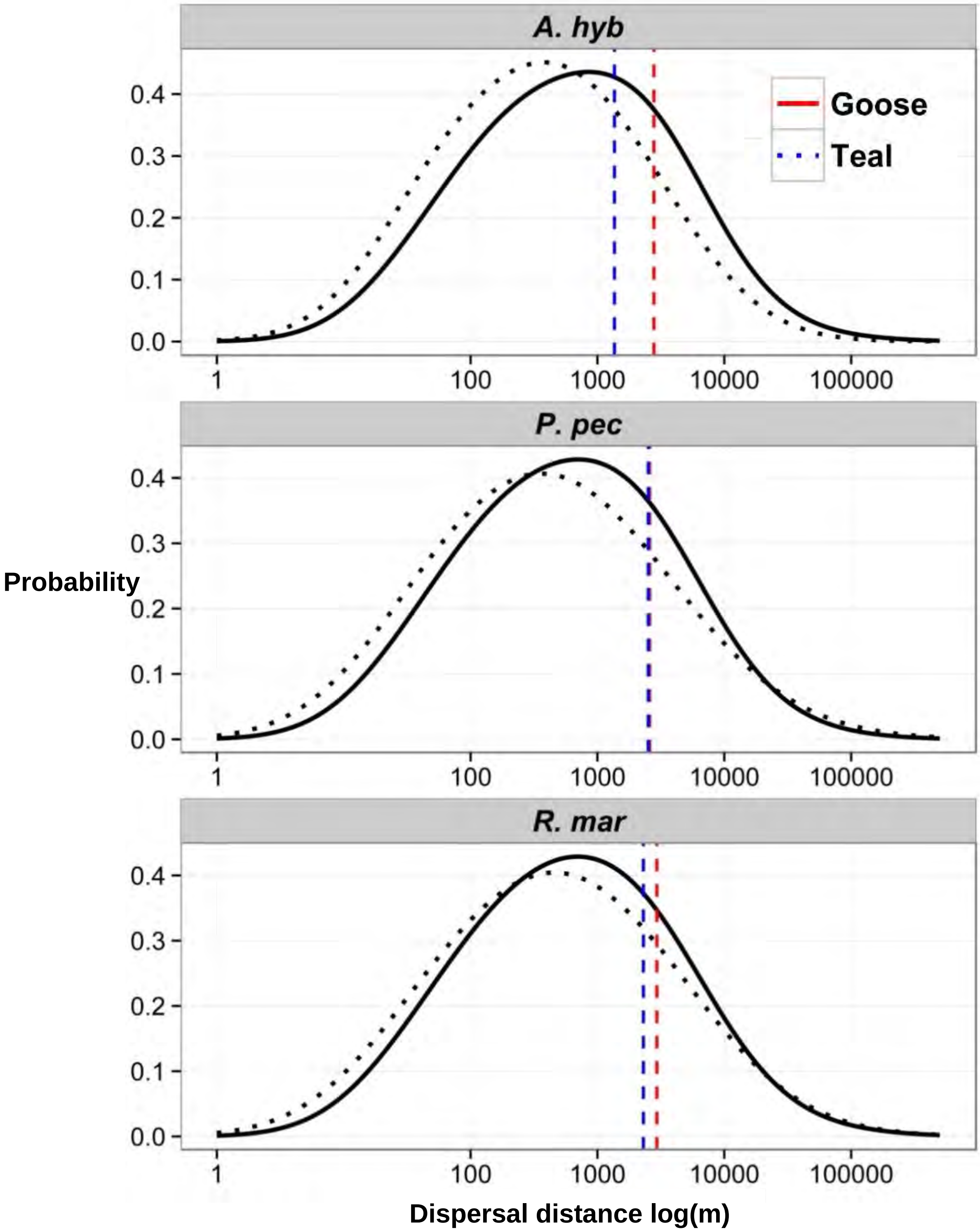

Figure 4a-c Dispersal kernels for *A. hyb* = *Amaranthus hybridus, P. pec* = *Potamogeton pectinatus* and *R. mar* = *Ruppia maritima*. Solid and dotted curve represent kernels of Egyptian Goose and Red-billed Teal respectively. Red and blue vertical-intercept represents the mean dispersal distances for each plant species by Egyptian Goose and Red-billed Teal respectively. Note: plotted kernels are modelled data.

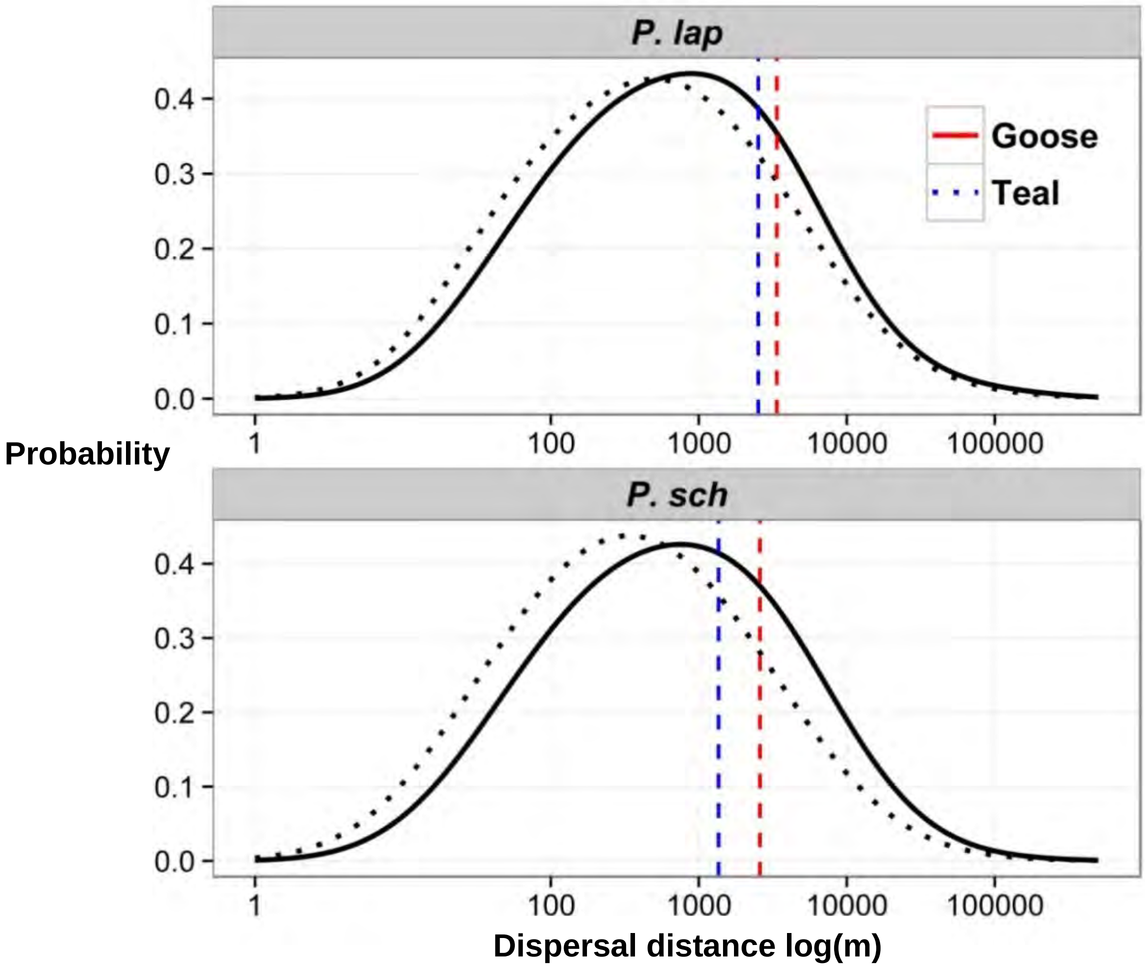

Figure 4d-e Dispersal kernels for *P. lap* = *Persicaria lapathifolia* and *P. sch* = *Panicum schinzii*. Solid and dotted curve represent kernels of Egyptian Goose and Red-billed Teal respectively. Red and blue vertical-intercept represents the mean dispersal distances for each plant species by Egyptian Goose and Red-billed Teal respectively

5.3.2 Differences between study populations

The dispersal kernels showed remarkably high variation between the study sites (Table 2 & Fig. 5). The kernels were again leptokurtic, with long tails to the right. The Weibull distribution was the best fit to the majority of kernels, with the exception of the dispersal kernels for the Barberspan and Jozini populations of Egyptian Goose, which were better fitted to a gamma distribution (Appendix 5C).

Pairwise comparisons of the dispersal kernels for each study site were all significantly different for both Egyptian Goose (all $D > 0.05$; all $p < 0.001$) and Red-billed Teal ($D > 0.06$; all $p < 0.001$). Note, pairwise comparisons were only conducted between sites for which tracking times were comparable, thus Voëlvlei and Jozini were excluded from this comparison. Egyptian Geese tagged at Barberspan had the highest mean and maximum dispersal distances, these birds showed a remarkable ability for long-distance dispersal with approximately 2% of all dispersal distances over 100 km (Table 2). Egyptian Geese tagged at Strandfontein had the shortest mean dispersal distances and a maximum dispersal distance of only 64 km. Voëlvlei and Manyame had much higher median dispersal values than from other sites. For Red-billed Teal, the mean, median and maximum dispersal distances were further for the Manyame site, and were similar for Barberspan and Strandfontein sites (Table 2). Similar differences occur for all other seed species across the study populations (Appendix 5D).

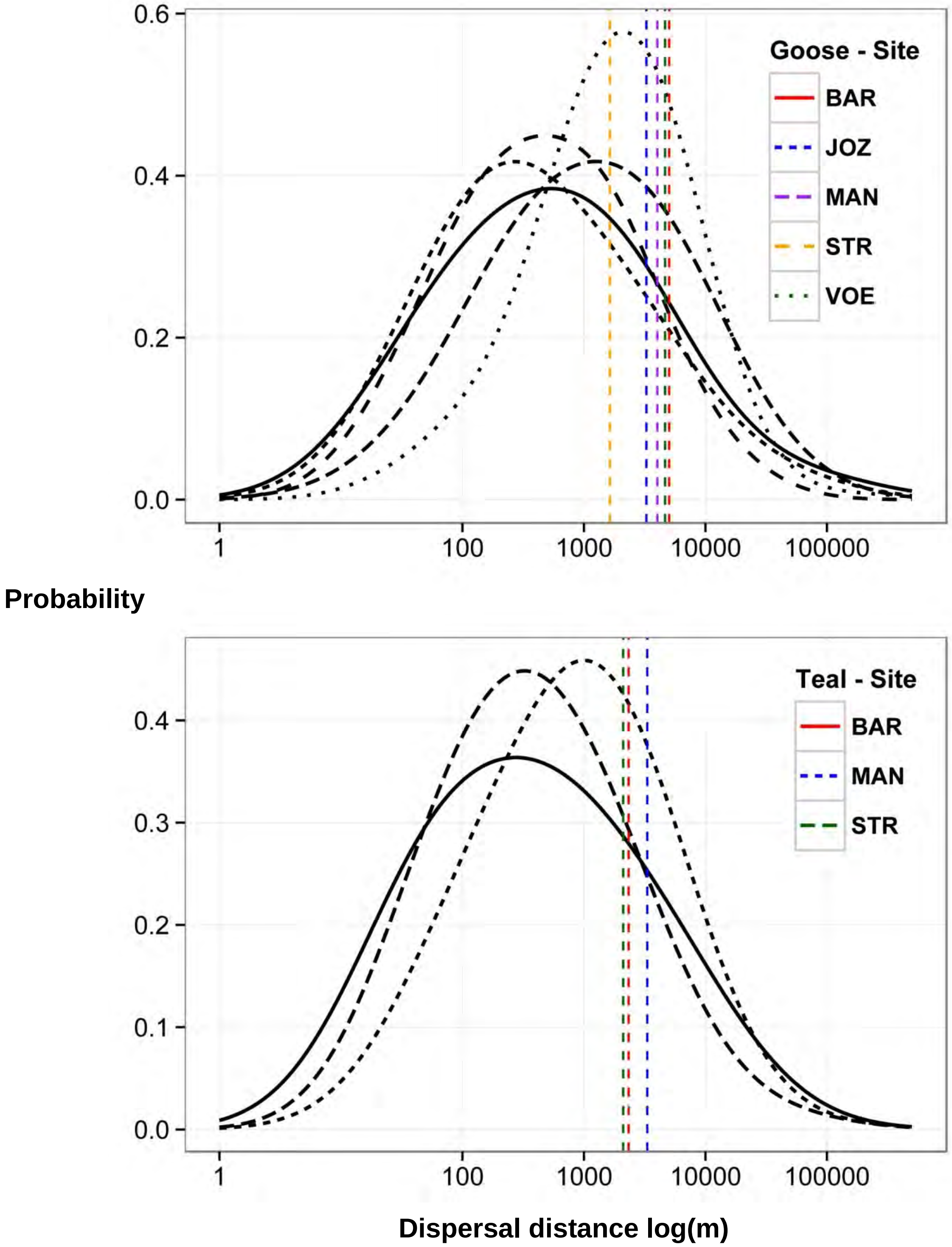

Figure 5 Dispersal kernels for *Persicaria lapathifolia* by Egyptian Goose and Red-billed Teal across different study populations. Line type represents the different study population. Vertical coloured line represents the mean dispersal value for each kernel. BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = False Bay Ecology Park/Strandfontein and VOE = Voëlvlei Dam. Note: plotted kernels are modelled data.

5.4 DISCUSSION

My simple mechanistic model incorporating gut retention data and GPS movement data illustrates the potential scale(s) of dispersal of wetland plants by waterbirds in southern Africa for the first time. The dispersal kernels were distinctly leptokurtic, suggesting that local dispersal on the scale of a few kilometres is most common. However, the kernels were also fat-tailed, demonstrating the potential extent of long-distance dispersal in the system (Fig 4 & 6), with wetland plants capable of being dispersed nearly 500 km from a source point. Whilst these LDD values might be surpassed by the incredible dispersal distances presented for migratory waterfowl in Europe and North America (up to 3000 km) (Viana *et al.* 2013b a), their value in connecting isolated wetland patches in arid southern Africa should not be underestimated. These LDD events may have an especially important role as climate and land-use change drive further fragmentation of wetlands, and by default the biotic communities they support (Strayer & Dudgeon 2010). Additionally, the LDD events could have important consequences for the spread of alien plants.

A substantial proportion of modelled dispersal events occur to >100 km from a point of origin. Considering the population sizes of Red-billed Teal and Egyptian Goose, which number in the millions of individuals in southern Africa, the frequency of LDD might be very high indeed, even if only 1 in every 2000 dispersal events is >100 km. The significance of these LDD events is however dependent on successful colonisation of the new habitat. While LDD is touted as the key factor describing why freshwater aquatic plants have particularly extensive geographic ranges (Santamaría 2002), it has also been shown that high levels of genetic differentiation still occur between these populations despite their excellent dispersal capacity (De Meester *et al.* 2002). Such patterns have not yet been explored for southern Africa, where the temporary nature of many wetlands might exclude common barriers to establishment such as priority effects (De Meester *et al.* 2002). Population genetics of aquatic plant communities across hydrologically isolated catchments might provide interesting insights into the relevance of LDD facilitated by waterbirds in arid landscapes.

5.4.1 Comparing approaches

To my knowledge, this study constitutes the first description of the patterns of seed dispersal by waterbirds using empirical movement data collected at fine resolution for several bird species and across different landscapes. Typical approaches in the past estimate dispersal curves by multiplying flight speeds with gut retention times and focus on variation introduced by seed characteristics or in the flight speeds of different vector species (Charalambidou *et al.* 2003c; Soons *et al.* 2008). These methods, which have been shown to produce estimates that are in the range of the dispersal distances predicted for migratory waterbirds (Viana *et al.* 2013b a), may grossly overestimate dispersal distances for non-migratory waterfowl. For example, based purely on the flight speeds of nomadic Grey Teal *Anas gracilis* and Pacific Black Duck *Anas superciliosa* in Australia, Raulings *et al.* (2011) reported that approximately 10% of dispersal events would occur at >100 km from the source. For southern Africa, the probability of dispersal events >100 km was much lower (between 1.5% and 0.05%; Table 1 & 2).

Reliable estimates of the scale of local dispersal cannot be determined utilising maximal flight speeds and travel distances alone. Although LDD can have effects which are disproportionally important to its low frequency (Higgins *et al.* 2003; Nathan *et al.* 2008b), local dispersal is by far the most common process. For example, Kleyheeg (2015) utilised GPS tracking data to model seed dispersal in non-migrating Mallard Duck *Anas platyrhynchos* in the Netherlands and found median seed dispersal distances between 600 m and 3 km in different landscapes. The cyclical daily movement patterns of non-migrating waterfowl, interpreted as a succession of foraging bouts and returns to a roosting area, constrain flight distances such that the majority of dispersal events occur within a few kilometres of the foraging and/or roosting sites. The use of GPS tracking technology here and in the Kleyheeg (2015) study allowed for the inclusion of specific patterns of daily bird movement into predictions of seed dispersal and provided a more accurate assessment of the scale(s) at which waterbirds disperse propagules. These results therefore suggest that aquatic plant meta-communities are likely to be relatively well connected over short distances with waterbirds utilising a well-defined core area (Raulings *et al.* 2011).

Typically mechanistic models are a useful indirect way of estimating where seeds may be deposited from a given origin (Cousens *et al.* 2010). However, as with all modelling approaches, limitations do arise from the simplifications and assumptions that are adopted. Firstly, the GRT data were acquired from birds in captivity and since vector activity (swimming or flying) moderates the time taken for propagules to pass through the gut, this model may underestimate dispersal distances (van Leeuwen, Tollenaar & Klaassen 2012; Kleyheeg *et al.* 2014). Secondly, seeds can be retained well beyond 36 hours (over 96 hours has been recorded (García-Álvarez *et al.* 2015) and maximum dispersal distances may have again been underestimated. Thirdly, the model assumes that seeds retrieved at a particular retention time were evacuated at that specific time. This is not the case, as seeds were evacuated sometime between the last collection and when the next sample is collected and, at longer time intervals we may overestimate the distances that seeds are dispersed. Lastly, the larger periods between successive relocations in the Red-billed Teal telemetry data made interpretation of the daily movement patterns more difficult and reduced the amount of GRT data that could be used in the analysis. Therefore, it is possible that the Red-billed Teal dispersal distances are also over- or underestimated.

5.4.2 Differences between vectors

The estimated dispersal kernels of the five wetland plants were different between the two waterfowl vectors. Red-billed Teal typically had shorter mean and median dispersal distances than Egyptian Goose (Table 1 & Fig. 4). This finding was not surprising given the longer mean daily movements, larger home ranges and further ranging movements of Egyptian Goose (Cumming *et al.* 2012), and matched my predictions. However, while variation in the dispersal distances is in part due to differences in the movement capacity between the two vector species, the influence of the shorter gut retention times and a lower recoverability of seeds for Red-billed Teal should not be discounted (Chapter 4). These results are consistent with studies exploring the roles of multiple frugivores on seed dispersal distances, which suggest that dispersal distance increases with body size as increasing size is correlated with larger home ranges and longer retention times (Westcott & Graham 2000; Jordano *et al.* 2007; Spiegel & Nathan 2007). Therefore, bird species can switch roles as a function of spatial scale and provide complementary dispersal services to a particular plant species (Spiegel & Nathan 2007). In addition, birds moving at different scales might themselves form different dispersal functional groups, i.e. long- and short-distance dispersal groups. A difference in the median dispersal distance of a few hundred meters may seem trivial for highly mobile waterfowl, but it suggests that Red-billed Teal disperse seeds two-thirds the distance that Egyptian Goose do. Furthermore, differences in mean dispersal distances can be up to 1.5 km further by Egyptian Goose. These seemingly small differences might have important consequences for plant communities during dry-downs, for example, as surface water becomes less available and seeds need to disperse further to reach new habitats.

Surprisingly, across all plant species the proportion of LDD events and the maximum dispersal distances was not significantly different between the vectors. However, if we consider each plant species separately then large differences in the scale of LDD emerge. For example, *A. hybridus* and *R. maritima,* have maximum dispersal distances in Red-billed Teal of half that shown for the same plant species in Egyptian Goose. Since we can assume that the vectors do not differ considerably in their long distance movement capacity as the other three plant species illustrate LDD on comparable scales, then it is likely that if ducks are their primary dispersal agent then GRT and recoverability of the plant species affect their scale of dispersal. For endozoochory of wetland plants this finding reiterates that dispersal is a complex interaction between the characteristics of the seeds and both vector movement and seed handling (Cousens *et al.* 2010).

Differences in the gut retention times of the various propagule species had a considerable influence on the dispersal kernels (Table 1). Variation between seed-producing plant species in dispersal is common. For example the seed dispersal kernels of 11 plant species dispersed by southern Cassowary *Casuarius casuarius* in Australia showed distinct differences in dispersal distances (Westcott *et al.* 2005). Seed characteristics such as size, shape and hardness mediate digestion resulting in small differences in gut passage times that can have important implications for patterns of dispersal (Wongsriphuek *et al.* 2008; Soons *et al.* 2008). In this study, *P. lapathifolia* had the longest dispersal distances across both vector species. The seeds of this plant are very hard with a high number of seeds retrieved and germinating at later time intervals (Chapter 4) that favour it towards longer dispersal distances. As landscapes become increasingly fragmented and the distribution of surface water changes through altered land-use or climate regimes these kinds of trait may come under increasing selective pressure as they facilitate successful dispersal and reduce inbreeding depression (Baguette *et al.* 2013). Therefore, certain wetland plant species may be more resilient to increasing fragmentation, whilst for others increased distances between habitable wetland patches results in negative feedbacks in selection, further exacerbating the lack of connectivity.

5.4.3 Differences between study populations

The variance observed in movement patterns across the different study populations for different vector species was enough to affect the estimated scale of seed dispersal (Table

2 & Fig. 5). For those study sites for which pairwise comparisons of the dispersal kernels were possible, significant differences in mean, median, and maximum dispersal distances across the study populations was considerable. Differences between the study populations also appeared to be more pronounced for Egyptian Geese. Interestingly, the scale of dispersal could vary by as much as six times when moving between study populations for this species in both local and long distance dispersal. The high proportion of dispersal events > 100 km in Egyptian Geese from Barberspan appears to be driven by the long distances that many of these birds move between the moult site and their "home" areas (Cumming *et al.* 2012). Alternatively, the longer dispersal distances seen for the Barberspan population may also be indicative of more arid landscapes, where surface water is less available than in wetter parts of the region. Median dispersal distances were longest for the Voëlvlei and Manyame populations. Dispersal distances have been shown to be longer for example in fragmented habitats as birds must move a greater distance between core habitat patches (Lenz *et al.* 2011; Kleyheeg 2015), and similar dynamics might explain the observed differences amongst these study populations. This may suggest that there is also a threshold distance above which waterbodies become increasingly isolated and connectivity depends on the rarer LDD events (*sensu* Breitbach *et al.* 2012). Red-billed Teal from Manyame similarly showed longer dispersal distances; a common element, landscape structure, is a driver of movement amongst waterbirds from this population. In any case, the variation in dispersal distances between the different study populations suggests remarkably different patterns of aquatic connectivity across these landscapes.

Birds in the different populations have differing movement strategies that are shaped by both intrinsic (e.g. navigation capacity) and external (e.g. rainfall) factors and result in different patterns of dispersal (Nathan *et al.* 2008a). These intrinsic and extrinsic drivers of animal movement provide a useful basis for formulating hypotheses about how dispersal distances might vary across different landscapes. For example, a key external factor that might affect waterfowl movement could be surface water availability. The presence of water is an essential habitat resource for all waterfowl and one might predict that dispersal distances would be larger in more arid landscapes, corresponding with vectors ranging further to find water (Roshier & Reid 2003). The study populations occur in markedly different landscapes, falling within different biomes, agricultural regions, and climatic zones. Therefore, there are a multitude of other environmental factors which may affect the scale of waterbird movement for example habitat fragmentation (Lenz *et al.* 2011; Kleyheeg 2015) or differing resource distributions (Campos-Arceiz *et al.* 2008). On the other hand Cumming *et al.* (2012) suggested that internal factors such as moult site fidelity and not resource fluctuations drive variation in Egyptian Goose and Red-billed Teal movement across the same study sites. Research on the drivers of waterbird movement in southern Africa, and how these factors affect the scale of seed dispersal, is a key future direction. Furthermore, despite obvious temporal variation in fecundity in many plant species (e.g. mast seeding), studies addressing temporal variation in seed dispersal are rare (Côrtes & Uriarte 2013). Acknowledging temporal variability in movement within a population for example between seasons (Campos-Arceiz *et al.* 2008) or life history stages (Mueller *et al.* 2014) and how these align with plant lifecycles will further enhance the accuracy with which we can make predictions about the scale of seed dispersal.

In conclusion, waterbirds in southern Africa have an important role in connecting aquatic communities at both local and landscape scales. Different waterbird vectors provide different dispersal services, and these differ greatly across landscapes. Furthermore, differences in dispersal services are likely to become more pronounced as we consider the effects of other waterbird vectors, both within the Anatidae and other waterbird families (e.g. Charadriiformes – waders, gulls and terns). My results reiterate the need to consider spatio-temporal and taxonomic variation in studies of seed dispersal and to identify important and unifying principals that govern movement and dispersal across a diversity of species (Côrtes & Uriarte 2013).

Appendix 5A Details of individual GPS-tagged Egyptian Geese (EG) and Red-billed Teal (RBT). Start and end date refers to the time period of the tracking data used in this study. Total fixes is the total number of relocations over the study period. Days refers to the total number of days used in this study with a full set of relocations per day (i.e. 12 for EG and 6 for RBT). The mean daily movement (mean/day) and maximum movement (max/day) distances was also calculated for each tracking period. PTT = transmitter identity. BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = False Bay Ecology Park/Strandfontein and VOE = Voëlvlei Dam.

PTT	Species	Site	Start (m/d/Y)	End (m/d/Y)	Total Fixes	Days	Mean/ day (km)	Max/ day (km)
77127	EG	BAR	06/07/2008	05/10/2010	5884	149	4.4	251
77128	EG	BAR	06/22/2008	12/02/2011	6199	254	11.4	272
77129	EG	BAR	06/07/2008	05/15/2009	3373	100	18.1	228
77130	EG	BAR	11/09/2008	06/04/2010	4427	180	14.7	177
77132	EG	BAR	06/07/2008	04/14/2010	4176	85	8	137
7712202	EG	BAR	10/23/2008	05/30/2009	2051	71	8.9	196
7711702	EG	JOZ	05/04/2012	09/20/2012	1661	136	2.4	43
7712002	EG	JOZ	05/04/2012	01/31/2014	6843	330	14.6	187
7712102	EG	JOZ	05/05/2012	09/03/2012	1300	104	1.1	8
7713302	EG	JOZ	05/04/2012	02/19/2013	2985	195	3.3	34
77125	EG	MAN	05/07/2008	05/31/2011	10400	410	14.1	262
77126	EG	MAN	05/07/2008	12/26/2008	2671	187	10.5	507
77094	EG	STR	01/12/2008	05/01/2009	3831	143	4.8	320
77095	EG	STR	01/12/2008	01/03/2009	3339	222	5.5	368
77134	EG	STR	12/01/2008	12/30/2013	6616	374	3.3	64
77135	EG	STR	12/01/2008	02/08/2011	8326	314	5.5	90
7711802	EG	STR	01/17/2009	10/11/2010	4257	193	6.6	76
7712302	EG	STR	12/05/2008	06/02/2009	1736	119	3.6	38
7713301	EG	STR	12/04/2008	04/27/2009	1474	55	8.7	94
7711602	EG	VOE	04/17/2013	10/27/2013	2265	180	10.1	287
7711902	EG	VOE	04/17/2013	08/30/2013	1595	128	8.4	194
7712402	EG	VOE	04/18/2013	07/29/2013	1201	96	8.7	59
7712602	EG	VOE	04/18/2013	01/31/2014	3261	262	7.1	31
77101	RBT	BAR	04/09/2008	09/28/2008	636	31	5.8	124
77102	RBT	BAR	04/10/2008	04/20/2010	4107	515	5.1	208
77111	RBT	BAR	07/25/2008	12/09/2008	651	60	1.5	5
77112	RBT	BAR	06/07/2008	05/15/2009	1772	210	4.5	17
77115	RBT	BAR	10/11/2008	07/15/2009	1360	143	6	70
77103	RBT	MAN	05/05/2008	08/24/2008	598	63	14	343
77104	RBT	MAN	05/05/2008	01/25/2009	1416	166	9.8	435

PTT	Species	Site	Start (m/d/Y)	End (m/d/Y)	Total Fixes	Days	Mean/ day (km)	Max/ day (km)
77106	RBT	MAN	05/06/2008	07/25/2009	2584	360	4.9	82
77108	RBT	MAN	05/06/2008	08/29/2008	624	85	6	37
77109	RBT	MAN	05/07/2008	12/24/2008	1294	168	5.6	30
77092	RBT	STR	03/12/2008	03/26/2009	1774	256	6.7	178
77093	RBT	STR	03/12/2008	09/07/2008	985	122	3.3	20
77098	RBT	STR	03/14/2008	11/24/2009	3531	472	3.5	83
77099	RBT	STR	03/14/2008	05/15/2009	985	122	3.3	20
77100	RBT	STR	03/14/2008	04/16/2009	2005	232	3.4	72

Appendix 5B

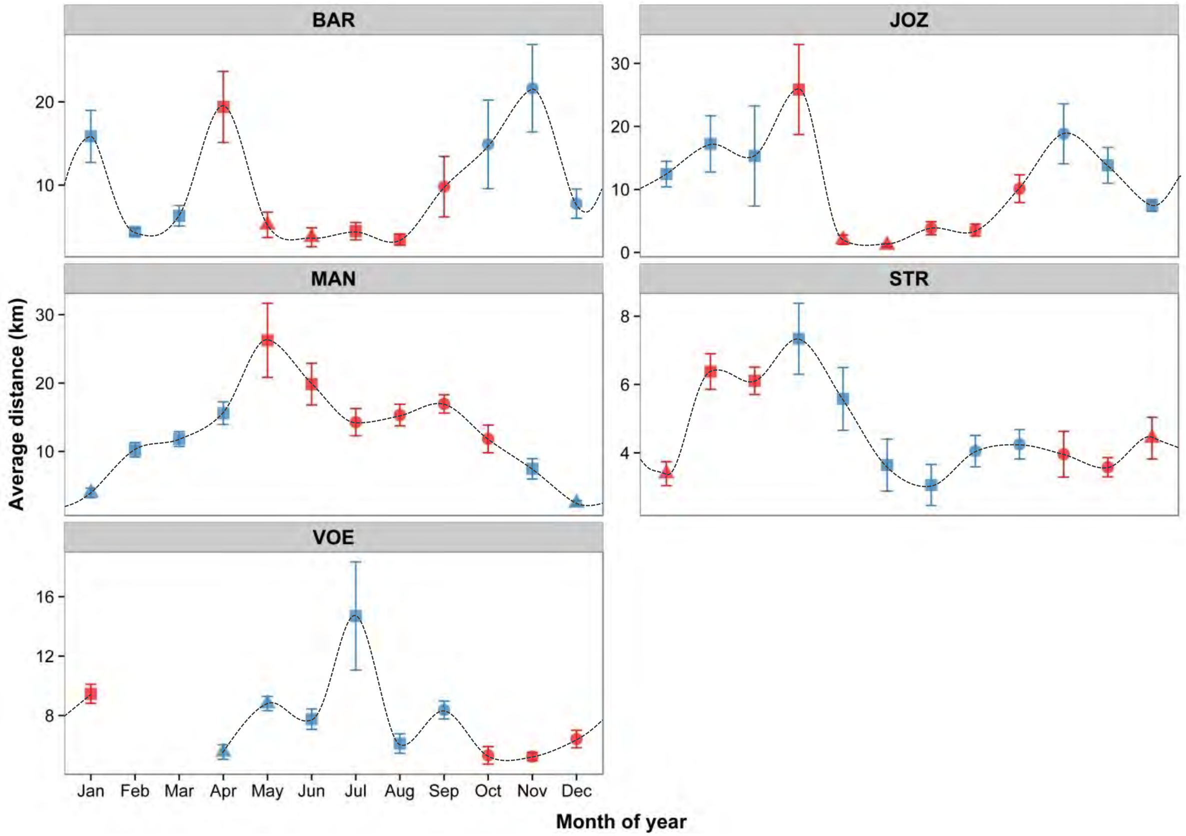

Figure 1a Mean (± se) daily movement per month for Egyptian Goose over the study period. Colour indicates seasonality of rainfall; red = dry and blue = wet. Symbols represent the three life history stages; circle = breeding, triangle = moulting and square = ranging. BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = Strandfontein and VOE = Voëlvlei Dam. *Two months of tracking data are missing for VOE. Dashed line indicates trend over time

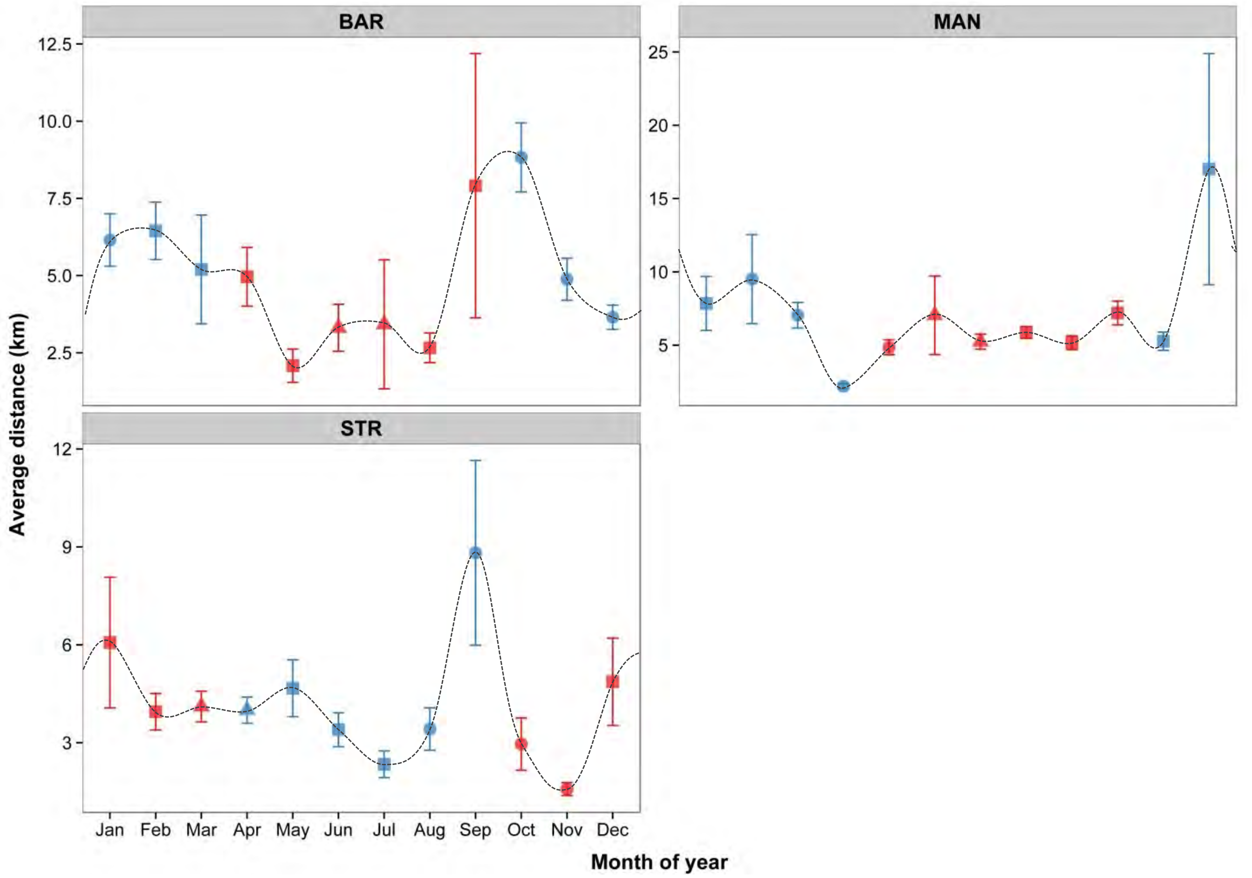

Figure 1b Mean (± se) daily movement per month for Red-billed Teal over the study period. Colour indicates seasonality of rainfall; red = dry and blue = wet. Symbols represent the three life history stages; circle = breeding, triangle = moulting and square = ranging. BAR = Barberspan Nature Reserve, MAN = Lake Manyame, and STR = Strandfontein. Dashed line indicates trend over time

Appendix 5C

Table 1 Comparisons of the Akaike information criterion (AIC) as a measure of goodness of fit for the five probability density functions fitted to the dispersal distribution of five wetland plants dispersed by Egyptian Goose and Red-billed Teal Best fitting distributions are shown in bold face.

Goose						
Plant	**AIC:**	**Normal**	**Weibull**	**Gamma**	**Lognormal**	**Cauchy**
A. hyb		192798	**192157**	196947	202718	229407
P. lap		275897	**275516**	280878	288870	325748
P. pec		113854	**113487**	116117	119456	135480
P. sch		119089	**118552**	121653	125136	142270
R. mar		101977	**101809**	103710	106528	120679
Teal						
A. hyb		61987	**61822**	62867	64544	74554
P. lap		123534	**123295**	124595	127575	146475
P. pec		23504	23515	**23422**	23838	27644
P. sch		23428	**23402**	23684	24281	28158
R. mar		23625	**23583**	23872	24463	27987

Table 2 Comparisons of the Akaike information criterion (AIC) as a measure of goodness of fit for the five probability density functions fitted to the dispersal distribution of *P. lapathifolia* dispersed by Egyptian Goose and Red-billed Teal across the different study populations. Best fitting distributions are shown in bold face.

Goose						
Site	**AIC:**	**Normal**	**Weibull**	**Gamma**	**Lognormal**	**Cauchy**
ALL		275897	**275516**	280878	288870	325748
BAR		47751	47703	**47634**	48627	55067
JOZ		53660	53715	**52813**	53507	61888
MAN		36272	**36079**	37469	38736	43199
STR		85046	**84814**	86616	89147	102362
VOE		41529	**41332**	44004	46069	47219
Teal						
ALL		123534	**123295**	124595	127575	146475
BAR		224196	**223382**	223994	228693	263027
MAN		176368	**175829**	181300	186580	209492
STR		345633	**345587**	349986	359115	414119

Appendix 5D

Table 1 Dispersal parameters for five wetland plants dispersed by Egyptian Goose and Red-billed Teal. The mean, median and maximum dispersal distances, and the confidence intervals as determined from a non-parametric bootstrap are shown, along with the percentage of all dispersal events that are further than 100 kilometres from the source. *A. hyb = Amaranthus hybridus, P. lap = Persicaria lapathifolia, P. pec = Potamogeton pectinatus, P. sch = Panicum schinzii* and *R. mar = Ruppia maritima*.

Goose	**Mean ± CI (km)**	**Median± CI (m)**	**Max ± CI (km)**	**> 100 km (%)**
A. hyb	2.79 ± 0.07	659 ± 1	371 ± 2	0.21
P. lap	3.37 ± 0.06	679 ± 1	373 ± 2	0.43
P. pec	2.59 ± 0.07	586 ± 1	307 ± 2	0.14
P. sch	2.59 ± 0.07	633 ± 2	283 ± 2	0.13
R. mar	2.95 ± 0.10	614 ± 2	493 ± 14	0.30
Teal				
A. hyb	1.34 ± 0.05	351 ± 1	217 ± 1	0.04
P. lap	2.52 ± 0.01	476 ± 2	426 ± 1	0.21
P. pec	2.53 ± 0.03	392 ± 2	422 ± 1	0.25
P. sch	1.36 ± 0.01	329 ± 1	204 ± 1	0.08
R. mar	2.28 ± 0.02	468 ± 3	222 ± 1	0.17

Table 2 Dispersal kernel parameters of four wetland plants dispersed by Egyptian Goose and Red-billed Teal across the different study population. The mean, median and maximum dispersal distances for each of the kernels are shown. BAR = Barberspan Nature Reserve, JOZ = Jozini Dam, MAN = Lake Manyame, STR = False Bay Ecology Park/Strandfontein and VOE = Voëlvlei Dam.

Goose	**Mean ± se (km)**	**Median (km)**	**Max (km)**
A. hybridus			
BAR	3.88 ±0.16	0.50	373
JOZ	2.40 ±0.06	0.31	184
MAN	3.71 ±0.12	1.20	118
STR	1.54 ±0.20	0.44	64
VOE	3.84 ±0.89	1.80	321
R. maritima			
BAR	4.22 ±0.20	0.49	542
JOZ	2.87 ±0.13	0.32	175
MAN	3.59 ±0.97	0.97	99
STR	1.60 ±0.15	0.43	64
VOE	4.00 ±0.06	1.60	346

P. schinzii			
BAR	3.05 ±0.15	0.48	286
JOZ	2.40 ±0.08	0.31	147
MAN	3.44 ±0.06	1.10	118
STR	1.44 ±0.02	0.41	64
VOE	3.82 ±0.09	2.02	189
P. pectinatus			
BAR	3.43 ±0.02	0.42	311
JOZ	2.32 ±0.09	0.31	157
MAN	3.55 ±0.04	1.06	122
STR	1.38 ±0.03	0.39	58
VOE	3.53 ±0.06	1.61	274
Teal			
A. hybridus			
BAR	1.35 ±0.06	0.29	50
MAN	1.70 ±0.07	0.67	204
STR	1.13 ±0.06	0.28	220
R. maritima			
BAR	2.39 ±0.06	0.36	203
MAN	2.47 ±0.12	0.85	88
STR	2.11 ±0.15	0.33	223
P. schinzii			
BAR	1.20 ±0.35	0.28	50
MAN	2.00 ±0.23	0.64	204
STR	1.03 ±0.39	0.26	136
P. pectinatus			
BAR	2.72 ±0.07	0.32	204
MAN	3.24 ±0.17	0.71	426
STR	1.80 ±0.06	0.28	220

CHAPTER 6

THE ROLE OF WATERBIRDS IN THE DISPERSAL OF AQUATIC ALIEN AND INVASIVE SPECIES

Photo by: Mike Haworth

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ABSTRACT

The aim of this chapter is to review existing literature on the ability of waterbirds to spread aquatic alien and invasive species, and to assess the relevance of bird-mediated dispersal for the conservation of freshwater ecosystems. The scope of this chapter is not restricted to southern Africa and instead draws on information from across the globe. A review of the literature revealed that quantitative studies investigating dispersal of alien organisms by waterbirds are rare. Most studies citing waterbird dispersal rely on anecdotes or inferences from morphological dispersal syndromes. However, evidence from each stage of dispersal (i.e., emigration, transport and immigration) shows that waterbirds can carry alien plants and invertebrates internally and externally; transport them between waterbodies at a variety of spatial scales; and deposit viable propagules in sites suited to aquatic invasive species. This review suggests that waterbirds can and do act as important dispersal vectors for freshwater invasive species. Further experimental and field based research on the numbers and viability of moved alien propagules, and the roles of different species in the bird community, is needed. Furthermore, consideration of the spatially explicit manner in which birds move is imperative to understanding invasive spread. Populations of alien aquatic species in seemingly isolated wetlands can no longer be considered contained if they are able to be spread through waterbird-mediated dispersal, and containment measures must recognise such opportunities for further spread. Changing waterbird movement patterns, driven by climate and land-use change further add to the challenge of managing invasive species and offers an interesting opportunity for future research. The study of waterbird-mediated dispersal of aquatic alien invasive species provides insights not only into species invasions, but more generally into movement ecology, population ecology and biogeography.

6. 1 INTRODUCTION

Biological invasions cause some of the most devastating and irreversible impacts on the world's ecosystems, ranking second only to habitat loss as a threat to global biodiversity (Sala *et al.* 2000; Mooney & Cleland 2001; Strayer 2010). The ecological impacts of biological invasions have prompted considerable research on the management and impacts of invasive species. Surprisingly, however, very little attention has been paid to the explicit role of dispersal in species invasiveness and management (Westcott & Fletcher 2011). Biological invasions are fundamentally driven by dispersal, which facilitates spread across a landscape

(Westcott & Fletcher 2011). Managing alien invasive species requires an understanding of spatial patterns of dispersal and the mechanisms that generate them (Sakai *et al.* 2001; Levin *et al.* 2003).

To date, biological invasions have had their largest impacts on freshwater ecosystems (Ruiz *et al.* 1999; Green *et al.* 2005). Freshwater systems provide vital ecosystem services and are the sole habitat for an extraordinarily rich, endemic and sensitive biota (Strayer & Dudgeon 2010). However, hundreds of alien species have been introduced into freshwater systems around the world (e.g., water hyacinth *Eichhornia crassipes*, zebra mussels *Dreissena polymorpha*, and Nile perch *Lates niloticus*), with extensive and long lasting ecological effects (Strayer 2010)

Freshwater systems can be viewed from a classical Island Biogeographic perspective as islands of freshwater in a sea of land (Magnuson 1976). Island Biogeography provides a useful framework for understanding connectivity relationships within wetland and river networks (MacArthur & Wilson 1967). For example biodiversity is expected to be higher in larger, more connected lakes and rivers and systems in which source pools of species are available following perturbations (Cumming 2004).Wetlands are in many cases connected by directional links; laterally by rivers, longitudinally across floodplains, and vertically through surface/ground water interactions (Fullerton *et al.* 2010). They are also connected functionally through the movements and behaviours of organisms (Haig *et al.* 1998; Amezaga *et al.* 2002).

In freshwater ecosystems, the most important processes contributing to the spread of alien species are those that connect waterbodies across catchments. Without these broader-scale links, invasions by species that lack significant dispersal mechanisms of their own would be far easier to contain. In many cases alien invasion involves an increased rate of spread that is only possible through human intervention (Wilson *et al.* 2009). Particular attention in this context has been paid to the role of ballast water release in the introduction of alien species into the American Great Lakes (e.g. spiny waterflea *Bythotrephes longimanus* and zebra mussel; (MacIsaac 2011) and the actions of fishermen and boats (e.g. live bait release of rusty crayfish *Oroconectes rusticus* and transport of submerged weed *Hydrilla verticulata* and zebra mussel larvae on boats; Lodge *et al.* 2000, Johnson, Ricciardi & Carlton 2001; Coetzee, Hill & Schlange 2008). However, natural passive dispersal processes across a range of spatial scales also contributes to the spread of alien invasive species between catchments. These include movements of prey species between catchments by predators (e.g., raptors dropping prey items (Higgins *et al.* 2003) and the more common mechanism of dispersal of aquatic organisms by waterbirds (Figuerola & Green 2002a).

6.1.1 Waterbirds as mobile links

Waterbirds are sometimes cited as driving the passive dispersal of alien invasive species (Figuerola & Green 2002a; Green & Figuerola 2005a; Green *et al.* 2008; Sánchez *et al.* 2012). However, empirical evidence for waterbird-mediated dispersal is rare (Table 1) (Appendix 6A) and its existence has largely been inferred on the basis of morphological dispersal syndromes (MacIsaac 2011) or the interactions of waterbirds with invasive species at a given site. To date the role of waterbirds in the dispersal of alien species has only been superficially assessed (Green *et al.* 2008; Brochet *et al.* 2009; Twigg *et al.* 2009).

Studies focusing on the dispersal of native aquatic plants and invertebrates have established that waterbirds are highly suitable dispersal vectors (see Figuerola & Green 2002a and van Leeuwen *et al.* 2012b for reviews). Waterbirds disperse a wide variety of native aquatic organisms that either pass intact through the gut (endozoochory) or attach to feet and feathers (ectozoochory) (Brochet *et al.* 2010b a; Raulings *et al.* 2011; van Leeuwen *et al.* 2012b). However, it remains largely unknown which invasive species waterbirds may be dispersing and whether the same relationships and traits that facilitate dispersal of native aquatic organisms are also relevant for invasive species. Alien species may have unique characteristics that facilitate rapid and wide spread (e.g., parthenogenesis versus sexual reproduction in aquatic gastropods; Miranda, Perissinotto & Appleton 2011). Waterbird-mediated dispersal may have been a key driver shaping the continental distribution of some aquatic plants and invertebrates (Brochet *et al.* 2009; Viana *et al.* 2013b). However, there is little knowledge of how waterbirds may contribute to the successful spread of invasive species and no published management recommendations on this specific subject.

I review quantitative and semi-quantitative evidence for the dispersal of alien and invasive aquatic plant and invertebrate species by waterbirds, critically evaluate the likelihoods and limitations of this process in light of the growing body of literature on waterbird-mediated dispersal of native aquatic organisms, and assess the importance of waterbirds relative to other dispersal vectors. I then discuss how anthropogenic factors such as land use and climate change can affect dispersal-related waterbird movement patterns and conclude by discussing priorities for future research.

6.2 HOW DO WATERBIRDS DISPERSE ALIEN SPECIES?

In order for invasive species to spread they must be effectively dispersed (i.e., dispersal followed by successful reproduction; Schupp, Jordano & Gómez 2010). Dispersal is a three-stage movement of organisms and/or their propagules (Ronce 2007) that consists of (1) emigration or uptake; (2) movement and transport; and (3) immigration or introduction. A propagule is defined as a structure acting as an agent of reproduction and propagation (seeds, vegetative bodies, spores, eggs, ephippia, gemmules, statoblasts, cysts).

6.2.1. Emigration

The first stage of dispersal entails the movement of alien species out of a site. Passively dispersing organisms can be taken up by a vector and remain intact upon departure from the site. Uptake by waterbirds can occur intentionally (e.g. ingested as part of the diet) or unintentionally (e.g. adhering to feet and feathers) (Figuerola & Green 2002a). The uptake of propagules via different modes has varying consequences for spatial patterns of spread.

Dietary studies can be used to determine the identity of alien propagules potentially dispersed by waterbirds. The number of seeds found in the oesophagus and gizzard is a significant predictor of the occurrence of intact seeds in the lower gut (Brochet *et al.* 2009). A review of 25 diet studies from Europe identified 14 alien plant seeds in the diet of four dabbling duck species. Seeds included several introduced species from the Gramineae family (e.g. *Paspalum miliaceum*), some weedy wetland obligates (*Najas gracillima* and *Heteranthera reniformis*), and the invasive Russian olive tree (*Elaeagnus angustifolia*) (Brochet *et al.* 2009).

Table 1 Summary of studies addressing waterbird dispersal of alien species. The specific alien organism, a summary of the main findings, the waterbird dispersal vector (sample size in parentheses) and location are identified. Summary information is based upon search of the ISI Web of Science which produced 1127 unique papers when combining search phrases based on seven synonyms for non-native status (non-indigenous, introduced, exotic, alien colonizing, non-native & invasive); a taxonomic identifier (aquatic macrophyte, aquatic plant, hydrophyte, aquatic invertebrate, aquatic insect) and four synonyms for dispersal (dispersal, movement, propagation & spread). We then systematically searched through the papers to target any studies which quantitatively or semi-quantitatively investigated the role of waterbirds in the dispersal of alien species. Only 14 studies up to and including November 2014 matched our search criteria. NA = North America; WE = Western Europe; EU = Europe; AU = Australia

Reference	**Method**	**Alien species**	**Summary of findings**	**Waterbird Dispersal Vectors (n) & Location**
Endozoochory				
Powers *et al*. 1978	Field study	*Cyperus iria **	20% of samples with ≥ one propagule, 17% viable	Green-winged Teal *Anas. carolinensis* (19); Mallard *A. platyrhynchos* (14); Ring-necked Ducks *Aythya collaris* (7); Northern Pintail *A. acuta* (5) Mottled Duck *A. fulvigula*(3); Gadwall *A. strepera* (2); Louisiana, NA
		Echinochloa colonum	6% of samples with ≥ one propagule, 50% viable	
		Eleocharis obtusa	6% of samples with ≥ one propagule, 50% viable	
		*Fimbristylis miliacea**	2% of samples with ≥ one propagule, 33% viable	
	Feeding trial	*Echinochloa crusgalli**	~1% passed intact, but 0% germination	Mottled Duck (5); Mallard (5); Northern Pintail (5); Louisiana, NA
		Echinochloa frumentacea	~2.5% passed intact, but < 1% germination	
		Oryza punctata	0% passed intact	
		Leptochloa fascicularis	18% passed intact, germination ranging from 7% - 57% dependent on bird species fed	
		Polygonum pensylvanicum	18% of seeds passed intact, but with no germination	
Sanchez *et al*. 2006	Field study	*Mesembryanthemum nodiflorum**	4% of samples contained intact propagules, 24% viable	Redshank *Tringa totanus* (295); Black-tailed Godwit *Limosa limosa* (56); Spotted Redshank *T. erythropus* (9); Spain, WE
		Sonchus oleraceus	7% of samples contained intact propagules, 76%	

			viable.	
Green *et al*. 2008	Field study	*Ranunculus scleratus*	17% of samples contained intact propagules, 67% viable	Grey Teal *A. gracilis* (30); Black Swan *Cygnus atratus* (20); Eurasian Coot *Fulica atra* (20); New South Wales, AU
		Medicago polymorpha	1.4% of samples contained intact propagules, 100% viable	
		*Polygonum arenasturm**	6% of samples contained intact propagules, 25% viable	
Twigg *et al*. 2009	Experimental feeding trial	*Ulex europaeus**	1.3% and 5.2 % recovered respectively, with 66.7% and 41.5% corresponding viability	Australian wood duck (3); Pacific black duck *Chenonetta jubata* (4)
		Brassica napus	0.3% recovered, but with a 45.5% viability	Australian wood duck *A. superciliosa* (3); Western Australia, AU
Brochet *et al*. 2010b	Field study	*Ludwigia peploides**	1 non-viable propagule recovered	Eurasian Teal *A. crecca* (366); France, WE
		Paspalum distichm	6 non-viable propagules recovered	
		Heteranthera reniformis	4 viable propagules recovered	
		Heteranthera limosa	2 non-viable propagules recovered	
Raulings *et al*. 2011	Field study	*Cotula cioronopifolia**	14 geminants from seedling emergence trial	Pacific Black Duck (21); Chestnut Teal *A. castanea* (24); Grey Teal *A. gracilis* (21), Eastern Australia, AU
		Lactuca serriola	1 germinant from seedling emergence trial	
		Sonchus oleraceus	3 germinants from seedling emergence trial	
		Trifolium glomeratum	1 germinant from seedling emergence trial	
		Trifolium cernuum	1 germinant from seedling emergence trial	
Green *et al*. 2005	Field study	*Artemia franciscana**	Very high recovery of intact cysts. Viability between 12- 68% dependent on location and vector	Redshank (122); Black-tailed Godwit (30); Dunlin *Calidris alpina* (103); Portugal & Spain, WE
Sanchez *et al*. 2012	Experimental feeding trial	*Artemia franciscana**	Recovered 8% of cysts fed, viability14%	Redshank (4); Dunlin (6); Spain, WE

Ectozoochory				
Sanchez *et al*. 2012	Experimental attachment	*Artemia franciscana**	0.3% of cysts attached to feathers remained	Black-tailed Godwit (4); Spain, WE
van Leeuwen & van der Velde 2012	Experimental attachment	*Potamopyrgus antipodarum**	74% of deliberately attached snails remained attached after 30 min; 1.2% after 8 h	Mallard (12); Netherlands, WE
		*Valvato pisinalis**	41% attached to tray in < 1min; 96 % attached < 7 min	
Raulings *et al*. 2011	Feather brushings	*Trifolium glomeratum*	1 germinant from seedling emergence trail	Pacific Black Duck (3); Chestnut Teal (22); Grey Teal (1); Eastern Australia, AU
		Plantago coronpus	1 germinant from seedling emergence trail	
		Senecia glomeratus	1 germinant from seedling emergence trial	
Coughlin *et al*. 2015	Experimental attachment	*Lemna minuta**	Prolonged retention and high viability of fronds inserted between feathers. High relative humidity between feathers	Mallard (9); United Kingdom, WE
Literature Review				
Brochet *et al.* 2009	Literature review of dabbling duck diet	*Amaranthus albus* *Amaranthus retroflexus* *Helianthus annuus* *Elaeagnus angustifolia** *Oryza sativa* *Panicum miliaceum* *Paspalum distichum* *Paspalum paspalodes* *Setaria italica* *Sorghum bicolour*	Identified 14 plant species alien to Europe	Eurasian Teal *A. crecca*; Northern Pintail; European Wigeon *A. penelope*; Mallard (25 diet studies); EU

		Zea mays *Najas gracillima* *Heteranthera reniformis* *Veronica persica*	
Genetic Analysis			
van Leeuwen *et al*. 2013	Microsatellite analysis	*Physella acuta**	Snail exploits several dispersal vectors, but waterbirds were responsible for long-distance dispersal; Spain, WE
Muñoz *et al.* 2013	Mitochondrial DNA analysis	*Artemia franciscana**	Bird-mediated dispersal had a significant historical role on the current species phylogeography; Europe
Muñoz *et al*. 2014	Microsatellite analysis	*Artemia franciscana**	Natural dispersal via flamingos between populations of shrimp in Mediterranean study region; Portugal, Spain, France and Italy, WE

*Considered an invasive alien species

The Anatidae (ducks, swans and geese) are considered the most influential dispersers (Green *et al.* 2002); however, they are not unique within the waterbird community. Faecal matter and regurgitated pellets from migratory Charadriiformes (also termed 'waders' or 'shorebirds') contained high numbers of intact seeds of *Mesembryanthemum nodiflorum* and *Sonchus oleraceus*, and constituted nearly 84% of all recovered seeds (Sanchez, Green & Castellanos 2006). Both plant species are widespread invasive aliens in the Americas and Australasia, and it appears that dispersal by migratory shorebirds may contribute to their rapid spread (Sanchez *et al.* 2006).

Examples of ectozoochory of alien species by waterbirds are very rare (Table 1). In general, endozoochory is presumed to be the prevailing form of dispersal for aquatic organisms by waterbirds (Brochet *et al.* 2010b) and it is true that higher numbers of seeds are evacuated from the gut than are recovered from feathers (Brochet *et al.* 2010b; Raulings *et al.* 2011). However, there has been much less research on ectozoochory (Table 1), including in the context of native organisms, and it is difficult to draw conclusions about the relative importance of each dispersal mode in the field.

Perhaps the best-known example of ectozoochory of an alien species by waterbirds is *Azolla filiculoides*. The red water-fern, *A. filiculoides*, is a small and widespread aquatic invasive weed (Lumpkin & Plucknett 1980). Waterbirds are commonly cited as dispersal vectors of *A. filiculoides* (McConnachie *et al.* 2004; Coetzee *et al.* 2011), but their role in the dispersal of this plant is not rigorously verified. Interestingly, however Green *et al.* (2008) found large amounts of *A. filiculoides* reproductive tissue in the faecal samples of waterbirds in Australia. The viability of the tissue was unfortunately never determined, but suggests that endozoochory may also play a role in the plants dispersal. Further examples of ectozoochory of alien species include the recovery of intact propagules of introduced pasture weeds, *Trifolium glomeratum* and *Plantago coronopus* on the plumage of waterbirds in Australia (Raulings *et al.* 2011).

Waterbirds do interact with and ingest alien organisms in the field. However, the limited spatial extent of sampling (Table 1), and the fact that most of the alien species were identified as part of a general review of waterbird-mediated dispersal, makes drawing conclusions about the sorts of alien organisms that birds disperse difficult. Dietary studies and faecal matter sampling can be important first steps in determining what waterbirds may be dispersing. However, such analyses need to be coupled with information on propagule abundance and availability, as well as the feeding ecology of the vectors. It remains unclear whether birds actively select the propagules of alien organisms or encounter them accidentally, and how uptake varies between bird species and across seasons.

Waterbirds are also capable of dispersing seeds into and from terrestrial habitats. Agricultural grains are commonly exploited food resources for waterbirds (Mangnall & Crowe 2001). Of the 14 alien plants found in dabbling duck diets, three were crop species and four were contaminants of ricefields (Brochet *et al.* 2009). The potential role of seed-eating waterbirds to establish and/or maintain feral populations of cultivated crops (e.g. canola *Brassica napus*) is thus of real concern (Twigg *et al.* 2009). The possibility exists for birds to spread genetically modified (GM) crops beyond containment boundaries, thereby enhancing the potential for transgenic flow to wild flora or to non-GM crops (Twigg *et al.* 2009). Additionally, the possibility exists for waterbirds to spread weeds within agricultural landscapes.

Examples of waterbird uptake of alien aquatic invertebrates remain scarcer than those of plants. The best known case is that of American brine shrimp, *Artemia franciscana.* This alien invasive species was introduced into the Mediterranean region for aquaculture and has spread very rapidly. The cestode parasites of native *Artemia* are unable to switch to *A. franciscana* (Georgiev *et al.* 2007) and foraging birds preferentially feeding on *Artemia* infected with cestodes (Sánchez *et al.* 2013). While this might suggest that native *Artemia* are selectively taken up and dispersed by waterbirds, as *A. franciscana* displaces native species it becomes the dominant dispersed species. High numbers of *A. franciscana* cysts pass through the gut intact and, depending on the sampling site, are recovered in higher quantities than native cysts (Green *et al.* 2005). *Artemia* cysts can be spread by people moving between saltpans (Waterkeyn *et al.* 2010) and wind (Persoone *et al.* 1980). However, endozoochory by waterbirds is thought to be the dominant dispersal mechanism (Sánchez *et al.* 2012)

6.2.2. Movement and transport

The transport distance of aquatic alien species by birds is a product of the movement distance of the avian vector and propagule retention time. Therefore, a crude measure of the maximum distance to which a propagule can be dispersed is the maximum time that a propagule remains in the gut (or on the feathers) multiplied by the speed at which the bird is capable of flying. Powers, Noble & Chabreck (1978) and Sánchez *et al.* (2012) demonstrated that rice weed seeds (*Persicaria lapathifolia* and *Leptochloa chinensis*) fed to several species of waterbirds, and cysts of *A. franciscana* fed to Redshank *Tringa tetanus* and Dunlin *Calidris alpina,* were present in the gut up to 12 h after feeding trials had commenced. Waterbirds such as ducks and shorebirds are extremely strong flyers, moving at speeds around 60-78 km/h and 48-60 km/h respectively (Welham 1994). These data suggest that alien organisms can remain in the gut of waterbirds and be transported over long distances. Long-distance dispersal (LDD) is a form of directed flight and is generally applicable only in the context of migrating birds. However, in the case of endozoochory, an important pre-requisite for dispersal is that birds fly with full guts (Clausen *et al.* 2002). Waterbirds tend to massively reduce the size of their digestive organs prior to long-distance migration (Piersma & Gill Jr. 1998) thus affecting the volume of propagules carried (Clausen *et al.* 2002). Furthermore, the activities of the vector have an effect on how long a propagule is retained; van Leeuwen *et al.* (2012a) suggest that previous long-distance dispersal estimates may be overestimated.

Stepping-stone dispersal, which refers to the movement of propagules at much smaller scales between adjacent sites, is highly relevant to aquatic biological invasions (Wilson *et al.* 2009). For example, the population structure and degree of gene flow between geographically and hydrologically isolated populations of the aquatic alien invasive snail *Physella acuta* suggests that dispersal on the scale of tens of kilometres is facilitated by waterbirds (van Leeuwen *et al.* 2013). Waterbirds that frequently moved between ponds and rice fields > 15 km away functioned as agents of gene flow between populations separated at this scale. The study did not determine whether endo- or ectozoochory was the main mechanism, but dispersal by waterbirds sufficiently explained genetic similarity between snail populations. More generally, alien aquatic snails demonstrate many necessary prerequisites for successful endo- and ectozoochory (e.g., van Leeuwen *et al.* 2012c; van Leeuwen & van der Velde 2012).

Movement by vectors is a poorly understood stage of both native and invasive species dispersal. Research on dispersal distances has primarily focused on unidirectional LDD of propagules down flyways by migratory waterbirds. This has likely been encouraged in part by the ability of birds to move parasites, microbes and zoonotic pathogens over long distances (Reed *et al.* 2003; Gaidet *et al.* 2010; Altizer, Bartel & Han 2011). Ducks are known to cover long distances during flight on occasion (Roshier, Robertson & Kingsford

2002; Cumming *et al.* 2012). Some satellite tracked Egyptian Geese, *Alopochen aegyptiaca*, in southern Africa moved > 650 km in a ten hour period (Cumming *et al.* 2012). Egyptian Geese movement patterns, however, primarily consist of shorter flights less than 10 km (Cumming *et al.* 2012) (Fig. 1). These shorter distance and relatively frequent dispersal events have not been well considered in the context of native and alien organisms. Detailed spatial movement data and the development of more realistic dispersal models, which account for the multi-directionality and small scale movement of waterbirds, are required to address spatial patterns of alien species spread.

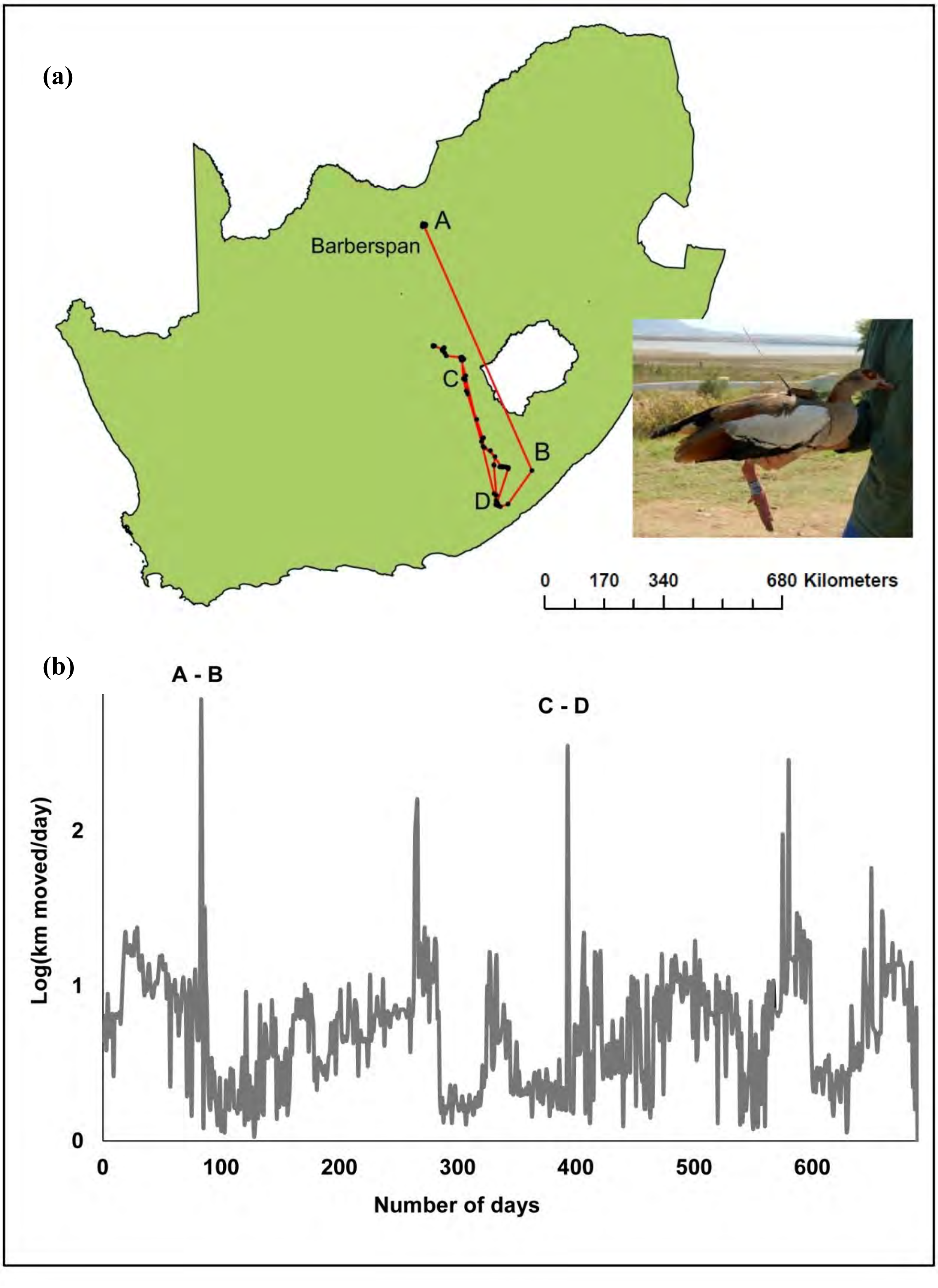

Figure 1 (a) Individual satellite track of Egyptian Goose *Alopochen aegyptiaca* tagged in Barberspan Nature reserve South Africa in June 2008. The individual made several long distance journeys, most notably A-B and C-D, which represent distances of 650 km and 400 km in under 12 hours respectively. These journeys can be seen in (b) a smoothed histogram of log (kilometres moved per day). Most daily movements are small scale movements.

6.2.3. Immigration

Immigration is a key step in the invasion process as it represents the final dispersal hurdle prior to invasive spread (Kolar & Lodge 2001). The study of biological characteristics that facilitate survival is crucial for understanding the dispersal capacities of potentially invasive aquatic organisms. To be effectively dispersed, alien species must enter suitable habitats where they may become established. Waterbirds are dependent on wetlands for at least some of their annual life cycle and therefore make directed movements between suitable habitats (Green *et al.* 2002).

Field and laboratory feeding studies indicate that the propagules of alien plants and invertebrates remain viable after passage through the guts of waterbirds. Green *et al.* (2008) showed that three alien invasive plant species could survive gut passage and germinate: celery-leaved buttercup *Ranunculus sceleratus*; burclover *Medicago polymorpha*; and oval-leaf knotweed *Polygonum arenstrum*. All three of these species are widespread and range-expanding in Australia and are considered invasive in the United States of America. Large quantities of viable seeds of alien plants can be found in the droppings of wading birds. A single Sow thistle plant, *Sonchus oleraceus,* can produce over 25 000 tiny seeds (each 2-3 mm in size) (Salisbury 1974) which are assumed to be mainly dispersed by wind (Jakobsson & Eriksson 2003). However, 76.3% of *S. oleraceus* seeds recovered from wading bird faecal matter were viable (Sanchez *et al.* 2006), suggesting that birds are overlooked vectors. It has been argued that non-standard mechanisms of dispersal are often responsible for LDD in plants (Higgins *et al.* 2003). Seeds that appear adapted mainly for wind dispersal may occasionally be transported at different spatial scales by birds. Small seed size is the most significant predictor of survival through the gut of waterbirds (Soons *et al.* 2008). The absence of obvious morphological adaptations for bird dispersal in aquatic seeds partially explains why waterbirds have been largely overlooked as vectors of alien plants. However, it is important to note that successful alien species are generally adept at exploiting multiple vectors, across a range of scales, and that morphological adaptations may not reveal all dispersal vectors.

For many aquatic alien plants, asexual reproduction is a key component of invasive potential (Kolar & Lodge 2001) allowing rapid establishment (Janes, Eaton & Hardwick 1996). Dispersal of asexual propagules on waterbird feathers has long been speculated. Ectozoochory by birds is most suited to small, adhesive propagules that are desiccationtolerant (Amezaga *et al.* 2002). Entanglement in the vector feathers or encapsulation in mud on feet may offer propagules protection against desiccation (Coughlan, Kelly & Jansen 2015) (Fig. 2). *Lemna minuta* (lesser duckweed) fronds inserted between the feathers of captive mallard duck *Anus platyrhynchos*, for example, showed both prolonged retention, viability and prevented desiccation. Retention of *L. minuta* in the feathers of waterfowl may thus be contributing to the dispersal of this "high impact" aquatic alien invasive species (Coughlan *et al.* 2015).

Figure 2 Lesser Duckweed *Lemna minor* attached to underwing feathers of Yellow-Billed Duck *Anas undulata***.**

Many aquatic invertebrates produce resistant propagules (ephippia, cysts, gemmules or statoblasts; Panov *et al.* 2004) that not only allow them to survive desiccation, but these same adaptations also facilitate dispersal via zoochory. Shorebirds were fed the cysts of a native and alien *Artemia* species showed 11% and 14% hatchability respectively. Green & Figuerola (2005) propose that the expansion of the alien invasive waterflea, *Daphnia lumholtzi,* in North America is a good opportunity to assess the role of birds in the dispersal of alien invasive organisms. *Daphnia* ephippia are well adapted for bird dispersal and survive gut passage by waterbirds (Green & Figuerola 2005a). Interestingly, *D. lumholtzi* may have been introduced to North America from tropical Africa via ephippia carried in the digestive tract of Nile perch which was itself introduced in 1983 (MacIsaac 2011). It is also possible that secondary dispersal has been facilitated by fish-eating birds (Mellors 1975; MacIsaac 2011).

It is important to determine the number of propagules that survive and remain viable upon entering a site. These data, coupled with the frequency with which waterbirds visit a site, can be used to calculate propagule pressure (see also Colautti, Grigorovich & MacIsaac 2006), a composite measure of the quality, quantity and frequency of alien organisms that are dispersed. Propagule pressure is a key determinant of whether an introduced alien species becomes established or an established alien species becomes invasive in a given habitat (Lockwood, Cassey & Blackburn 2005). Furthermore, priority effects may play a role in establishment. In systems prone to disturbance, like arid zone wetlands which constantly face dry downs, the early arrival of a highly competitive weed could monopolise all resources and prevent the establishment of other species (Symons & Arnott 2014).

6.3 CHANGING CONNECTIONS

As global climate changes, large-scale hydrological changes are expected to occur (Strayer & Dudgeon 2010). There is substantial evidence that climate change alters movement patterns, the timing of migrations, waterbird abundance, and diet (Sutherland 1998; Lehikoinen *et al.* 2013), all of which will have implications for alien species introduction and spread. The Bean Goose *Anser fabalis* and Greylag Goose *A. anser* have shortened their migratory routes in the last few decades, wintering in central Europe instead of southern Europe (Amezaga *et al.* 2002). Climate change affects pathways of introduction, the impact of alien species and the effectiveness with which we can manage these species (Hellmann *et al.* 2008). Proper assessment of the role waterbirds play in alien invasive spread and prediction of future bird movements are imperative for effective management.

Human activities are key drivers of biological invasions, directly through the introduction of organisms and propagules and indirectly through environmental changes that affect the ecological integrity of the recipient habitats and influence animal movement and behaviour. Land use change can affect how waterbirds utilise and move within a landscape. In southern Africa, the building of small impoundments has resulted in changes in waterbird abundance and movement patterns (Okes *et al.* 2008). Year round water availability in a typically arid environment has altered the patterns that would ordinarily drive waterbird movement (Okes *et al.* 2008). Furthermore, agricultural activities often lead to increased nutrients in farm dams, particularly increased concentrations of nitrate and phosphate compounds, creating suitable habitats for many aquatic plant invaders (e.g. *A. filiculoides*) (Hill 2003; McConnachie *et al.* 2004; Strayer 2010). Farm dams are also problematic from a management standpoint as they are often poorly monitored and on private lands where the presence of alien species is often not noticed or reported until it presents an ecological problem. Management of alien species via mechanical and biological control is best undertaken during the early stage of invasion (Olckers 2004; Henderson 2011). Education and awareness programs amongst stakeholders of aquatic environments (e.g., farmers and fishermen) on emerging pests could provide a better early warning system to better control aquatic invaders.

6.4 DISCUSSION AND FUTURE PRIORITIES

Waterbirds are poorly-considered as dispersers of aquatic alien organisms. However, waterbirds can facilitate effective dispersal (and hence spread) of alien organisms. Most published studies have inferred capacity to disperse alien organisms by *post hoc* identification of a few intact and viable propagules (Green *et al.* 2008; Raulings *et al.* 2011) and few studies have actively explored this research focus (Green *et al.* 2005; Sánchez *et al.* 2012). The case of the invasive American brine shrimp *Artemia franciscana* remains the only example to date which addresses the explicit role of waterbirds in the spread of an alien aquatic organism (Green & Figuerola 2005a; Green *et al.* 2005; Sánchez *et al.* 2007, 2012; Muñoz *et al.* 2013) (Table 1).

Westcott & Fletcher (2011) found a similar under-representation of vertebrate dispersal in the spread of terrestrial alien invasive fruiting plants. They attributed this failure to the mismatch of scales at which dispersal ecologists and invasion biologists operate. Dispersal ecologists tend to focus primarily on the description of individual processes for one dispersal vector, whilst invasion biologist have focused more on the outcomes of these processes at population levels (Westcott & Fletcher 2011). Unfortunately, a weak scientific foundation leads to management objectives for alien species that are reactive rather than proactive. Dispersal is a pivotal process driving invasion and determination of dispersal mode is thus fundamental to describing spread potential (Westcott & Fletcher 2011). A mechanistic understanding of the underlying processes facilitating effective dispersal can potentially improve our predictions of alien invasive spread. In the context of waterbirds and aquatic alien species this requires an understanding of the nature and scale of waterbird movement, waterbird community and foraging ecology and analyses of plant and invertebrate traits which aid uptake or survival. Research into these areas will be useful for determining the invasive potential of alien organisms and developing management priorities (Gosper, Stansbury & Vivian-Smith 2005).

The lesser extent to which birds are thought to drive invasive processes in comparison with anthropogenic drivers partially explains why bird dispersal has been neglected. However, even a low frequency of waterbird-mediated dispersal has consequences for the management of alien organisms. A lack of structural connectivity between waterbodies is not sufficient to contain waterbird-dispersed alien invasive species. Seemingly immobile plants and invertebrates can be viewed as highly mobile species if they can take advantage of the movements and habits of birds (Coughlan *et al.* 2015). Whilst it may be difficult to avoid the spread of invasive species by waterbirds without affecting the connectivity provided to native aquatic species, better recognition of the frequency and scale of dispersal does offers a first line of defence. Understanding how invasive species might spread amongst a network will allow better monitoring schemes and quicker responses at impacted wetlands.

Biological invasions provide opportunities for empirical research across large spatial and temporal scales (Sax *et al.* 2007), addressing processes such as directed dispersal. Priorities for future research involve the baseline identification of invasive organisms dispersed by waterbirds and the invasive species traits that facilitate such dispersal. Dispersal determines the potential for spread, but realised spread is dependent largely on post-dispersal processes (Nathan & Muller-Landau 2000). Thus, the directionality and scale of dispersal and the viability and condition of propagules landing at new sites are important determinants of effective spread. Understanding the problem will require a combination of field studies to identify alien propagules and source populations and to quantify their abundance and viability, experimental studies to investigate propagule selectivity and retention times, and spatially explicit tracking of waterbirds to determine movement patterns. A further priority is to determine whether multiple bird species may be spreading a particular alien organism. Multiple dispersal agents increase invasiveness (Sakai *et al.* 2001) and facilitate spread at different scales e.g. in the case of *A. franciscana*. Dunlin *Calidris alpine* which migrate through the region only disperse cysts between sites differing in latitude, whilst Redshank

Tringa totanus present in the region year round may affect dispersal longitudinally (Sánchez *et al.* 2012). Finally, genetic comparisons between recently established populations of aquatic alien species offer excellent opportunities for assessing the frequency of gene flow and evaluating the scales of movement of the propagules (e.g. Figuerola *et al.* 2005; van Leeuwen *et al.* 2013).

Within the general context of invasive species, I have focused on the invaders themselves. However, waterbird-mediated dispersal may also be an effective management tool through the dispersal of the biological control agents of certain alien organisms. For example, the frond weevil *Stenophelmus rusticus* controls *A. filiculoides* in South Africa. The weevil has a natural dispersal distance of approximately 20 km, but within a short period after a controlled release was found over 300 km from the original release site. The movement was attributed to a waterbird (McConnachie *et al.* 2004). Waterbirds have since been implicated in the continued dispersal of the weevil and may have been instrumental in what is likely one of the most successful biological control campaigns ever undertaken (Coetzee *et al.* 2011).

There are many examples of alien species thought to be dispersed by waterbirds (Bilton *et al.* 2001; McConnachie *et al.* 2004; Appleton, Forbes & Demetriades 2009). These anecdotes offer opportunities to develop our understanding of connectivity in aquatic systems and the explicit roles waterbirds play in alien species spread. The dispersal of aquatic alien organisms by waterbirds is a viable, overlooked, and valuable field of enquiry.

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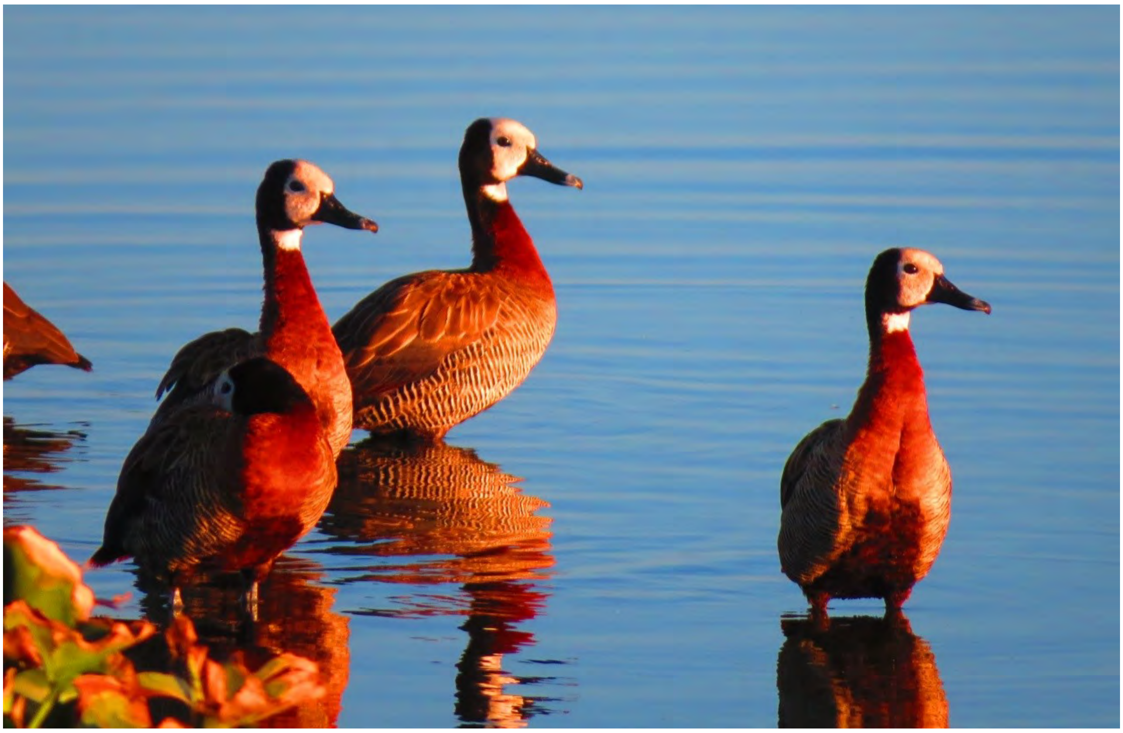
CHAPTER 7

DEFINING FUNCTIONAL GROUPS USING DIETARY DATA: DIET COMPARISON SUGGESTS FUNCTIONAL CLASSIFICATION FOR SEED-DISPERSING WATERFOWL



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ABSTRACT

Recent years have seen considerable advances in ecological understanding of the functional role(s) of biodiversity and the connections between biodiversity, ecosystem function and ecosystem service provision. Functional approaches have become important tools for simplifying biodiversity-ecosystem function relationships, but they also have some obvious weaknesses. In particular, since analyses that use functional groups treat members of a group as ecologically interchangeable, functional groups must be defined at a level that simplifies ecological complexity yet retains key ecological distinctions between groups of species. I developed a data-driven approach to functional group definition and applied it to a case study of 16 species of seed-dispersing Afrotropical waterfowl for which seed dispersal functional groups were created using both *a priori* categories, as typically done in previous studies, and a hierarchical clustering approach. Relevant functional differences and similarities occur among the waterfowl, particularly in the types of plant family dispersed. There was evidence for at least five functional groups of seed disperser. The different groupings have important implications for both wetland and terrestrial plant dispersal. This analysis suggests that even for a relatively data-scarce study system, using quantitative approaches to generate functional groups offers a feasible and ecologically rigorous approach and is a useful alternative to simple *a priori* classification schemes. This approach is capable of capturing variation across several functional traits and suggests that existing datasets may be useful in exploring variation in biodiversity-ecosystem function relationships. Since functional classification schemes may affect conclusions about biodiversity, ecosystem function and ecosystem service provision, considerable care should be given to ensuring that functional groups are not defined in such a way as to mask important ecological differences among supposedly similar species.

7.1 INTRODUCTION

Research in ecology and conservation is placing increasing emphasis on the functional roles of organisms in ecosystem processes and the provision of ecosystem goods and services to people (Hooper *et al.* 2005; Reiss *et al.* 2009; Cadotte, Carscadden & Mirotchnick 2011; Gagic *et al.* 2015). Although functional roles in animal communities were originally defined in terms of trophic and nutrient-related interactions (e.g., using foraging guilds or contributions to nutrient cycling; Simberloff & Dayan 1991; Wilson 1999), functional definitions have been extended to consider a wider range of processes and services (Sekercioğlu 2006; Kremen *et al.* 2007; Green & Elmberg 2014; Whelan, Şekercioğlu & Wenny 2015). The growing emphasis on functional roles in the ecosystem services literature has been accompanied by a tendency to combine multiple species into broad functional groups for analysis. These simplifications are considered essential if functional classifications are to be useful in simplifying and analysing the complexity of ecosystems.

A considerable amount of research has been conducted on how to define functional groups (Díaz *et al.* 2003; Hooper *et al.* 2005; Wright *et al.* 2006; Petchey & Gaston 2006; Villéger, Mason & Mouillot 2008), but there is still little clarity on the closely related question of what level of detail represents an acceptable level below which species can be considered functionally interchangeable (Petchey & Gaston 2002; Wright *et al.* 2006). For example, the generic functional group of 'pollinators' may describe a variety of organisms (e.g., ants, beetles, bees, birds, bats, and rodents) that perform a pollination function in different ways, have very different life histories, and respond differentially to environmental change. These functional differences may be irrelevant for some kinds of analysis, for example in coarse descriptions of avian ecosystem functions and services (Whelan *et al.* 2008, 2015; Green & Elmberg 2014). However, if we seek to answer specific questions about the relationships between biodiversity and function or to explore the resilience of ecosystem service provision to biodiversity loss, understanding the details of relevant differences in functional roles and responses becomes essential (Wright *et al.* 2006; Billeter *et al.* 2007).

Typical approaches to measuring the role of biodiversity in ecosystem function have relied on the creation of functional groups or guilds using *a priori* classifications. These classifications are based on the similarity of specific traits deemed relevant to the function or service being investigated (Chalcraft & Resetarits 2003). Organisms with similar traits are assumed to carry out ecosystem functions in comparable ways. Such approaches are largely insufficient for determining where relevant interspecific functional dissimilarities occur, as the groups are pre-defined and arbitrarily decided on the part of the researcher (Bernhardt-Römermann *et al.* 2008). Additionally, these kinds of classification have been shown to make predictions of ecosystem functioning which are no better than if species were randomly assigned to functional groups (Petchey 2004; Wright *et al.* 2006).

How do we comprehensively but simply describe functional variation between species for a given ecosystem service? In this chapter, it is argued that a data-based approach with no *a priori* assumptions of group membership offers an alternative way to determine an optimal level of functional analysis between the species level and a broad functional grouping. For many kinds of biodiversity-ecosystem function relationships, useful data that can capture variation between species across multiple functional traits may already exist. If the use of a more detailed functional classification has strong ecological support and a significant impact on analyses of functional relationships and ecosystem service provision, then by implication, the next generation of ecosystem service models will require an approach that takes better account of functional differences.

7.1.1 Case Study: The seed dispersal function of waterfowl

As a test case, I use the seed dispersal function of southern African waterfowl to explore the significance of finer level functional classifications. Birds provide approximately 11 core functions (Sekercioğlu, Daily & Ehrlich 2004), of which seed dispersal is considered among the most ecologically important. Seed dispersal has important implications for connectivity, gene flow, and the structure of plant communities (Nathan & Muller-Landau 2000). Although only recently the subject of empirical studies, waterbirds have long been considered key dispersal agents of aquatic plants (Darwin 1859; Ridley 1930). Amongst the waterbirds, the waterfowl (Anatidae - ducks, geese and swans) are considered to be the most influential seed dispersers because of the importance of seeds in their diets, their wide-ranging movements, and their generally high abundance (Green *et al.* 2002). In the last decade, several studies have shown that waterfowl have the ability to transport large numbers of viable seeds in the gut or attached to the feathers (Figuerola, Green & Santamaria 2003; Green *et al.* 2008; Brochet *et al.* 2010b; van Leeuwen *et al.* 2012b). This dispersal function has significant consequences for aquatic community dynamics (Amezaga *et al.* 2002), especially given the ability of waterbirds to transport alien and invasive species (Chapter 6). Differences in the seed dispersal function between waterbird species are thus important for the ecosystem services and disservices provided by wetland plants and the resilience of freshwater systems.

Dietary studies can provide useful insights into the propagules that waterfowl disperse (Brochet *et al.* 2009). Most studies of waterfowl diets are based on the contents of the foregut and do not consider whether seeds survive beyond the muscular gizzard employed to crush them (Figuerola & Green 2002a). However, these data can be used as proxies for dispersal potential because the presence of seeds in the oesophagus and/or gizzard is a significant predictor of seeds in the lower gut (Brochet *et al.* 2009). Stomach content analysis allows for the identification of plant species in the diet of multiple different waterfowl species and across a wide geographic region (Brochet *et al.* 2009, 2010b). Therefore it seems plausible that in southern Africa, with its rich historical and well-documented interest in waterfowl foraging ecology (e.g. Mitchell 1983; Petrie 2000; Petrie & Rogers 2004), plant species composition in the diet would be a useful functional trait against which to measure variation in seed dispersal function by waterfowl.

A detailed analysis of waterfowl diet and potential for seed dispersal might provide one of three outcomes: (1) waterfowl (as exemplified by the 16 common indigenous southern African species) do not show significant differences in their seed dispersal potential and should be considered as a single functional group of seed dispersers; (2) waterfowl exhibit significant functional differentiation and functional grouping within the clade, and hence should be considered as comprising not one but several functional groups of seed dispersers; or (3) the differences in seed dispersal between waterfowl species are sufficiently large that each species should be analysed as performing a different kind of seed dispersal function. These three different outcomes have implications for how we think about and analyse seed dispersal by waterfowl.

Here I use cluster analysis to test for finer level functional classifications of seed dispersal within the southern African waterfowl and compare the ability of both the empirically defined clusters and an *a priori* functional classification to resolve the presence of plant species in the diet. The *a priori* classification is based on the commonly used trait of foraging mode: dabbling, grazing, or diving (Hockey *et al.* 2005; Lisney *et al.* 2013). The dabbling, grazing, diving (DGD) classification is used because primary foraging mode is considered a means of resource partitioning amongst a waterfowl community and indicates the types of plant species which can be accessed; it should therefore reflect differences in seed dispersal (Green 1998; Green *et al.* 2002). In addition, I explore the versatility of this data-driven approach in simultaneously capturing variation in multiple functional traits pertaining to dispersal.

7.2 MATERIALS AND METHODS

7.2.1 Diet Data

The analysis was based on published information from all the diet studies I was aware of (N = 28), and comprised records for 16 commonly occurring and indigenous waterfowl species in southern Africa (Appendix 7A). Most diet studies included here specified the occurrence of the seeds of a particular plant species in the diet. However, some studies noted only the presence of a plant species in the diet and these species were included in the analysis only if listed as seed-producing flowering plants (Angiosperms). A similar approach was adopted for studies noting the presence of herbaceous material in the diet. The rationale for including these plant species was that when waterfowl ingest shoots and leaves for example, they are also likely to ingest seeds in the process (e.g. Bruun, Lundgren & Philipp 2008) ("Foliage is the fruit" hypothesis - Janzen 1984). I also included two studies from the Kafue Flats, Zambia, and one from Lake Chilwa, Malawi. Although not strictly southern Africa as delineated in Robert's Birds of southern Africa (Hockey *et al.* 2005), these locations share many of the same waterfowl species and cosmopolitan aquatic plants.

Since I sought to be comprehensive rather than selective in the inclusion of diet studies, the data were highly variable across location, time and number of plant species identified and needed to be standardised prior to analysis. There was no correlation between the number of plant species present in the diet and the number of diet studies included (Spearman's correlation: r_s 0.37, p = 0.161). However, White-faced Whistling Duck *Dendrocygna viduata* had nearly double the number of observations as Red-billed Teal *Anas erythrorhyncha* and Spur-winged Goose *Plectropterus gambensis*, the waterfowl species with the next highest number of observations (Appendix 7B). White-faced Whistling Duck was the most commonly researched species, with greater than one-third of the total plant species listed present in the diet, reflecting a very thorough study on the nutrition of this species by S.A. Petrie (Appendix 7A). Cluster analysis on the full suite of data was not useful for this purpose as it produced only two clusters; one containing White-faced Whistling Duck and the other cluster containing the other 15 southern African waterfowl species. To account for this sampling bias the final clusters were therefore determined using a nonparametric bootstrap over 1000 iterations. In each iteration, 18 observations from the White-faced Whistling Duck data were selected at random (and without replacement in any single iteration), and used in conjunction with the full dataset for the other 15 southern African waterfowl species. I used

18 observations because this corresponded to the number of observations for Red-billed Teal and Spur-winged Goose.

Data analysis was conducted at the plant family level, allowing for further standardisation of the dataset. The plant families in our analysis are widespread across the region and represent a variety of growth forms, habitats, seed sizes and seed quantities.

7.2.2 Statistical Analysis

Two independent methods of classification were used to create seed dispersal functional groups: an *a priori* approach and a hierarchical clustering approach. In the *a priori* functional group approach I assigned each waterfowl species to a group based on similar foraging behaviour (the DGD classification) (Hockey *et al.* 2005) (Table 1). In the hierarchical clustering approach, waterfowl species were grouped on the basis of empirical similarities in diet.

Data were standardised to presence/absence of plant family in the diet and binomial deviance was used as measure of similarity as it handles variable sample sizes well (Anderson & Millar 2004). Agglomerative hierarchical cluster analysis with complete linkage was performed on the similarity matrix and the optimum number of groups k selected based on the highest Mantel correlation coefficient (Borcard, Gillet & Legendre 2011). This same procedure was repeated 1000 times, and in each case, I determined the maximum Mantel correlation coefficient and corresponding optimum number of groups, as well as the resulting dendrogram. In 86% of cases the Mantel correlation coefficient was maximised at $k = 5$ (r_p: mean ± sd: 0.65 ± 0.01), and in approximately 10% and 4% of cases the Mantel correlation coefficient was maximised at $k = 3$ and 4 respectively (r_p: 0.67 ± 0.01 and 0.64 ± 0.03). I therefore chose five as the optimal number of clusters. However, these five clusters showed multiple alternative arrangements (although very similar) and the most frequent configuration of the dendrogram was thus chosen for interpretation of the clusters and for defining the functional groups (Fig. 1). In 33% of cases, the configuration of the dendrogram was as illustrated in Figure 1. Alternative configurations are represented in Appendix 7C, as well as a pairwise comparison of the percentage of cases in which waterfowl species were ascribed to the same cluster (Appendix 7C: Fig. 1 & Table 1).

Table 1 The number of diet studies considered and the species richness of plants recorded in the diet of waterfowl in southern Africa (including a subset from White-faced Whistling Duck). Functional groups were created by grouping waterfowl according to primary foraging mode, dabbling, grazing or diving as outlined in Hockey et al. (2005). The overall number of plant species in each functional group and the number of plant species shared between each pair of functional groups is indicated. The functional group into which waterfowl are placed by hierarchical clustering is also indicated. Abbreviations of waterfowl species names are shown in parentheses.

	No. of Studies	Species Richness	Clustered Functional Group
Dabbling ducks total		**38**	
Cape Teal *Anas capensis*	3	1	3
Red-billed Teal *Anas erythrorhyncha*	4	18	4
Hottentot Teal *Anas hottentota*	1	11	5
Cape Shoveler *Anas smithii*	2	1	3
African Black Duck *Anas sparsa*	2	3	2
Yellow-billed Duck *Anas undulata*	2	4	4
Knob-billed Duck *Sarkidiornis melanotos*	2	13	5
Diving ducks total		**43**	
Fulvous Whistling Duck *Dendrocygna bicolor*	4	16	5
White-faced Whistling Duck *Dendrocygna viduata*	6	18	1
Southern Pochard *Netta erythrophthalma*	2	9	5
African Pygmy Goose *Nettapus auritus*	4	11	5
Maccoa Duck *Oxyura maccoa*	1	2	3
White-backed Duck *Thalassornis leuconotus*	3	7	5
Grazing ducks total		**22**	
Egyptian Goose *Alopochen aegyptiaca*	6	11	4
Spur-winged Goose *Plectropterus gambensis*	1	18	4
South African Shelduck *Tadorna cana*	1	5	4
Shared species			
Dabbling & Diving		**16**	
Dabbling & Grazing		**7**	
Diving & Grazing		**1**	
Total		**80**	

To compare how each functional grouping resolved differences in seed dispersal functionality across waterfowl species, I applied both classifications to the diet dataset of plant species presence, including the 18 most commonly selected species from bootstrapping the White-faced Whistling Duck data. The plant species richness within a functional group was calculated, as well as the number of species shared between the functional groups for both the DGD and clustered classifications (Table 1 & Fig. 2). Shared species is used as a proxy for the "uniqueness" of a functional group and the assumption is that functional differences between groups are better represented by a classification with little overlap in plant species. Plant species for which only the genus was listed were not added to the total species richness unless they were the only representative of the genus.

Finally, to test if these types of data-based techniques capture multiple traits simultaneously and are therefore useful in the determination of ecologically relevant functional groups, I used distance-based redundancy analysis (dbRDA) (Legendre & Anderson 1999). In particular, the relative contributions of habitat, diet preference and foraging mode to variation in plant assemblage composition between waterfowl species was examined, again using the binomial deviance similarity matrix derived from plant family presence/absence in the diet. Permutational ANOVAs which produced a pseudo-*F* statistic and associated *p-value* were used to determine the overall significance of the ordination, and the significance of the explanatory terms (Borcard *et al.* 2011). All explanatory variables were factors. The primary habitat and diet preference data were also based on classifications from the Robert's birds of southern Africa (Hockey *et al.* 2005). Primary habitat for each waterfowl species was classified as open water, vegetated wetland and/or mixed terrestrial/aquatic habitat, whilst diet preference was classified as herbivorous, omnivorous and/or insectivorous. I maintained foraging mode as in the DGD classification.

All statistical analysis was performed in R statistical software version 3.2.2 (R Core Team, 2015). Dissimilarities, dbRDA and shared species were calculated using functions from the *vegan* (Oksanen *et al*. 2015) and *rich* (Rossi 2012) packages. Mantel correlation coefficients were calculated using functions from the *cluster* package (Maechler *et al*. 2015).

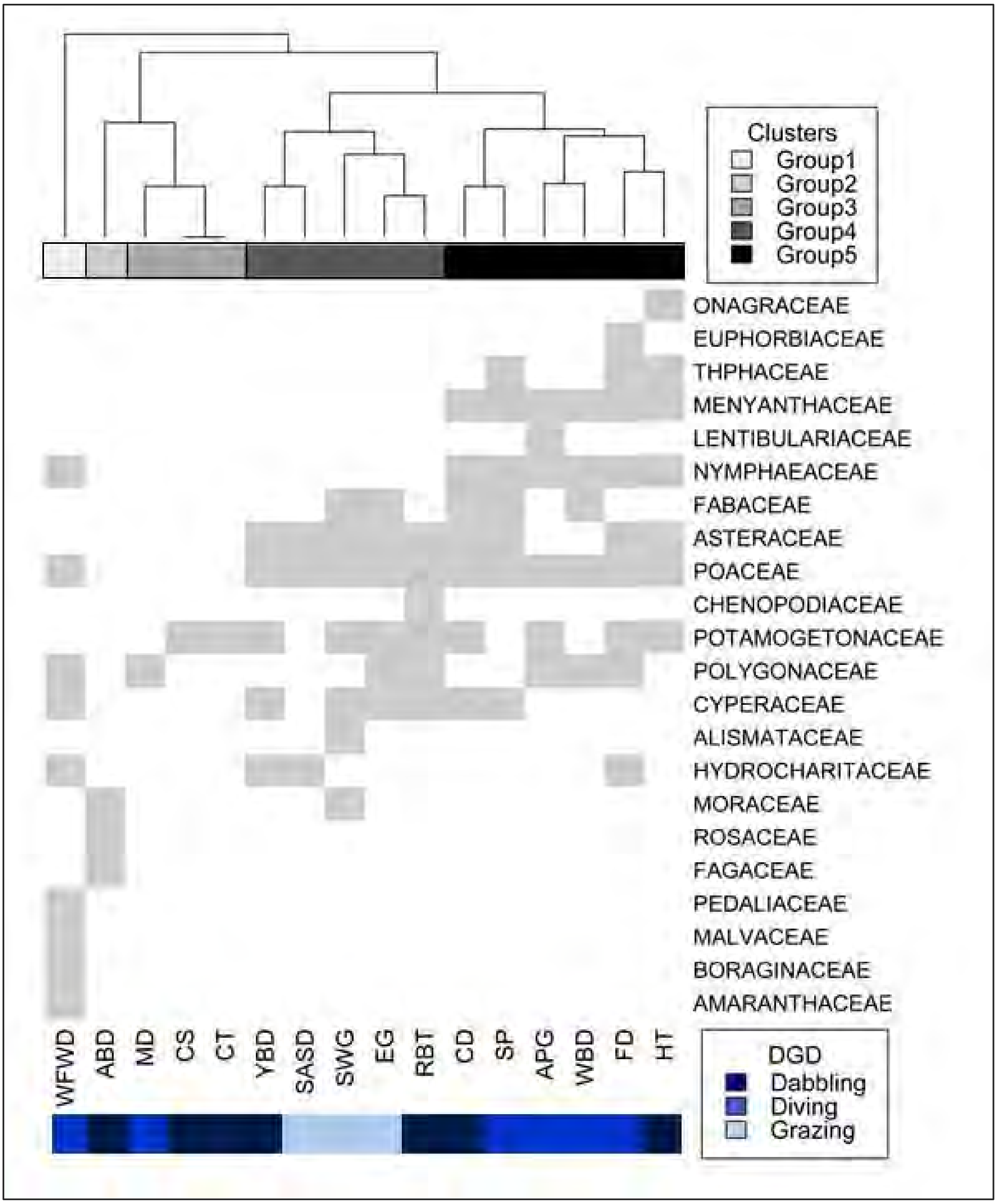

Figure 1 Dendrogram based on binomial deviance and complete linkages illustrating the five functional group clusters of waterfowl based on plant family presence/absence in the diet. Grey shading indicates presence of plant family in diet. WFWD = White-faced Whistling Duck, ABD = African Black Duck, MD = Maccoa Duck, CS = Cape Shoveler, CT = Cape Teal, YBD = Yellow-billed Duck, SASD = South African Shelduck, SWG = Spur-winged Goose, EG = Egyptian Goose, RBT = Red-billed Teal, CD = Knob-billed Duck, SP = Southern Pochard, APG = African Pygmy Goose, WBD = White-backed Duck, FD = Fulvous Whistling Duck and HT = Hottentot Teal. Blue shading represents the *a priori* classification of waterfowl according to the DGD definitions.

7.3 RESULTS

7.3.1 General

A total of 89 plant species from 24 families were recorded in the diets of 16 common southern African waterfowl species (Appendix 7B). Commonly recorded aquatic plants included sago pondweed *Potamogeton pectinatus* and blue waterlily *Nymphaea nouchali*. A total of 20 plant species were non-indigenous to the region and included many naturalised exotic crop species such as maize *Zea mays* and sunflower *Helianthus annuus*, the invasive species white mulberry *Morus alba* and many weedy exotics including Indian heliotrope *Heliotropium indicum* and Willow-weed *Persicaria lapathifolia*. There was also an abundance of terrestrial plant species in the diets, including many species from the Poaceae, but also woody species such as sicklebush *Dicrostachys cinerea* and Oak *Quercus sp*. The most frequently represented plant family in the diet of waterfowl was the Poaceae with 32 plant species identified, followed by the Cyperaceae with 7 plant species identified.

7.3.2 Functional groups

Hierarchical cluster analysis suggested five groups based on plant family presence/absence in the diet of 16 waterfowl species. The clusters maintain a little of the structure suggested by the *a priori* DGD classification (for example, group-5 loosely represents the diving waterfowl and group-4 the grazing waterfowl), but suggest that other factors apart from foraging mode are structuring the plant family assemblages that are dispersed (Fig. 1). The clustering in group-4 is driven by the presence of Poaceae, Asteraceae and Cyperaceae, amongst others, in the diet, whilst the clustering in group-5 by the presence of Nymphaeaceae and Menyanthaceae. White-faced Whistling Duck, despite the precautions taken with the use of the data, formed a unique cluster (group-1), but did show overlap with both group-4 and group-5 in terms of plant family presence in the diet. However, there were also a good number of plant families unique to this species, e.g. Amaranthaceae and Malvaceae that probably drove the formation of the additional cluster. Only in 1% of cases did White-faced Whistling Duck share a cluster with other waterfowl species (Appendix 7C: Table 1). African Black Duck *Anas sparsa* is the region's only true riverine species and formed a single cluster (group-2), showing little overlap with other groups (Fig. 1). Again, the presence of unique families drives the formation of this cluster. Finally, the clustering in group-3 is likely due to a lack of plant components in the diet as these waterfowl species are primarily insectivorous.

The *a priori* classified diving and dabbling waterfowl had similar total numbers of plant species present in the diet, and had almost double the total species present as those classified as grazing (Table 1). However, this result may be confounded by having fewer waterfowl species in the grazing group. Dabbling waterfowl shared 20% and 8% of recorded plant species with diving and grazing waterfowl respectively, but these two groups had very little overlap (< 1%) with each other (Table 1). In comparison, the clusters resolved the plant species data very well with overlap between most of the groups less than 7% in all cases. In five instances, there was no overlap whatsoever (Fig. 2).

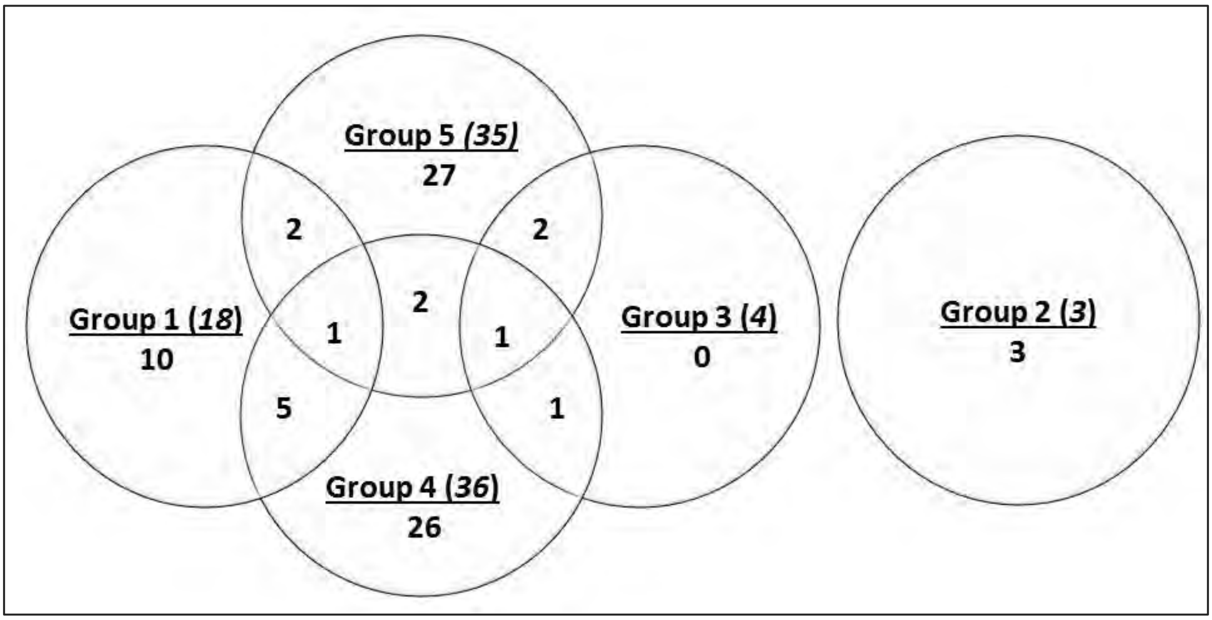

Figure 2 Venn diagram of plants species shared between and unique to each of the functional groups empirically defined by hierarchical clustering of plant family presence/absence in waterfowl diet. Total species richness for each cluster is indicated in parenthesis. Group-2 has no overlap with any of the other functional groups.

Distanced-based redundancy analysis (dbRDA) indicated that differences between the waterfowl species in the composition of plant assemblages in the diet were driven by multiple traits (pseudo-$F_{6,9}$ = 3.23, $p < 0.001$) with three explanatory factors accounting for 68% of the variance (Fig. 3). The effects of all three explanatory variables, primary habitat (pseudo-$F_{2,9}$ = 3.96, p = 0.002), diet preference (pseudo-$F_{2,9}$ = 3.14, p = 0.004) and foraging mode (pseudo-$F_{2,9}$ = 2.89, p = 0.006) on plant assemblage composition in waterfowl diet were all highly significant and accounted for 28%, 20% and 20% of the variance respectively.

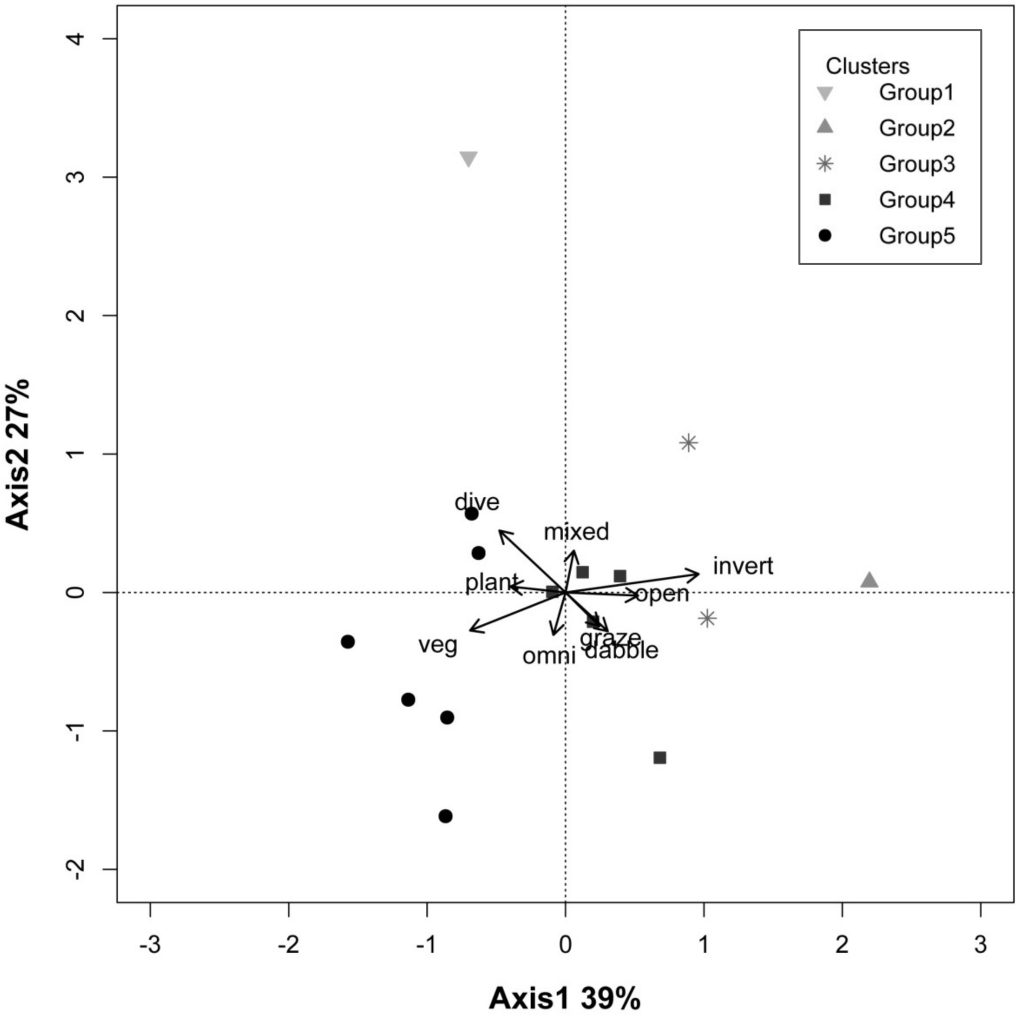

Figure 3 Distance-based redundancy analysis (dbRDA) biplot based on the three explanatory variables of habitat, diet preference and foraging mode fitted to the variation in plant family composition within the diet of different waterfowl species. Vectors indicate the relationship direction between the explanatory factors and the ordination of the clustered waterfowl species represented by the symbols. Grayscale symbols represent the functional groups as determined by cluster analysis. Habitat = *mixed*, *veg* and *open*; diet preference = *plant*, *omni* and *invert*; foraging mode = *dive*, *graze* and *dabble*. Note: Cape Teal and Cape Shoveler plot directly on top of each other, and hence only two points are visible for group-3

7.4 DISCUSSION

The results demonstrate the possibility of several finer-level seed dispersal functional groups within the waterfowl, and suggest that differences are neither so large that we need to resort to species level classifications nor so small that waterfowl can be considered a homogenous group of seed dispersers. There are important differences between the species in their seed dispersal function, with certain plant families uniquely dispersed by a particular suite of waterfowl. These kinds of dietary specialisations yield important insights into the need for a finer level of functional classification beyond the broad "catch-all" of seed dispersal. Furthermore, the use of this data-driven approach is a useful alternative to *a priori* functional group classification as it can readily differentiate species into ecologically meaningful groupings and simultaneously capture variation across multiple functional traits.

7.4.1 Seed dispersal functional groups

The studies included here record a large number of plant species in the diet of southern African waterfowl. Whilst the diet studies do not test for recoverability and viability of seeds, nor do they contain information about transport of seeds, they suggest that waterfowl are capable of dispersing a great diversity of plant species. A surprising number of terrestrial plant species were recorded in waterfowl diets (~ 50% of all seeds). Brochet *et al.* (2009) similarly noted high numbers of terrestrial seeds in the diets of waterfowl across Europe and suggested that they were excellent vectors for terrestrial plants surrounding aquatic habitats. The Poaceae was the most commonly recorded plant family in the diet of southern African waterfowl, suggesting that waterfowl may be important dispersal vectors of grassland plants typically thought to be dispersed by wind (Howe & Smallwood 1982) or large herbivores (Janzen 1983). In addition to terrestrial plants, waterfowl also consumed a number of exotic plant species, with nearly 25% of all species recorded classified as non-native. This finding is of particular interest as waterbirds are often cited as culprits of aquatic invasive species dispersal despite a lack of empirical studies testing this idea (Chapter 6). Many of the exotic species were terrestrial domesticated crop species such as maize, sunflower *Helianthus annuus* and wheat *Tritium sp*., which were prevalent in the diets of the group-4 waterfowl species (Appendix 7B). Waterfowl in this functional group are commonly found in agricultural fields and could therefore more readily contribute to the maintenance of feral populations of domestic crops through dispersal (Twigg *et al.* 2009).

There was evidence for the presence of at least five seed dispersal functional groups based on the presence/absence of particular plant families in the diet. These results support the second prediction, that waterfowl exhibit significant functional differentiation within the clade and should be considered as several separate functional groups of seed dispersers. This suggests that finer-level groupings can be formed that exist at a level of analysis between the broad function of seed dispersal and a species-level classification.

White-faced Whistling Duck formed its own separate group (group-1). It is difficult to ascertain if this species does indeed play a unique role as a seed disperser or if the differences emerge as the other waterfowl species are undersampled. However, comparison with the other well sampled waterfowl species which readily formed multi-species clusters, i.e. Red-billed Teal, Spur-winged Goose and especially the ecologically similar Fulvous Whistling Duck *Dendrocygna bicolor*, suggested that the high number of unique families observed for White-faced Whistling Duck may not just be an artefact of the data. White-faced Whistling Duck are highly nomadic and have a strong preference for ephemeral wetlands (Petrie & Rogers 1997), which may require flexibility in the food items ingested to survive in a highly variable environment. Alternatively, the breadth of habitats which this species occupies (Hockey *et al.* 2005) may result in a variety of different plant species being frequently encountered and ingested. In any case, White-faced Whistling Duck was an interesting outlier amongst the seed dispersing waterfowl and would be an important species to focus on in future studies.

The second major split in the classification was indicative of a diet dichotomy across the waterfowl species. Some waterfowl species are considered principally herbivorous and have plenty of plant species recorded in the diet (group-4 and group-5), whilst others feed predominantly on invertebrates (group-2 and group-3) (Fig. 1). African Black Duck formed its own unique group (group-2). Although the diet of this species is presumed to be primarily benthic invertebrates (Hockey *et al.* 2005), they did have a few seeds in their diet that were mainly from terrestrial fruiting plant species. As southern Africa's only true riverine duck species, they may play an irreplaceable functional role in the seed dispersal of riparian tree species. For example, African Black Duck might facilitate the upstream dispersal of seeds which would ordinarily be dispersed downstream by longitudinal movement of the river (Pollux *et al.* 2005) and play a pivotal role in the re-colonisation of upstream areas.

Waterfowl in group-4 and group-5 are the primary seed dispersers. Group-4 waterfowl were a mixture between our *a priori* defined dabbling and grazing waterfowl. The dabbling Yellow-billed Duck *Anas undulata* and Red-billed Teal as well as the grazing Egyptian Goose *Alopochen aegyptiaca*, Spur-winged Goose and South African Shelduck

Tadorna cana all forage in terrestrial habitats and are the functional group most likely responsible for dispersal at the terrestrial/aquatic interface. Group-5 waterfowl are largely aquatic plant dispersers and, although there were similarities with group-4 in plant families consumed, they also consumed plant species from several unique families (Fig. 1). For example, seeds of the waterlily or Nymphaeaceae family were found exclusively in the diets of group-5 waterfowl. Thus, population declines in waterfowl species represented by group-5, such as African Pygmy Goose *Nettapus auritus* (Okes *et al.* 2008), are of concern not only from a waterbird conservation standpoint, but are suggestive of a possible decrease in ecosystem function (e.g., nitrate removal) when certain aquatic plants are less effectively dispersed. However, dispersal of these plant species may be somewhat resilient to changes in waterfowl community composition as potential functional redundancy within the groupings may exist. The effect of waterbird community composition on dispersal is not well considered in the literature (Raulings *et al.* 2011) and their differences in diet suggest that this is an important consideration in future research.

7.4.2 Comparing classifications

The *a priori* DGD classification has some ability to discriminate between functionally relevant groups (e.g., grazing versus diving waterfowl), but fails to capture important overlap between dabbling and both grazing and diving waterfowl. The hierarchically defined clusters were able to resolve the plant species in the diet into functional groups with minimal overlap and perhaps more convincingly capture variation in the seed dispersal function. The particular value of this clustering approach lies in its ability to resolve the dispersal function of the dabbling waterfowl, which appear to lie on a gradient from non-seed eating species through those foraging in terrestrial habitat and finally to those preferring purely aquatic habitat. Many studies still use *a priori* classifications to produce functional groups (Robertson *et al.* 2013; Sheaves *et al.* 2013; Trueman *et al.* 2014) and thus I reiterate that the choice of trait(s) is critical to the relevance of the classification (Petchey & Gaston 2006; Bernhardt-Römermann *et al.* 2008). The use of the dietary data demonstrates that for some biodiversity-ecosystem relationships the choice of an appropriate and ecologically suitable trait for which we can gather empirical data will better describe variation in function. The assembled data captured information about several functional traits pertaining to seed dispersal that we may not have measured or even considered. In this case study, differences in plant assemblages in the diet of waterfowl could be explained by at least three traits (i.e., habitat, diet preference and foraging mode) which together explained nearly three-quarters of the variance in diet composition (Fig. 3). Therefore, in some instances it seems possible to base functional classifications on data-rich ecological traits and avoid *a priori* groupings.

This approach can be considered useful in demonstrating two things: (1) important functional differences between groups of waterfowl species suggest that finer-level classifications of biodiversity-ecosystem relationships are meaningful and potentially useful; and (2) data-driven approaches of relevant traits can be generally useful in determining ecologically important functional groups. However, several caveats need to be addressed. Firstly, these data do not include information on seed quantities, seed handling or dispersal distances, which are pivotal components of seed dispersal (Wang & Smith 2002). Unfortunately, quantitative data were not always available for this case study, and I would recommend its use in other studies of this nature. Secondly, although I did the best to standardise the data, there are likely to still be biases in sampling effort and sample sizes across species and sampling location. Thus, this approach waits testing on how data of improved quality might affect the predictions and outcomes. Furthermore, the data did not include any information about the role of other waterbird groups (for example shorebirds Charadriiformes and grebes Podicipediformes) which have been known to transport propagules (Green *et al.* 2002). These would be important in a more general analysis of seed dispersal by waterbirds.

These results provide a clear indication that aggregating the seed dispersal functions performed by waterfowl together under a single functional category of ‘seed disperser’ glosses over a set of functionally important distinctions between different species. Failing to recognise these differences will have important implications for our understanding of how dispersal services might change when the distribution and abundance of waterfowl change (*sensu* Dennis & Westcott, 2006), for example due to altered water availability through the building of impoundments. These changes will influence the dispersal of both wetland and terrestrial plants and affect the ecological functions and ecosystem services that they in turn perform and provide. At the same time, there are sufficient similarities between the diets of different waterfowl species that a lower level of functional grouping can reasonably be developed and used without losing important ecological information. For many kinds of problem it is not necessary to consider each species individually; for example, identifying the group of waterbirds most relevant to the spread of exotic plants might be key to predicting invasive spread. This approach is therefore useful in summarising some of the complexity of biodiversity-ecosystem function relationships. It is also interesting to note that I was able to obtain such clear results from published data for a group and study system that are not considered particularly well studied.

In general, therefore, this analysis supports the argument that before basing policy or management decisions about ecosystem services centred on a single broad functional group e.g. seed dispersers, it is important that variation within the functional group is considered in greater depth and using a more organism-focused perspective. If this analysis supports the creation of ecologically meaningful functional groups within a particular analytical context and focal question, there is a sufficient scientific basis for treating the species as functionally interchangeable. A more nuanced, ecologically informed approach to defining functional groups is needed in the future (Wright *et al.* 2006).

Appendix 7A Waterfowl species considered in the review and references to the diet studies

Species	**References**
African Black Duck *Anas sparsa*	Mckinney et al. 1978, Patten 1981
African Pygmy Goose *Nettapus auritus*	Douthwaite 1977; 1980; Brown et al. 1982; Bell 1996
Cape Shoveler *Anas smithii*	Brand 1961; Mitchell 1983
Cape Teal *Anas capensis*	Brand 1961; Winterbottom 1974; Mitchell 1983
Egyptian Goose *Alopochen aegyptiaca*	Taylor 1957; Douthwaite 1978; Halse 1984, 1985; Eriksson 1990; Mangnall & Crowe. 2002
Fulvous Whistling Duck *Dendrocygna bicolor*	Schluten 1974; Douthwaite 1977; Clark 1978; Rogers & Breen 1990
Hottentot Teal *Anas hottentota*	Douthwaite 1977
Knob-billed Duck *Sarkidiornis melanotos*	Douthwaite 1978; Rogers & Breen 1990
Maccoa Duck *Oxyura maccoa*	Brown et al. 1982
Red-billed Teal *Anas erythrorhyncha*	Skead 1977; Woodall 1979; Mitchell 1983; Petri 1996
South African Shelduck *Tadorna cana*	Geldenhuys 1977
Southern Pochard *Netta erythrophthalma*	Douthwaite 1977; Skead & Mitchell 1983
Spur-winged Goose *Plectropterus gambensis*	Halse 1985
White-backed Duck *Thalassornis leuconotus*	Schulten 1974; Douthwaite 1977; Wintle 1981
White-faced Whistling Duck *Dendrocygna viduata*	Douthwaite 1977; Brown et al. 1982; Rogers & Breen 1990; Petrie & Rogers 1996; Petrie 2000; Petri 2005
Yellow-Billed Duck *Anas undulata*	Skead 1981; Brown et al. 1982

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Appendix 7B The presence of plant species recorded in the diet of 16 waterfowl species from across southern Africa. The total number of species per a plant family is also indicated. Habitat and status refers to the primary habitat and status listed in the Red List of South African Plants (SANBI, 2014). *exotic species $^{+}$ terrestrial species.CT = Cape Teal, RBT = Red-billed Teal, HT = Hottentot Teal, CS = Cape Shoveler, ABD = African Black Duck, YBD = Yellow-billed Duck, CD = Knob-billed Duck, FD = Fulvous Whistling Duck, WFWD = White-faced Whistling Duck, SP = Southern Pochard, MD = Maccoa Duck, APG = African Pygmy Goose, WBD = White-backed Duck, EG = Egyptian Goose, SWG = Spur-winged Goose and SASD = South African Shelduck

	CT	RBT	HT	CS	ABD	YBD	CD	FD	WFWD	SP	MD	APG	WBD	EG	SWG	SASD	Total
ALISMATACEAE															**1**		**1**
*Alisma plantago-aquatica**															1		1
AMARANTHACEAE									**1**								**1**
Amaranthus sp.+									1								1
ASTERACEAE		**3**	**1**				**1**	**1**	**2**	**1**				**1**	**1**	**1**	**12**
Ambrosia artemisiifolia+*		1	1				1	1	1	1							6
Ambrosia sp.+									1								1
Helianthus annuus+*		1												1	1	1	4
Schkuhria pinnata+*		1															1
BORAGINACEAE									**1**								**1**
Heliotropium indicum+*									1								1
CERATOPHYLLACEAE									**1**								**1**
Ceratophyllum demersum									1								1
CHENOPODIACEAE		**1**							**1**								**3**
Atriplex sp.+		1							1								2
Chenopodium sp.+									1								1
CYPERACEAE		**3**				**1**	**1**		**3**	**1**				**2**	**1**		**12**
Cyperus articulatus														1			1
Cyperus difformis									1								1

	CT	RBT	HT	CS	ABD	YBD	CD	FD	WFWD	SP	MD	APG	WBD	EG	SWG	SASD	Total
Cyperus esculentus							1							1			2
Cyperus laevigatus															1		1
Cyperus sp.									1								1
Eleocharis sp.+		1				1											2
Fuirena sp.+		1															1
Scirpus littoralis										1							1
Scirpus sp.		1							1								2
EUPHORBIACEAE								**1**									**1**
Acalypha segetalis+								1									1
FABACEAE							**2**		**1**	**1**			**1**	**1**	**1**		**7**
Aeschynomene fluitans+							1										1
Aeschynomene nilotica+							1										1
Aeschynomene nodulosa+													1				1
Aeschynomene pfundi+										1							1
Dichrostachys cinerea+									1								1
Medicago sativa+*														1	1		2
FAGACEAE					**1**												**1**
Quercus sp.+*					1												1
HYDROCHARITACEAE						**1**		**1**	**1**							**1**	**4**
Lagarosiphon sp.						1										1	2
Najas horrida								1	1								2
LAMIACEAE									**1**								**1**
Salvia sp.+									1								1
LENTIBULARIACEAE												**1**					**1**
Utricularia inflexa												1					1

	CT	RBT	HT	CS	ABD	YBD	CD	FD	WFWD	SP	MD	APG	WBD	EG	SWG	SASD	Total
MALVACEAE									**2**								**2**
Hibiscus sp.+									1								1
Sida rhombifolia+									1								1
MENYANTHACEAE			**1**				**1**	**1**		**1**		**1**	**1**				**6**
Nymphoides indica			1				1	1		1		1	1				6
MORACEAE					**1**										**1**		**2**
Ficus sp.+															1		1
Morus sp.+					1												1
NYMPHAEACEAE			**1**				**1**	**1**	**1**	**1**		**1**	**1**				**7**
Nymphaea nouchali							1	1		1		1	1				5
Nymphaea sp.			1						1								2
ONAGRACEAE			**1**														**1**
Ludwigia stolonifera			1														1
PEDALIACEAE									**1**								**1**
Sesamum triphylum+									1								1
POACEAE		**8**	**5**			**1**	**6**	**7**	**12**	**3**		**6**	**2**	**5**	**11**	**3**	**69**
Avena sativa+*														1	1		2
Brachiaria xantholeuca+							1										1
Cynodon dactylon+														1	1		2
Dactyloctenium aegyptiu+		1							1								2
Digitaria ciliaris+*			1				1	1				1					4
Digitaria ternata+												1					1
Digitatria sp.+		1															1
Echinochloa colona+			1				1										2
Echinochloa crus-galli+									1								1

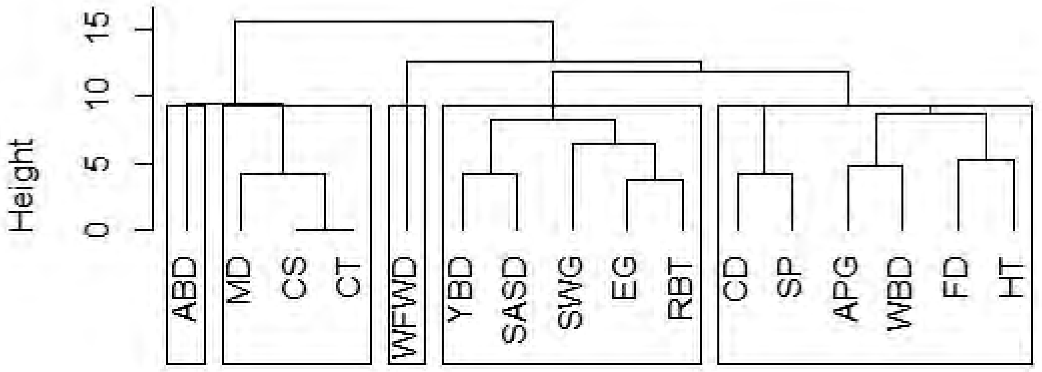
	CT	RBT	HT	CS	ABD	YBD	CD	FD	WFWD	SP	MD	APG	WBD	EG	SWG	SASD	Total
Echinochloa pyramidalis+									1								1
Echinochloa stagnina+								1		1		1	1				4
Eleusine indica+															1		1
Eriochloa sp+									1								1
Eriochloa stapfiana+		1															1
Hordeum vulgare+*														1	1		2
Leersia sp.+		1							1								2
Oryza barthii								1									1
*Oryza sativa**								1		1							2
Oryza sp.															1		1
Panicum coloratum+									1								1
Panicum repens+															1		1
Panicum schinzii+		1							1								2
Panicum subalbidum+												1					1
Paspalidium geminatum+			1					1		1			1				4
Paspalum scorbiculatum+		1	1						1								3
Paspalum urvillei+*												1					1
Phragmites australis															1		1
Sacciolepsis africana+			1				1					1					3
Sorghum bicolor+								1									1
Sorghum halepense+*									1								1
Sorghum sp.+									1						1	1	3
Sorghum verticilliflorum+							1										1
Triticum sp.+*		1												1	1	1	4
Urochloa panicoides+															1		1

	CT	RBT	HT	CS	ABD	YBD	CD	FD	WFWD	SP	MD	APG	WBD	EG	SWG	SASD	Total
Urochloa sp.+									1								1
Vossia cuspidata							1	1									2
Zea mays+*		1				1			1					1	1	1	6
POLYGONACEAE		**3**						**2**	**3**		**2**	**1**	**2**	**1**			**14**
Persicaria lapathifolia+*		1							1								2
Persicaria limbata+*												1	1				2
Persicaria serrulata+									1								1
Persicaria sp.+								1			1						2
Polygonum aviculare+*		1							1								2
Polygonum senegalense+*														1			1
Polygonum sp.+								1			1		1				3
POTAMOGETONACEAE	**1**	**2**	**1**	**1**		**1**	**1**	**1**				**1**		**1**	**2**		**12**
Potamogeton crispus	1		1				1	1							1		5
Potamogeton pectinatus		1		1		1								1	1		5
Potamogeton sp												1					1
ROSACEAE					**1**												**1**
Pyracantha sp.+*					1												1
THPHACEAE			**1**					**1**		**1**							**3**
*Typha domingensis**			1					1		1							3
Total	**1**	**18**	**11**	**1**	**3**	**4**	**13**	**16**	**32**	**9**	**2**	**11**	**7**	**11**	**18**	**5**	

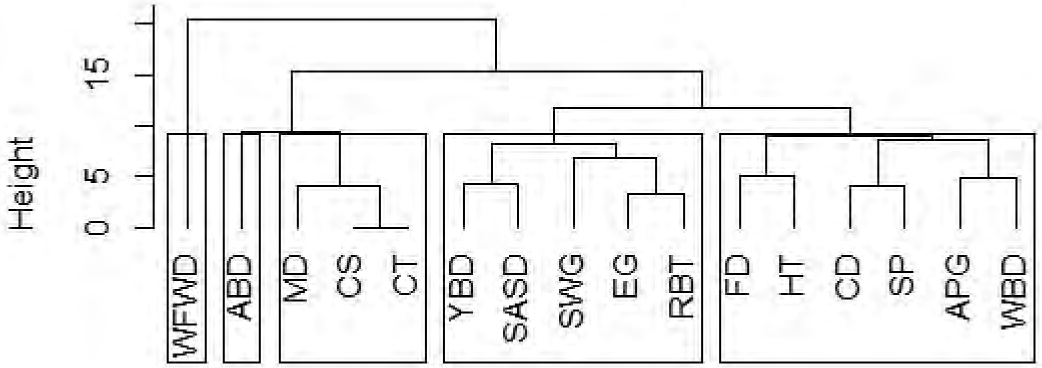
Appendix 7C

Figure 1 Three additional alternative configurations of the dendrogram based on 1000 iterations of plant family presence/absence in the diet of southern African waterfowl. Black borders denote cluster membership as determined by Mantel's correlation coefficient. (a) The second most common configuration, occurring in 24% of cases; (b) the third most common configuration, occurring 10% of cases; and (c) the fourth most common configuration occurring in 8% of cases. WFWD = White-faced Whistling Duck, ABD = African Black Duck, MD = Maccoa Duck, CS = Cape Shoveler, CT = Cape Teal, YBD = Yellow-billed Duck, SASD = South African Shelduck, SWG = Spur-winged Goose, EG = Egyptian Goose, RBT = Red-billed Teal, CD = Knob-billed Duck, SP = Southern Pochard, APG = African Pygmy Goose, WBD = White-backed Duck, FD = Fulvous Whistling Duck and HT = Hottentot Teal.

(a)



(b)



(c)

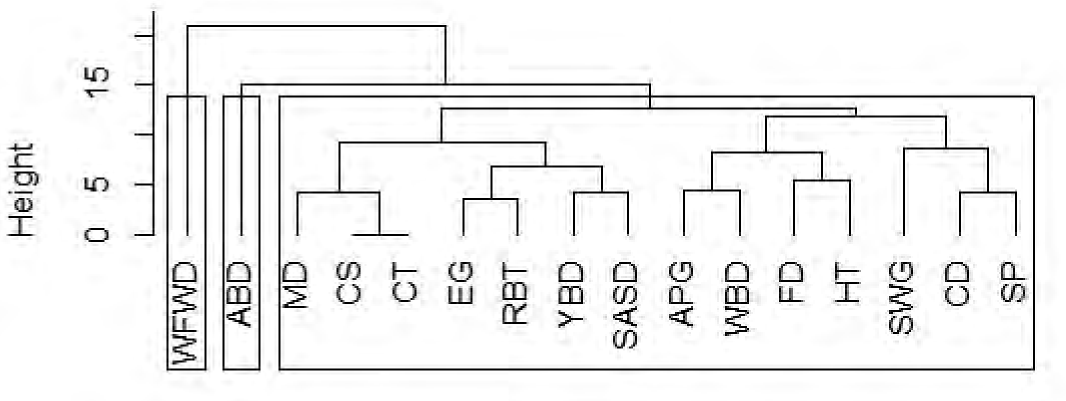

Height
0
5
15
WFWD
ABD
MD
CS
CT
EG
RBT
YBD
SASD
APG
WBD
FD
HT
SWG
CD
SP

Table 1 Pairwise comparison of the percentage of cases in which waterfowl species were ascribed to the same cluster over 1000 iterations. Darker shading indicates high overlap between the waterfowl species in group membership, and lighter shading indicates poor overlap. WFWD = White-faced Whistling Duck, ABD = African Black Duck, MD = Maccoa Duck, CS = Cape Shoveler, CT = Cape Teal, YBD = Yellow-billed Duck, SASD = South African Shelduck, SWG = Spur-winged Goose, EG = Egyptian Goose, RBT = Red-billed Teal, CD = Knob-billed Duck, SP = Southern Pochard, APG = African Pygmy Goose, WBD = White-backed Duck, FD = Fulvous Whistling Duck and HT = Hottentot Teal.

	WFWD	**ABD**	**MD**	**CS**	**CT**	**YBD**	**SASD**	**SWG**	**EG**	**RBT**	**CD**	**SP**	**APG**	**WBD**	**FD**	**HT**
WFWD																
ABD	0															
MD	0	1														
CS	0	1	100													
CT	0	1	100	100												
YBD	1	0	13	13	13											
SASD	1	0	13	13	13	100										
SWG	1	0	12	12	12	98	98									
EG	1	0	13	13	13	100	100	98								
RBT	1	0	13	13	13	100	100	98	100							
CD	1	0	11	11	11	12	12	15	13	13						
SP	1	0	11	11	11	12	12	15	13	13	100					
APG	0	0	11	11	11	11	11	12	11	11	98	98				
WBD	0	0	11	11	11	11	11	12	11	11	98	98	100			
FD	0	0	11	11	11	11	11	12	11	11	98	98	100	100		
HT	0	0	11	11	11	11	11	12	11	11	98	98	100	100	100	

CHAPTER 8

SOWING THE SEEDS OF SUCCESSION: A SYNTHESIS OF WATERBIRD-MEDIATED DISPERSAL IN SOUTHERN AFRICA

Photo by: Anon

8.1 OVERVIEW

The ability of organisms to reach and persist in isolated habitats has long fascinated scientists (Darwin 1859; Ridley 1930), from the colonisation of oceanic islands (Nogales *et al.* 2012) to the occupation of rock pools across expansive deserts (Jocque, Vanschoenwinkel & Brendonck 2010). However, in recent years this curiosity has developed into an obsession, in part driven by a need to understand the movement of organisms that are threatened by habitat fragmentation and global climate change, as well as reduce the spread of invasive species (Higgins & Richardson 1999; Trakhtenbrot *et al.* 2005; Pearson & Dawson 2005; Gosper *et al.* 2005). A simple search in the ISI Web of Science for the keyword "dispersal" indicates that since the turn of the millennium over 24 000 publications have addressed this topic on some level. It seems almost unimaginable that amongst such an abundance of information, the dispersal capacity of many species is still largely unknown. In this thesis, I attempted to address one such knowledge gap; the role of waterbirds as vectors in the dispersal of seeds and aquatic invertebrates in southern African.

This research is timely in that it extends on the recent interest in waterbird-mediated dispersal in the literature (see Santamaría & Klaassen 2002), and address an obvious gap in our knowledge of this phenomenon on the African continent. In studying the mechanisms underlying the dispersal of both indigenous and exotic propagules by waterbirds, I have been able to expand on previous work to show commonalities and differences between the southern African system and what is known from studies in the northern hemisphere. Additionally, this work will allow future studies to address previously unexplored hypotheses that focus on differences in waterbird movement strategies or on differences in the ecology of seeds across continents. This thesis has demonstrated that differences in propagule traits and waterbird ecology interact to influence the patterns of dispersal in aquatic systems. Determining the causes and consequences of the high intra- and interspecific variation amongst propagules and vectors are important areas of future research.

This study also demonstrates the important and underappreciated role of waterbirds in connecting isolated wetland environments. The scale of connectivity has important ecological implications as dispersal is a key process for the organisation of communities (Leibold *et al.* 2004). Additionally, dispersal is predicted to be an important factor facilitating the persistence of populations in spatially and temporally variable environments, such as ephemeral wetlands (Levin *et al.* 1984; McPeek & Holt 1992). The results of this thesis show that waterbirds have a high capacity for the dispersal of aquatic propagules across multiple scales and lay the foundation for future studies to further address questions related to dispersal and its role in aquatic community assembly and persistence in heterogeneous environments. Finally, understanding the scale of dispersal in wetlands brought about through waterbird-mediated dispersal has important conservation implications, especially in managing the risk of aquatic invasive spread.

8.2 GENERAL DISCUSSION

8.2.1 The dispersal framework

Understanding dispersal requires measuring the spatial patterns of dispersed propagules and exploring the mechanisms that generate them (Levin *et al.* 2003). I utilised a mechanistic framework, which describes the dispersal of propagules as following three consecutive stages (propagule uptake by the vector, transport by the vector and deposition of viable propagules), to synthesise my findings on waterbird-mediated dispersal in southern Africa. Qualitative and quantitative elements of the capacity and scale of dispersal are evaluated by identifying: (1) *what* propagules are dispersed, (2) *how* propagules are dispersed and (3) *where* viable propagules are deposited. In summary, multiple waterbird species have the capacity to disperse seeds of terrestrial and aquatic plants and the resting eggs of aquatic invertebrates, of both native and alien species, via ecto- and endozoochory and can facilitate dispersal across multiple spatial scales (Fig. 1).

8.2.1.1 Emigration - What propagules are dispersed?

The first task in studying waterbird-mediated dispersal in a new region is to establish baseline information on the identity of propagules dispersed. The results from Chapters 2 and 7 show that an incredible diversity of plant propagules are taken up by a variety of waterfowl species in southern Africa, with over 132 unique species of plant seed identified from a field study and a literature review of waterfowl diet. This estimate alone surpasses the 97 plant species identified as waterbird dispersed by van Leeuwen *et al.* (2012) and suggests that as additional studies are undertaken in different regions the list of propagules will continue to grow. What these results also revealed was the capacity of waterfowl to disperse the seeds of terrestrial plants; from woody plant species such as oak *Quercus sp.* through a variety of grass seeds to the agricultural grains of maize *Zea mays* and wheat *Triticum sp*. Furthermore, many of the plant species identified are considered exotic to the region, and some are classified as invasive species e.g. cockleburr *Xanthium strumarium*. These results were similar to other studies conducted in the northern hemisphere and Australia where a significant proportion of propagules dispersed were exotic species and/or terrestrial species (Green *et al.* 2008; Brochet *et al.* 2009; Raulings *et al.* 2011). The dynamics of waterbird-mediated dispersal thus supersede the expected effects on just aquatic communities, reach into terrestrial ecosystems, and should be acknowledged in the spread of exotic species (Bruun *et al.* 2008; Green 2015).

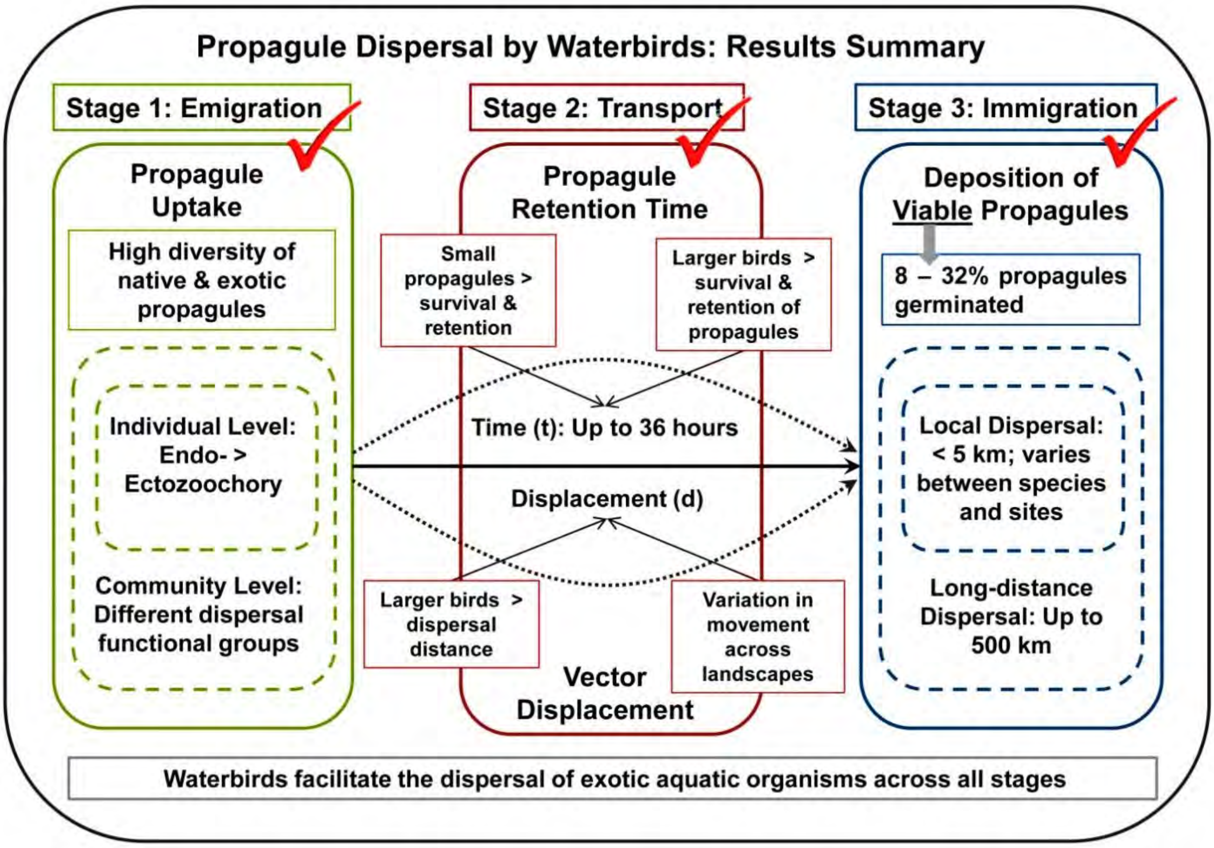


Figure 1 Summary of main findings in the context of the three stage mechanistic framework describing waterbird-mediated dispersal in southern Africa. Each stage is represented in a separate colour. Dashed boxes indicate where a single process has been addressed at different scales or levels. Red ticks indicate that waterbirds facilitate dispersal across all three stages.

Similarly to other studies, I was also able to quantitatively conclude that endozoochory, rather than ectozoochory, is the main dispersal mode in the field (Brochet *et al.* 2010b). The results of Chapter 2 show that many more seeds are taken up through foraging activities than inadvertently adhere to the feathers and feet. One may be tempted to "give up" on ectozoochory as a dispersal mode altogether, but ectozoochory may be somewhat complementary to endozoochory in terms of the species of propagules dispersed. The structures of the different propagules did not follow strict dispersal syndromes (Howe & Smallwood 1982) in that barbed seeds attached externally were also sometimes identified in the faecal samples, and hard, round seeds generally found in faecal samples were occasionally attached to the feet encased in sticky mud. This makes it difficult to predict *a priori* how a particular seed species might be dispersed. However, as noted by Tackenberg, Poschlod & Bonn (2003) dispersal is plastic and ascribing certain species to particular dispersal modes may not be useful in addressing ecological questions. Instead, quantifying the dispersal potential across different modes may be a valuable alternative approach (Tackenberg *et al.* 2003). If we review the results in light of this approach then individual seed species can be seen to have different capacities for dispersal by different modes, which will influence the quantity of propagules dispersed, the scale of transport, and the condition of propagules on arrival at a new site, and ultimately affect the spatial patterns of seed dispersal.

The broad range of plant species identified as dispersed by waterfowl, which extend across multiple habitat types and lack apparent adaptations for dispersal, may lead one to conclude that waterfowl play a generalist role in dispersal. However, the findings in Chapter 7 indicate that amidst this general dispersal ability is a more nuanced, specialist role. At a community level these results show that amongst the indigenous southern African waterfowl there are several seed dispersal functional groups. There was overlap in dispersed plant families between several of the functional groups, but there were also a number of plant families dispersed exclusively by certain suites of waterfowl. What is more, these functional groups represented differences in diet preference, habitat preference, and foraging mode between the waterfowl and suggest that what is ingested and ultimately dispersed is representative of differences in the ecology of the waterfowl. This well-known hypothesis (Green *et al.* 2002) has proved difficult to demonstrate as it requires comprehensive data on diet and/or dispersal across a complete set of waterbirds, but is an important area of future research.

Whilst the above summary focusses on the dispersal of seeds by waterfowl, many of the conclusions can be applied in the dispersal of aquatic invertebrate propagules. The findings in Chapter 3 demonstrate that southern African waterfowl take up the propagules of aquatic invertebrates and again supports the conclusion that endozoochory is the more effective mode of dispersal in the field. The dispersal of aquatic invertebrates by waterbirds has particular relevance in the spread of invasive species, as some of the world's worst aquatic invaders are invertebrates (Lowe *et al.* 2000). For example, in Chapter 6 the invasive American brine shrimp *Artemia franciscana* was identified as actively taken up by waterbirds, and dispersed via both endo- and ectozoochory.

Several studies have identified propagules of exotic species in the diet of, or attached externally to, waterbirds (Green *et al.* 2008; Brochet *et al.* 2010b; Raulings *et al.* 2011), It was thus surprising that the explicit role of waterbirds in the spread of invasive species had not been well investigated. In Chapter 6, I looked for quantitative evidence to critically evaluate the role that waterbirds play in the dispersal of aquatic invasive species. Although studies empirically addressing this topic were rare, there was good evidence that waterbirds actively take up the propagules of exotic species and suggest that this is a worthwhile direction for future enquiry.

8.2.1.2 Transport - How are propagules dispersed?

The transport stage of dispersal comprises two subcomponents: (1) the retention time of the propagule and (2) the displacement of the vector over that time. Each subcomponent in turn is affected by propagule traits and vector traits. The transport of propagules can be better described by addressing factors affecting gut retention times and vector displacement. Therefore, as a starting point, I wanted to determine how propagule traits mediate gut retention and recovery and how vector size and behaviour affects the distances propagules are dispersed.

In Chapter 4, I explored how the seed characteristics of size and hardness influence the retention time and recovery of seeds passing through the gut of two differently sized waterfowl species, Egyptian Goose and Red-billed Teal. Small seed size appears to enhance endozoochory by two complementary mechanisms: (1) small seeds have higher recoverability, and (2) small seeds are retained longer in the gut and are thus likely to be dispersed further. Seed hardness played a secondary role in facilitating the recovery of seeds after gut passage. The observed role of small seed size in facilitating endozoochory reiterates the findings of other studies (Mueller & Valk 2002; Soons *et al.* 2008; Figuerola *et al.* 2010), and is perhaps evidence for the emergence of a “dispersal syndrome” amongst waterbird-dispersed plants. If small seeds almost exclusively enjoy higher recovery and longer retention times and these outcomes promote successful dispersal, then there will be selection for small-seeded plants or small-seeded phenotypes. Support for this argument comes from a recent meta-analysis suggesting that 1 mm propagules have double the probability for dispersal via endozoochory by waterbirds than a 10 mm propagule (van Leeuwen *et al.* 2012b). However, at least for terrestrial plants the potential for seedling establishment is considered to vary positively with seed size (Levin & Muller-Landau 2000), and these trade-offs between establishment and dispersal must therefore also be considered before determining the effectiveness of small seeds as a dispersal syndrome. Additionally, trade-offs in seed size and attractiveness to the waterbird vector must also be considered as larger seeds are generally more nutritious and therefore preferentially selected. In terrestrial systems it is well-established that larger seeds are more commonly predated upon (Moegenburg 1996; Gómez 2004). Therefore, it is likely that there is an optimal size (or optimal size range) of seeds effectively dispersed by waterbirds as a result of the conflicting trade-offs between dispersal ability and establishment and/or attractiveness.

Ingested seeds were retained for longer and recovered in higher numbers from the larger Egyptian Goose than Red-billed Teal, and were attributed to a longer digestive tract and poor digestive efficiency amongst herbivorous waterfowl respectively (Chapter 4). Furthermore, Egyptian Geese have a faster flight speed and greater mean daily movements than Red-billed Teal (Cumming *et al.* 2012). These two factors, combined with the longer retention times, resulted in higher average dispersal distances for wetland plants dispersed by the Egyptian Goose (Chapter 5). Thus, in this study it seems reasonable to conclude that larger birds are better vectors as they retain seeds longer, digest fewer seeds, and fly further. However, these trends are not consistent across studies, for example Viana *et al.* (2013a) showed that dispersal distances decreased with increasing body mass during migratory flight due to trade-offs in distance and speed undertaken to optimise migratory efficiency. Additionally, García-Álvarez *et al.* (2015) demonstrated that seed retention was actually longer in the smaller Mallard Duck than for Greylag Goose. We appear to have made good progress in unravelling the propagule traits that facilitate dispersal (at least for endozoochory), but much more work needs to be undertaken on elucidating the role of the vector in terms of both digestive physiology and movement.

Movement is an incredibly complex behaviour, and influenced by both internal and environmental factors (Nathan *et al.* 2008a) which will have consequences for the spatial patterns of propagule dispersal. The individual dispersal kernels produced for each study population in Chapter 5 showed high variation in mean and maximum dispersal distances. Whilst I did not explicitly quantify landscape effects on waterbird movement, it is clear from just glancing at the land cover data and individual trajectories (Chapter 5 – Figure 1) that movement strategies vary remarkably across the study sites and between individuals. These differences have implications for the distances that seeds are moved, and it is therefore imperative that dispersal is assessed at multiple spatio-temporal scales. Typically, studies have modelled dispersal during one period of the annual cycle, migration, and viewed it as a long-distance unidirectional movement that has consequences for the continental distributions of aquatic species (Charalambidou, Santamaría & Figuerola 2003b; Soons *et al.* 2008; Viana *et al.* 2013b). In contrast, very little attention has been paid to the nomadic wanderings of non-migratory waterbirds or even the daily movements of waterbirds. The dispersal of aquatic propagules need not only be addressed in the context of long-distance dispersal, and determining the scales at which waterbirds disperse propagules on a local level will have important implications for our understanding of wetland community dynamics.

Finally, whilst this thesis primarily explored the role of waterfowl in the dispersal of aquatic plants and invertebrates, it must be acknowledged that other waterbird vectors (grebes, gulls, shorebirds etc.) can and do disperse the propagules of aquatic organisms (Green *et al.* 2008; Sánchez *et al.* 2012; van Leeuwen *et al.* 2012b). Southern Africa does not support any inter-continental migratory waterfowl, but there are numerous inter-continental migratory shorebirds that frequent the region (Hockey *et al.* 2005). In comparison to the waterfowl, these migratory shorebirds are capable of connecting wetlands at much larger spatial scales, and over evolutionary time may have contributed to the cosmopolitan distribution of many aquatic invertebrates across the African continent (Mergeay *et al.* 2006). However, there is still some debate as to the long-distance dispersal capacity of migratory shorebirds as they tend to decrease the size of the digestive organs prior to long-distance migration (Piersma & Gill 1998), thus likely reducing the ability to transport propagules via the gut. Other waterbird vectors, such as coots and grebes, are generally sedentary within the region and typically inhabit more permanent wetlands; however they may also undertake occasional nomadic movements of up to a few hundred kilometres to find productive habitat

(Hockey *et al.* 2005). The realised waterbird-mediated dispersal distances in the region will therefore likely include a much wider range then when considering only waterfowl as dispersers, and might vary from long-distance dispersal facilitated by migratory shorebirds to local dispersal within a wetland. Thus, more research on a variety of waterbirds is needed to fully describe the scale(s) at which waterbirds transport propagules of aquatic organisms.

8.2.1.3 Immigration - Where are viable propagules deposited?

The final stage of dispersal requires the deposition of viable propagules in a new habitat, but this is very difficult to quantify given the challenges of tracking seeds over large distances. Furthermore, high biotic resistance to immigrating seeds, for example through priority effects (De Meester *et al.* 2002), makes determining the success of dispersal with molecular techniques problematic. The ecological significance of immigration depends on whether dispersal results in the successful establishment of new individuals, and is a poorly considered topic in dispersal. Whilst I could not explicitly measure the establishment of dispersed seeds in the field, I did use germination as a proxy for ability to establish. Seed dispersal effectiveness is the product of the quantity and quality elements of dispersal and encompasses the number of propagules dispersed by a vector and the probability that the dispersed propagule produces a new reproductive adult (Schupp *et al.* 2010). Viability, a measure of quality, does appear to be high with germination trials conducted in Chapter 2 indicating that 15% and 8% of ecto- and endozoochory samples respectively contained at least one germinating seed. Additionally, Chapter 4 revealed that for some seed species up to 86% of all seeds recovered germinated. Thus, there appears to be good potential for the dispersal of viable seeds by waterfowl, especially considering the abundance and diversity of waterfowl in the region. Although many more studies are needed, seed dispersal effectiveness appears to be very high for waterbird-mediated dispersal as both large numbers of seeds are deposited and many of these remain viable.

To measure the spatial scale at which viable seeds could be dispersed I used a simple mechanistic model combining two sets of data: the gut passage times of viable seeds and high-resolution movement data from GPS satellite telemetry of Egyptian Goose and Red-billed Teal. The modelling results in Chapter 5 indicate that this dispersal most commonly occurs over the scale of a few kilometres (< 5 km). Additionally, if we consider the median and not the mean, then the dispersal distance decreases to a few hundred meters. The dispersal distances were constrained by the daily movement patterns of the waterfowl, moving between foraging areas and roost sites. What this suggests is that waterbirds connect wetlands well on a small-scale (300 m – 5 km) with directed movements between productive foraging wetlands. Whilst it remains to be tested in southern Africa, we would expect gene flow across populations of commonly dispersed aquatic plants and invertebrates to be high at this scale.

While less common than local dispersal, long distance dispersal was modelled at distances of nearly 500 km from a source (Chapter 5), although this also varied remarkably between the different study populations. This type of long distance dispersal may explain why many aquatic organisms are widely distributed (Santamaría 2002). Long-distance dispersal is a commonly invoked mechanism for explaining why some organisms have widespread ranges (Cain 2000; Nathan 2006), and for migratory waterbirds modelling attempts have shown the potential of these species to influence continent wide distributions of aquatic plants and invertebrates (Viana *et al.* 2013b). My results demonstrate that, in southern Africa, waterfowl can facilitate not only local dispersal, but also regional dispersal.

8.2.2 Revisiting the dispersal framework - the movement ecology of plants

The dispersal framework is a useful tool for conceptualising the movement of propagules from a source, but is perhaps too simple in that it does not focus on the complexities of vector movement or the evolutionary drivers of dispersal. The process that underpins both active and passive dispersal is the movement of organisms through space, thus key to a deeper understanding of dispersal is unravelling the causes and consequences of movement for both vector and propagule. The new emerging "movement ecology" paradigm aims to unify both ecological and evolutionary processes in organismal movement into a single cohesive theory (Nathan 2008). A four part theoretical framework was proposed by Nathan *et al.* (2008) for addressing organismal movement which integrates three movement components related to a focal individual (the internal state, motion capacity and navigation capacity) with various abiotic and biotic environmental factors. The framework embraces both proximate and ultimate drivers of movement, seeking to understand how, why and where organisms move and how these factors are influenced by interactions with the environment. To apply the movement ecology framework to seed dispersal we need to link the movement ecology of seeds to the movement ecology of vectors (Damschen *et al.* 2008;

Wright *et al.* 2008; Trakhtenbrot, Katul & Nathan 2014). Damschen *et al*. (2008) proposed a revised movement ecology framework (Fig. 2) which includes the movement ecology of dispersal vectors as a second class of external factors influencing the movement of propagules (the other being environmental factors).

Applying this framework to waterbird-mediated dispersal, we must first consider the internal state of the plants or the "why disperse" component. As seen in Chapter 5 the majority of individuals settle relatively close to their natal site, but a few are spread out over large distances. This strategy is considered an adaptation to living in ephemeral habitats and allows a species to spread risk in variable environments while also taking advantage of currently favourable conditions (Burgess *et al.* 2015). As shown in Chapter 4, certain propagule traits can perhaps influence the success of this strategy and drive selection for particular dispersal syndromes. However, dispersal also has costs, including deposition in unfavourable habitats or risk of digestion (Matthysen 2012). Any assessment of the drivers of dispersal thus requires consideration of the trade-offs between the advantages of the spatial displacement of individuals and the costs of such movements (Burgess *et al.* 2015).

Next we would turn our attention to the motion and navigation capacities of the vector or the "how and where" components respectively. We have already established that the distance and direction that propagules are dispersed is a result of an interaction between vector traits and propagule traits. This in my opinion is where the movement ecology paradigm has the ability to best enhance our understanding of waterbird-mediated dispersal. Through encouraging hypothesis driven research about how internal factors (e.g. hunger), the navigation and motion capacities (e.g. age or sex-related) and environmental factors (e.g. landscape configuration or season) influence vector movement we can gain a better understanding of the influence of vector behaviour on the spatial distribution of dispersed seeds. The use of GPS satellite telemetry and accelerometers linked with high resolution land cover and environmental data sets has the ability to provide incredible insight into the movement decisions of vectors (Kays *et al.* 2015). Studies in frugivory have already begun incorporating such technologies into models of seed dispersal and have revealed the importance of considering animal behaviour at multiple spatio-temporal scales (Kays *et al.* 2011; Côrtes & Uriarte 2013; Mueller *et al.* 2014). Additionally, the results of Chapter 5 showed how variable dispersal distances were between different populations of waterbirds, and determining what combination of internal and external factors influence these movement decisions is a vital next step. At the same time, there is scope to develop our understanding of propagule motion and navigation capacity as a function of vector digestive physiology (e.g. digestive plasticity during moult), allometric scaling (e.g. size of gizzard between species) and vector activity (e.g. roosting versus flying), amongst other factors. The digestive system of waterbirds is very plastic and the size of digestive organs change during certain life history stages such as migration or moult (Piersma & Gill 1998; Ndlovu *et al.* 2010). Furthermore, several studies have shown that vector activity such as swimming or walking decreases the digestive efficiency leading to higher recovery of propagules (van Leeuwen *et al.* 2012a; Kleyheeg *et al.* 2014). These studies suggest that there is considerable variation in the number of propagules that survive through the gut or in gut passage times, which ultimately affect where propagules are deposited.

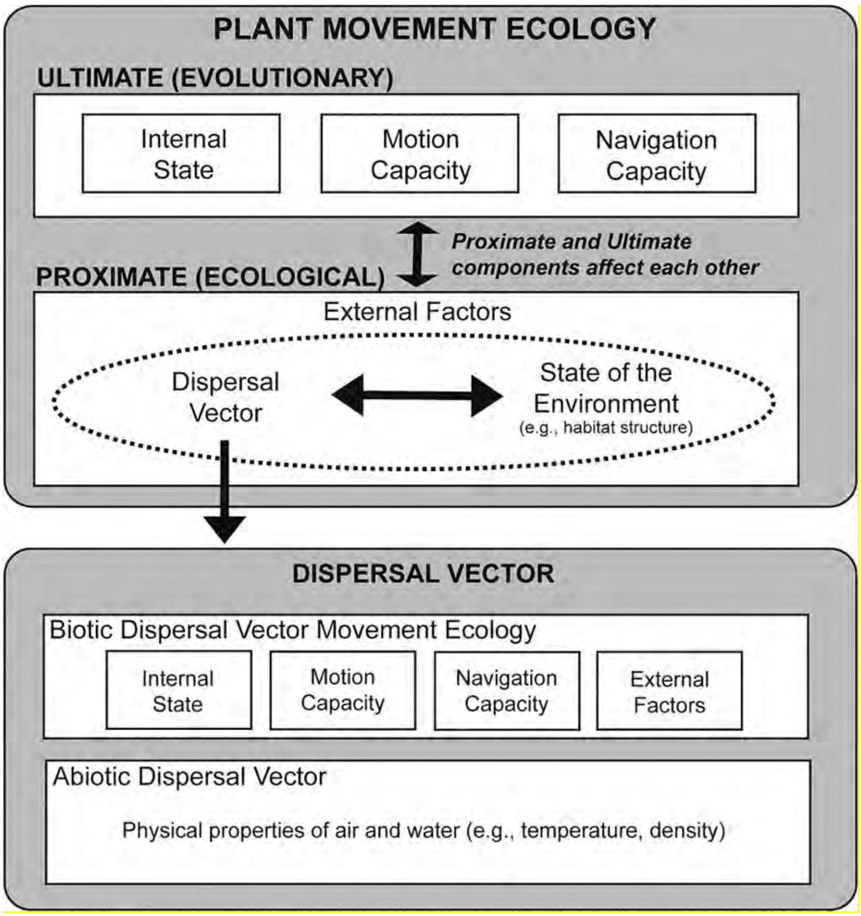


Figure 2 A movement ecology framework for plants showing both ecological (proximate) and evolutionary (ultimate) processes in propagule dispersal. The interactions between proximate and ultimate factors and between external factors and seed dispersal vectors are critical to the understanding of propagule dispersal. Figure and caption from Damschen *et al.* 2008.

Finally, the movement ecology framework not only recognises the influence of the environment on the movement of the vector, but also on the propagule. Thus environmental factors can influence the "decision" to disperse, for example, decreasing food availability and photoperiod causes the production of resting egg phases in *Daphnia* (Kleiven, Larsson & Hobek 1992). The environment may also affect the motion capacity of the propagules by influencing the size or quality of propagules produced, for example the parental growing environment has been shown to influence seed size (Galloway 2001; Halpern 2005). In environments such as wetlands, the spatio-temporal variation in resources and its effects on dispersal have yet to the considered.

As already mentioned, perhaps the main advantage in applying the movement ecology framework will be in unpacking some of the complex interaction between the two external factors (vectors and environment) and their effect on propagule motion and navigation capacity. Navigation capacity in plants may refer to choosing specific vectors for example small migratory waders as opposed to larger sedentrary waterbirds by altering size and colour. Furthermore, the use of standardised mechanistic frameworks such as this one will better enable interactions to be described in a way that facilitates comparison with other studies and therefore supports the formulation of much needed general principles for dispersal (Wright *et al.* 2008). Future work in dispersal could benefit from evaluating the stages of dispersal within the context of movement ecology.

8.3 THE RELATIVE ROLE OF DISPERSAL IN AQUATIC COMMUNITIES

A fundamental goal in ecology is to understand what controls the distribution and abundance of species (Pianka 1966; Gaston 2000; Gilbert & Lechowicz 2004). Communities are thought to be structured by both local (such as competition, predation and environmental conditions) and regional (such as dispersal and extinction) processes (Ricklefs 1987), and disentangling the relative roles of these processes is key to understanding how communities are assembled.

For nearly a century ecologists have debated the relative importance of local processes (deterministic factors) and regional processes (stochastic factors) in explaining the distributions and abundances of species (Chase 2014). Beginning with the early ecological works of Gleason (1926) versus Clements (1936), the "Theory of Island Biogeography" (MacArthur & Wilson 1967) then swayed the debate towards the role of regional processes in community assembly. This theory, highlighted the importance of dispersal from a regional species pool and laid the foundations for the study of the mechanisms underpinning community assembly (Vellend 2010). However, important works by Diamond (1975) and Tilman (1976) reintroduced the role of local processes in the community assembly debate, providing evidence for the importance of biotic interactions and environmental conditions. These ideas became the forerunners of the current niche theory, the perspective that communities assemble according to ecological niche differentiation through interspecific competition and species sorting along ecological gradients (Rees *et al.* 2001; Tilman 2004). The most recent counter argument to niche theory is neutral theory, which suggests that species are ecologically equivalent and community dynamics are governed by stochastic processes such as immigration and local extinction (Hubbell 2001, 2005; Bell 2001). Although neutral theory has been strongly criticised (Dornelas, Connolly & Hughes 2006), it is still argued as a good starting point for an explanation of the patterns of species distribution and abundance (Halley & Iwasa 2011; Rosindell, Hubbell & Etienne 2011; Rosindell *et al.* 2012). Unfortunately, after nearly a century of research there is still little consensus on the debate, and it likely that the scale of observation alters our conclusions of the relative importance of local and regional processes and that these processes operate together to influence the patterns of species abundance and diversity over different spatial and temporal scales (Levin 1992; Boulangeat, Gravel & Thuiller 2012; Chase 2014).

In freshwater communities, the relative importance of local versus regional processes in determining community structure is largely unknown. Dispersal limitation is a key regional process, and in fragmented and naturally isolated ecosystems (wetlands, islands and mountain tops) it is especially important in explaining community structure (Cottenie & De Meester 2004; Leibold *et al.* 2004; Viana *et al.* 2014). Several studies have also provided evidence that dispersal limitation is the major determinant affecting assemblages of zooplankton (Dodson 1992; Frisch *et al.* 2012) and plays a part in determining the structure of aquatic plant assemblages (Capers, Selsky & Bugbee 2010). However, other studies have shown that local environmental conditions are the most important determinant of community composition within wetlands (Declerck *et al.* 2011; Alahuhta & Heino 2013; Viana *et al.* 2014). Overall, the consensus is that in aquatic environments, such as lakes and permanent ponds, community structure is best explained by a combination of local and regional processes, and the relative importance of the different processes are taxon and scale dependent and affected by the strength of the environmental gradient (Alahuhta & Heino 2013; Heino *et al.* 2015). For example, the greater the spatial extent under consideration the larger the role of dispersal limitation (Soininen *et al.* 2011). Additionally, in species with high dispersal ability we expect that environmental conditions would better explain variation in community structure (Heino 2013), and intuitively the greater the environmental gradient the larger the role of environmental factors (Jackson, Peres-Neto & Olden 2001; Heino *et al.* 2015). In this thesis, I have demonstrated that waterbirds have the capacity to facilitate the dispersal of non-mobile plants and aquatic invertebrates. Thus, from a waterbird-mediated dispersal perspective, the propagules of many aquatic plants and invertebrates have high dispersal abilities and are capable of being dispersed over large spatial extents. Therefore, across a network of permanent wetlands, waterbird-mediated dispersal of aquatic propagules might result in broad distributions for many aquatic plants and invertebrates, but be less important at small spatial scales where local factors are more influential (e.g. Viana *et al.* 2014).

In patchy environments, which experience high spatial and temporal heterogeneity, dispersal is predicted to have an important effect on the structure of ecological communities (Levin *et al.* 1984; Snyder 2011; Baguette *et al.* 2013). Therefore, in ephemeral wetlands, such as those that characterise much of southern Africa, spatial and stochastic processes are thought to play a much larger role in structuring aquatic communities (Heino *et al.* 2015). Dispersal processes are thought to be especially important during the re-wetting phase of the hydrological regime (Heino *et al.* 2015), as this may provide a new template for colonisation by incoming propagules with little competition for niche space (Connell & Slatyer 1977). Thus, in arid zones where waterbirds undertake opportunistic movements that allow them to capitalise on recently inundated and newly productive environments (Roshier *et al.* 2002; Roshier & Reid 2003), waterbird-mediated dispersal to re-filling wetlands will have important consequences for community structure. Additionally, different waterbirds will capitalise on these newly productive habitats at different times and dispersed propagules will thus arrive at varying stages of wetland succession. Therefore, it is possible that waterbird vectors such as White-faced Whistling Duck and Red-billed Teal, which are generally the first waterbird species to arrive at recently flooded wetlands in southern Africa (Hockey *et al.* 2005), will have a greater overall impact on community structure. However, the degree to which the arriving propagules are met with resistance by the propagule bank will be an important and worthwhile avenue of future enquiry. Nonetheless, waterbird-mediated dispersal appears to be an essential process for aquatic community assembly, and may be of particular importance in arid regions where it is a source of resilience, reorganisation and persistence in wetland ecosystems.

8.4 CONSERVATION IMPLICATIONS

Freshwater ecosystems are identified as perhaps the most endangered ecosystems in the world (Dudgeon *et al.* 2006). The conservation of water resources is of critical importance for maintaining ecosystem processes and freshwater diversity (Strayer & Dudgeon 2010). Traditionally wetland conservation efforts have focused on the preservation of special sites (for example Ramsar sites) that are managed as isolated units (Amezaga *et al.* 2002). However, wetland conservation initiatives now seek to go beyond the conservation of discrete sites to recognise the ability of individuals to move across a network of patches and develop all-inclusive conservation strategies more comparable to terrestrial protected area networks (Baguette *et al.* 2013). The results of this thesis, and the work of others, have shown that waterbirds are a major component of biotic connectivity in freshwater ecosystems. Waterbirds disperse a high diversity of plant and invertebrate propagules, which can influence community dynamics and facilitate gene flow between populations (e.g. Brochet *et al.* 2009; Viana *et al.* 2013b; Green & Elmberg 2014). On a local scale, developing spatially explicit models of dispersal that incorporate the movement of key waterbird vectors will be a useful first step in delineating wetland conservation networks within a landscape. These practices can also be applied on a regional scale, where perhaps key wetland sites that act as important regional source pools for propagules - for example, stopover sites during shorebird migrations or waterfowl moult sites – are identified and protected.

In many areas there has been an increase in surface water due to the building of impoundments, which has affected waterbird movement patterns and hence dispersal and connectivity. In southern African this is of particular relevance as the construction of farm dams in previously arid environments has contributed to range expansion of certain waterbird species (for example Egyptian Goose) (Okes *et al.* 2008). Additionally, by providing a constant source of water throughout what would normally be considered the dry-season, the usual dynamics in arid landscapes of following productive patches and thus dispersing propagules to newly inundated wetlands are changing (Kingsford, Roshier & Porter 2010).

An enhanced understanding of how land-use change is affecting waterbird movements is required as it has important implications for freshwater biodiversity conservation.

Perhaps one of the most noteworthy conservation concerns identified in Chapter 6 is the ability of waterbirds to disperse exotic and invasive species in both freshwater and terrestrial habitats. Biological invasion to date has had some of its greatest impacts on freshwater biodiversity (Ruiz *et al.* 1999; Green & Figuerola 2005a), and the role of waterbirds in facilitating the spread of invasive organisms can no longer be underestimated. Thus managing wetland networks requires acknowledging that waterbirds facilitate the spread of aquatic invasive species.

Finally, there seems to be some noticeable parallels between the dispersal of propagules and the spread of pathogens by waterbirds. Therefore, the mechanisms of dispersal explored here might have important applications in understanding the epidemiology of waterbird-borne diseases such as avian influenza. For example, the viral latency period of waterbirds carrying avian influenza virus could be viewed as equivalent to gut retention time and coupled with spatially-explicit movement data in mechanistic models to determine the spatial dynamics of disease spread (Gaidet *et al.* 2010). However, there are also some important differences between dispersal and disease spread. For example, in disease spread an infected migratory waterbird may experience an alteration in its ability to fly and feed that effects the capacity of the individual to migrate over long distances (Bauer & Hoye 2014), but this would not be a consideration in propagule dispersal. Nonetheless, waterbirds are known vectors of pathogens that are of relevance to human health and can affect biodiversity by altering resident host-pathogen dynamics (Altizer *et al.* 2011; Bauer & Hoye 2014). It is important to consider the full set of ecological functions, and ecosystem services and disservices brought about by waterbirds to determine their value for wetland conservation and potential trade-offs that may occur.

8.5 RECOMMENDATIONS FOR FUTURE WORK

Throughout this synthesis, I have highlighted areas for future research that will enhance our understanding of the mechanisms underlying waterbird-mediated dispersal. However, it is my opinion that there are three major avenues of future enquiry that will be the most valuable and insightful: (1) analysing the dispersal function of the waterbird community as a whole; (2) explicitly assessing spatio-temporal variation in vector movement; and (3) determining the relative contribution of waterbird-mediated dispersal to population and community dynamics. Each of these three topics are further discussed below.

Not all dispersers are equal. Studies of frugivory have shown that changes in disperser community, for example the loss of megafauna by poaching, can have devastating effects for forest tree species (Galetti *et al.* 2006; Peres & Palacios 2007). Similarly, not all species in a waterbird community will perform the dispersal function equally and there will be differences in what is taken up, how it is moved, and ultimately where it deposited. The focus in waterbird-mediated dispersal has largely been on the waterfowl, and amongst the waterfowl largely on the dabbling ducks (van Leeuwen *et al.* 2012b). Whilst it is understood that there are methodological restrictions, for example diving ducks which are relatively more difficult to capture, a concerted effort must be made to quantify similarities and differences in dispersal function across multiple species of waterbirds if we are to begin to assess the resilience of freshwater systems to future challenges. On a fine scale, this will require more autecological research into the feeding ecology of various waterfowl, shorebird, heron, and gull species, amongst others, and experimental research on how variation in digestive organs, vector activity, and propagule characteristics affect retention times and recoverability.

There needs to be consideration of other types of waterbird movement beyond long-distance migrations. It is tempting to focus on migration and long-distance dispersal given the incredible distances which some species can achieve. For example the Bar-tailed Godwit *Limosa lapponica* migrates over 11 000 km non-stop each year (Battley *et al.* 2012). However, waterbirds move at a variety of different scales throughout the annual cycle and their movements can affect community dynamics at both local and regional scales. It is unwise to draw conclusions about waterbird-meditated dispersal from a limited number of spatial scales and geographical regions and advancing our understanding of the extent and consequences of dispersal will require explicitly addressing spatio-temporal variation in waterbird movement (Côrtes & Uriarte 2013). Addressing these questions requires detailed information on how internal and environmental factors influence waterbird movement (Nathan *et al.* 2008a). Advances in technology, such as GPS satellite telemetry and accelerometers coupled with remotely-sensed environmental data on water availability or land-use change will provide key insights into the drivers of movement and how they vary in space and time (Kays *et al.* 2015). Only once we have a firm understanding of the drivers of waterbird movement can we begin to predict how waterbirds might facilitate the persistence of species in fragmented landscapes or aid range shifts with changing climates.

Perhaps the most pressing and challenging question is to determine the contribution of waterbird-mediated dispersal to aquatic community structure and population persistence at various scales. Currently molecular techniques, such as population genetic methods, offer the best option for directly quantifying gene flow between isolated populations (Heino *et al.* 2015). Coupling these estimates with measurements of dispersal ability by different dispersal mechanisms, such as hydrochory or anemochory, will provide insight into the relative contribution of waterbird-mediated dispersal (van Leeuwen *et al.* 2013). However, due to biotic resistance mechanisms such as priority effects, propagules may be dispersed to a wetland but never establish. This will affect our conclusions about the scale of dispersal. Future methods could assess gene flow at longer temporal scales to circumvent this problem or genotype entire propagule banks. Finally, by exploring the relative roles of waterbirds (amongst other dispersal mechanisms) and local environmental factors in structuring aquatic communities there is scope to further our theoretical understanding of community assembly. Just as islands provided excellent model systems with which to study dispersal and meta-population dynamics (MacArthur & Wilson 1967), so can wetlands be considered "islands in a sea of land" (Darwin 1859).

The importance of dispersal in the diversity, abundance and composition of communities is generally accepted (Robledo-Arnuncio *et al.* 2014). However, there are still few studies that persuasively demonstrate the role of dispersal in community dynamics and structure (Levine & Murrell 2003; Côrtes & Uriarte 2013; Robledo-Arnuncio *et al.* 2014). This is most likely due to simplifications that have to be made when modelling and measuring dispersal and the actual complexity of the dispersal process itself. To advocate for the role of dispersal in community structure, perhaps there needs to be an integration of dispersal ecology with the fields of movement ecology (Nathan *et al.* 2008a) and community ecology (Vellend 2010), such that the spatial patterns of dispersal are more realistically determined and the biotic and abiotic interactions of dispersed propagules are explained. This is not a simple undertaking, however, important technological advances such as high resolution GPS satellite-tracking devices, population genetics, isotopic methods, and advances in computing and data analysis provide the tools to begin tackling such complicated dynamics. In addition, new theories and concepts need to be developed. Mathematical advances such as the use of moment methods, a statistical technique for estimating a single quantitative measure for the shape of a set of points, have led to relevant theoretical advances in elucidating the role of dispersal in community structure (Detto & Muller-Landau 2013; Robledo-Arnuncio *et al.* 2014). Advancing our understanding of the importance of dispersal in community processes and patterns thus represents a dynamic interplay between new tools and new ideas. Dyson (2012) and Nathan (2015) summarised this relationship most eloquently and suggested that we are fortunate to experience a time where the philosophies of Thomas Khun (progress in science is driven by new paradigms) and Peter Galison (progress in science is driven by new technologies and tools) are both going strong. Therefore, by exploiting cutting-edge tools and relevant new theories researchers are presented with a unique opportunity to make important contributions to much needed research into the role of dispersal in determining community structure.

8.6 CONCLUSIONS

The objective of this thesis was to describe and quantify the role of waterbirds in the dispersal of plants and aquatic organisms in southern Africa for the first time. This work has shown that waterbirds in the region take up a variety of different propagules, move them over multiple spatial scales and are capable of depositing good numbers of viable propagules in suitable habitat. However, not all waterbird vectors perform the dispersal function equally, and this is an important consideration when evaluating the dispersal capacity of a waterbird community. Additionally, a high number of terrestrial and exotic propagule species were identified, and I reiterate that the dynamics of waterbird-mediated dispersal thus surpass effects on just wetland communities, and waterbirds should be considered as legitimate dispersers in terrestrial environments and of exotic species. Dispersal is a complicated interaction between the disperser and the vector, and I have shown that both differences in propagule characteristics and vector traits affect spatial patterns of dispersal. Furthermore, these spatial patterns of dispersal are markedly different to that shown for long-distance dispersal by migrating birds in the northern hemisphere, and demonstrate the need to extend research of waterbird-mediated dispersal into new geographic regions. Whilst there still remains much to uncover about the mechanisms underpinning the successful dispersal of aquatic organisms by waterbirds, perhaps the most important next step will be to determine the contributions of waterbird-mediated dispersal to structuring aquatic communities.

Despite their apparent isolation, important ecological connections exist between wetlands. Waterbirds play an important role in connecting wetlands through dispersal and in doing so influence aquatic community organisation and provide a means of recolonisation in ephemeral habitats. Changes in the distribution, abundance, and movement patterns of waterbirds will therefore have important consequences for aquatic communities and affect wetland biodiversity on both regional and local scales. Additionally, these changes will influence the spread of aquatic invasive species. Unfortunately, land-use and climate change will continue to alter the distribution of resources and increase fragmentation between aquatic habitats, however, waterbirds will have an important role to play under these conditions by helping species to shift their ranges and in facilitating reorganisation after drought. Therefore, I conclude that waterbird-mediated dispersal is a significant and overlooked mechanism of resilience in aquatic ecosystems.

Musings of a PhD student

An informal perspective on dispersal and ecology

I am in awe of the complexity with which the natural world functions. When I first proposed this research as the topic of my PhD thesis, I had a rather simple and perhaps romanticised view of how waterbirds might connect wetland systems and contribute to the resilience of ephemeral habitats. A thorough review of available research and three years of fieldwork and data analysis has shown me that whilst, in essence, there is truth to these relationships, they are also not so straightforward and are an oversimplification of the processes taking place. As ecologists, we need to simplify ecological processes in order to make generalisations about the natural world, but it seems that in doing this we tend to overlook the role that variation amongst individuals can have on a particular outcome. In this study, I looked for generalisations about the numbers of seeds transported, the seed traits that would generally facilitate survival through the digestive tract and the average distances that waterbirds dispersed seeds – all of which provide critical information for conservation recommendations and for furthering our understanding of wetland ecology. However, what I could not measure or account for were instances of $N = 1$ that may have significant overall implications beyond predictions based on the mean. For example, an Egyptian Goose from our sample population flew over 1 000 km in a few hours, a single event never recorded again for that individual or for any other of our tracked waterbirds. When Higgins *et al.* (2003) suggested that rare long-distance dispersal events are often driven by non-standard means of dispersal they were primarily referring to cases where, for example, humans introduce aquatic invertebrates into lakes, or when birds move plants usually dispersed by wind. Nevertheless, this idea can be extended to include instances of rare long-distance movements by standard vectors or extraordinary variations in disperser phenotype that account for unprecedented dispersal events. What this study has revealed to me is the importance of individual variation in driving processes and the difficulty of measuring and describing it. However, if we seek to understand how biodiversity is going to respond to current threats we must strive to account for individual variation in our predictions. Perhaps, there is thus still a place for natural history type observations at the individual level, which coupled with current technological advances in data capturing, storage and access can provide not just mere anecdotes of species responses, but the foundations for understanding the value of individual variation in ecology.

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"There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable. There is another theory which states that this has already happened."

Douglas Adams, The Hitchhiker's Guide to the Galaxy

"All you really need to know for the moment is that the universe is a lot more complicated than you might think, even if you start from a position of thinking it's pretty damn complicated in the first place."

Douglas Adams, The Hitchhiker's Guide to the Galaxy