The Impacts of Corvids on Biodiversity

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Pied crow (*Corvus albus*); Source: C. Madden

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Abstract

Corvids are often referred to as efficient nest predators with potential negative impacts on biodiversity. Despite the plethora of literature focusing on the impact of corvids on their potential prey, no review has been conducted on the genus *Corvus* to synthesis these relationships, and to explore their likely impacts on biodiversity. This thesis conducts a systematic literature review on the impacts of corvids on biodiversity by collating information from two study types: experimental studies and correlative studies. The impacts of corvids were diverse and varied between studies, countries and species. The vast majority of studies were on impacts on birds, and of these passerines were the most frequently studied, followed by waders. Collating the results from both experimental and correlative studies revealed a negative impact for 29% (n=50) of cases, whereas no impact was detected in 63% (n=107) of cases, and I found a positive impact (suggesting a beneficial relationship) in 8% (n=13) of cases. Thus, from the studies that have been investigated, the main findings indicate that corvids most frequently have no detectable impact on target species, and that their impacts are certainly not consistently negative.

Concerns of corvid impacts have been raised in South Africa, as one indigenous species, the pied crow (*Corvus albus*) seems to be increasing. The aim was to explore whether changes in pied crow abundance in South Africa correlate with certain covariates which have been suggested to be involved in their increase. These covariates include transmission lines, climate change (temperature and rainfall), and land cover. Using data from the South African Bird Atlas Project (SABAP) in two surveyed periods (SABAP1: 1987-1991; SABAP2: 2007-2012), I examined changes in pied crow reporting rates (a proxy for relative abundance), describing both the overall change between these time periods, and exploring whether these changes were associated with biomes, transmission lines, climate variables, or land cover. A significant overall increase in this proxy for pied crow abundance was found across South Africa in the last 25 years. Increases differed between different habitat types, with increases being greatest in shrublands and urban areas. A full model, including all the potential covariates, found significant relationships between both temperature and rainfall change, with reporting rates. Pied crows are increasing in regions that are becoming hotter and a little wetter, which are predominantly areas in the west and the interior. There were simultaneous decreases of pied crows in the eastern regions of the country. Thus, change appears to be operating at a broad scale associated with large-scale changes in climate (rainfall and temperature). These analyses represent the first attempt to quantify the changes in abundance and range shifts of pied crows in South Africa, and also represent one of the first studies in South Africa empirically to relate bird population changes to medium-term climate change data.

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CHAPTER 1

UNDERSTANDING THE IMPACTS OF CORVIDS IN RELATION TO PREDATION, ABUNDANCE AND RANGE CHANGES

Introduction – Scope of thesis

Concerns have been raised about the loss of biodiversity in the face of anthropogenically induced changes primarily from habitat loss through fragmentation, climate change and introduced species (e.g. Chapin *et al.* 2000). Concerns about the impacts of introduced species on native fauna and flora have been widely described and identified (Blackburn *et al.* 2004). Synergistic effects of climate change on non-native (e.g. Beans *et al.* 2012) and native (e.g. Simmons *et al.* 2004) species range change can further drive biodiversity loss (e.g. Sheppard 2012). A species' ability to adapt to and exploit novel environments determines the rate and their capability to expand or shift their range (Anson & Dickman 2013). Generalist species tend to have the capacity to increase in abundance and are prone to expand their range because they are able to maintain their foraging efficiency by switching to alternative prey if their main prey populations decline (Sims *et al.* 2008). Therefore, they are often not limited by the range of their main prey species. In a changing environment, the effects on different species can further drive biodiversity loss, especially if predatory species respond by increasing their numbers or range when favoured by these changes.

One such generalist avian group showing a positive response to landscape changes by altering both their abundance and range are the corvids (Manzer & Hannon 2005). This thesis focuses on corvids in a changing environment, and aims to understand the impacts of corvids on their prey in relation to predation pressure and increasing abundance.

The potential for a species to cause population declines of other species, or biodiversity loss, is not confined to introduced, alien species. Regional increases in several indigenous species' range limits allows new areas to be colonised, thus showing a similar pattern (Marzluff *et al.* 2001; Hockey & Midgley 2009; Duckworth *et al.* 2010). Reasons for such increases are often species-and context-specific. However, frequent hypotheses include increases in food availability (Robb *et al.* 2008), introduction of new nest sites (Robb *et al.* 2008), and changes to climate (Hamer 2010) which provide suitable environments in which novel species can survive and thrive.

One group of particular concern are the corvids – the avian family including crows, ravens, rooks, magpies, treepies, choughs, nutcrackers and jackdaws (dos Anjos 2009). Corvids are known predators that are responsible for nest robbing, mobbing and preying upon a variety of species (Newton 1998; Gibbons *et al.* 2007). Being generalists with advanced cognitive capabilities, several corvid species show complex adaptations to their environments (Emery & Clayton 2004). Corvids are fascinating as they are highly adaptable and able to survive in various habitats with harsh conditions – from arctic tundra, to tropics and deserts (dos Anjos 2009), and human settlements - certain corvid species are tightly associated with people especially crows and ravens (Marzluff *et al.* 2001). With human population growth and the resulting urban sprawl, corvids adapting to new environments and tracking human expansion. The increase in abundance and range change of several corvid species can potentially impact biodiversity as prey species may now be faced with a novel predator, or a predator maintained above usually experienced densities.

The increase in corvid abundance is, in general, a global phenomenon (Marzluff *et al.* 2001). Because of this, and because many corvid species are predatory, concerns are often raised on the impact of corvids on biodiversity. Corvids are often cited as the dominant predator of bird species, especially ground-nesting birds, and management plans to control corvids are often implemented in an attempt to improve breeding success of target species (Gibbons *et al.* 2007; Klausen *et al.* 2009). However, experimental studies on the impacts of corvid removal have provided different, often contradictory results (e.g. Erikstad *et al.* 1982; Parker 1984). Inconclusive trends are problematic as land managers can selectively choose findings that support a pre-determined management option.

In this thesis, I carry out a systematic literature review, drawing on the global literature of experimental and correlative studies to assess the validity of concerns about corvids and their potential to affect target species' breeding success or population size. Additionally, I investigate a local South African issue, and explore the changes in range and abundance of the pied crow (*Corvus albus*) in South Africa to assess whether this species is increasing its range and/or abundance, as many believe, and what the drivers of population changes might be. Scientifically defendable data are imperative to make informed decisions about whether corvids are increasing, and if so, if they have the potential to affect prey populations. Understanding the impacts of increasing predator populations, and what drives these increases, is essential for the management and preservation of biodiversity in the face of rampant ecosystem change.

Predation – Can it limit populations?

Several factors can limit a species' population size; namely starvation, disease, competition for nest sites or shelter, and predation (Newton 1998). However, predation is arguably the most fundamental ecological interspecific interaction (Ramanantoanina *et al.* 2011). Predation has been hypothesised to limit prey populations in certain contexts (Chesness *et al.* 1968; Tapper *et al.* 1996; Littlefield 2003; Fletcher *et al.* 2010) and, where this may happen, can act to keep prey populations below carrying capacity. When predation is at a level where only those individuals are consumed that would have died anyway from other factors (the aptly named 'doomed surplus') it is termed 'compensatory' predation (Errington 1946). In other cases, predation is an essential part of regulating and controlling populations; without such controlling factors our planet, in theory, would be over-run by prey. A classic example demonstrating the importance of predators, and their roles in trophic cascades, is illustrated in the localised extinction of the sea otter (*Enhydra lutis*) in the north Pacific due to over-hunting (Estes & Duggins 1995). Without top-down control by this predator, the sea urchin (*Stronglycentrotus* spp.) population exploded resulting in widespread overgrazing of kelp beds. Thus, in this case, predation was 'additive' to other forms of mortality and once the predator was removed the prey population size increased. Functional predator-prey relationships are therefore essential in maintaining ecological functioning. Altering the dynamics and balance of these interactions can flip ecosystems into alternative, potentially undesirable, states (Holling 1973).

Bird populations tend to remain relatively stable over time despite inter-annual variability (Newton 1998). Small-bird densities show greater variation between years compared to larger species, but show less fluctuation compared to some insects, which can display inter-annual changes in population size by 100-fold or more (Newton 1998). Caution should therefore be exercised when quantifying population size, which can fluctuate widely within a single year. For example, the post-breeding population can often be almost double that of the population that is leftover at the beginning of the next breeding season (Newton 1998). Half the population therefore dies or emigrates before the next year. Without an adequate understanding of the dynamics of such populations, mortality by predation alone may seem excessive and the main cause for limiting, or decreasing prey populations. For example, Meslow & Keith (1968) noted a drastic decline per square-mile from 622 adult snowshoe hare (*Lepus americanus*) in 1962 to 3 by the summer of 1965. Initially this appeared to be the result of unsustainable predation, however, long term data have revealed that such fluctuations are part of long-term natural cycles, and not a result of excessive predation.

Several processes that affect mortality may occur simultaneously in conjunction with predation. It is therefore futile to assess the impacts of predation simply by comparing breeding and post-breeding prey population sizes (Newton 1998). It is also essential to recognise that several factors reduce post-breeding population sizes. In a review of 42 published papers, Ripple & Beschta (2012) illustrate that top-down control by large predators is a strong force limiting herbivore populations in northern forest ecosystems. The reduction of predators in North American ecosystems resulted in large herbivore populations, increasing by six-fold in some cases, increasing grazing pressure and stress on ecosystem integrity (Ripple & Beschta 2012). This demonstrates that predators in some systems can be responsible for limiting prey populations, through additive mortality, and depicts the importance of such interactions in maintaining a healthy ecosystem.

Despite this natural ‘trimming’ of populations (through compensatory and additive predation) down to a lower level in keeping with the supporting environment, there are several factors (anthropogenic, biotic and abiotic) that can exacerbate a particular mortality agent with far-reaching consequences. Prey density can influence predation through a density-dependent relationship, and the availability of alternative prey may also affect this relationship. The classic predator-prey interactions show oscillating prey numbers, with predator numbers lagging behind (Figure 1). This depicts a numerical response of changes in predator numbers following changes in those of their prey (Redpath & Thirgood 1997).

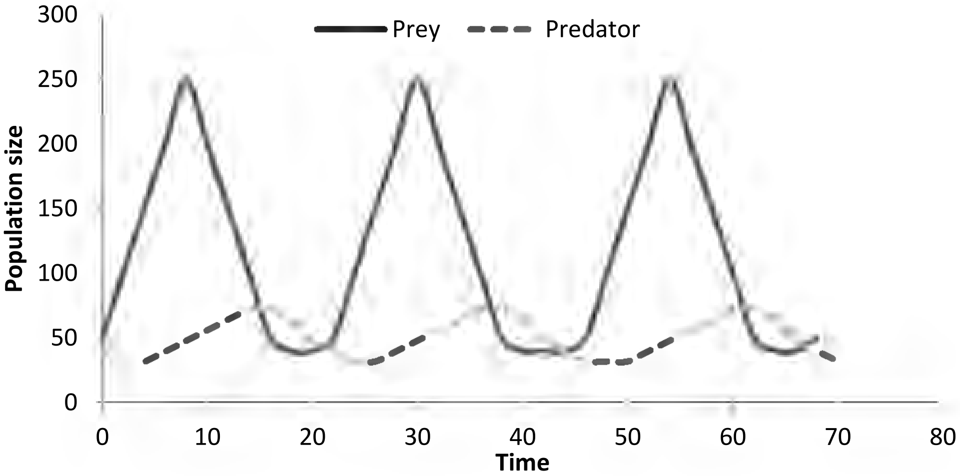

Figure 1: Graph showing hypothetical data to illustrate a typical relationship between predator and prey populations, where predator abundance tracks prey abundance with a lag.

At higher predator densities, the number of prey killed per predator can increase because of the associated increase in predation pressure (Valkama *et al.* 2005). Eventually the prey will decrease. If predator numbers remain constant, this can cause a larger proportion of the prey population to be affected by predation (Newton 1998). Reduced prey should, theoretically, result in reduced predation on that species as alternative food resources become more attractive and available. This decrease is a functional response where predator consumption rates fluctuate with changes in density of prey (Holling 1959). Generalist species are able to switch to alternative prey and therefore can have a disproportionately large influence on rare or vulnerable prey species despite the prey's low numbers (Norrdahl 2000). This 'alternative prey hypothesis' therefore describes how increasing populations of predatory generalists can increase the predation pressure on less common species (Newton 1998). In California, the introduction of feral pigs (*Sus scrofa*) provided a de facto artificially supplemented food source for golden eagles (*Aquila chrysaetos*) that in turn led to the reduction of another prey species, an endemic island fox (*Urocyon littoralis*) through excessive predation (Roemer *et al.* 2001). Here predators display a functional response to increased prey densities by increasing the predation rate (Roos 2002). Understanding the response of populations to predation allows for greater understanding of the complex dynamics of predator-prey interactions and can assist management strategies should intervention be necessary (Moleón *et al.* 2012).

Unsustainable predation is well-documented in instances when prey species are exposed to a novel predator. For example, at least 110 bird species have gone extinct due to predation since *ca.* 1600, and the release of novel predators onto oceanic islands resulted in the extinction of at least 31% of those (Groombridge 1992; Redpath & Thirgood 1997). Understanding what proportion of each mortality agent is responsible for limiting the population and to what extent density-dependent interactions are maintaining the population needs to be explored. Only then can effective management and conservation strategies be implemented.

It is important to recognise that predators do not necessarily have an effect on prey populations (Newton 1998). When populations are limited by resources within a given habitat, then any extra individuals entering the population through birth or immigration will die because resources are the ultimate limiting factor. Yet, predation can play an important role in shaping avian reproductive strategies, as non-lethal impacts by predators can act as selective pressures (Fontaine & Martin 2006). Species have evolved life-history strategies and behavioural traits to buffer intense predation rates (Snow 1978; Fontaine & Martin 2006). High egg mortality in birds has had a strong influence on the reproductive strategy of several species to withstand high nest predation such as producing tiny, inconspicuous eggs to lessen detection and loss from predators (Snow 1978). Conversely, experimentally reduced predation risk has increased egg size, clutch mass, provisioning rates and decreased incubation time among several birds implying that heightened risk of nest predation could impact the breeding success of avian species (Fontaine & Martin 2006). Since nest predation is the primary cause of nest failure, reproductive and behavioural strategies have evolved to compensate or prevent such predation from causing an unsustainable negative impact on species' populations (Martin 2007). Predation must therefore be assessed in relation to breeding and population parameters, because certain bird species may be unaffected by apparent high predation rates. Thus, different species have different strategies to cope with predation, so it can be uninformative or potentially misleading to report predation rates without the knowledge of species' tolerances. Predation-related mortality can therefore be very high without limiting populations, as adaptations in life-history and behavioural traits have evolved to cope with such intense predation. Predators can therefore have no effect on the population if they kill the ´doomed surplus´ only (Errington 1946). However, when predation levels are in excess of what is most commonly experienced, they can be "additive" and will likely limit population sizes (Errington 1946). As long as predation, disease, resource limitation and other factors that result in mortality do not exceed the 'doomed surplus', they will have no effect on the population.

As I have described, simply quantifying predation rate alone is not sufficient to conclude whether predators might be limiting a population. It is often difficult to detect species-specific impacts of predation, due to uncertainties in decoupling effects of other mortality agents and other predators. Compensatory predation and prey switching among generalist predators, coupled with difficulties in identifying which predator is responsible for prey mortality, makes it difficult to quantify what effect a predator has on a prey population (Draycott *et al.* 2008). The impact of predation also differs depending on age-classes and timing, where breeding adults killed just before the breeding season can have a disproportionately larger impact on the population than the loss of an egg or nestling, as replacing adults is more difficult than young (Newton 1998; Gibbons *et al.* 2007).

The impact of predation also cannot really be considered in isolation from habitat quality, as several studies have shown these factors interact to influence the impact of predators on prey populations (Evans 2004). Habitat quality is the most common underlying determinant of population size in 20 studies, most of which reported habitat fragmentation, degradation and decline, rather than predation, as the primary cause of diminishing bird populations (Côte and Sutherland 1997). The reduction in habitat quality can compromise the carrying capacity for an ecosystem. Poorly managed and impoverished habitats can increase resource competition, forcing individuals to forage in exposed and dangerous habitats that increase their vulnerability to predation (Martin 1992). Predation is also more common along forest edges (Paton 1994; Lahti 2001;but see Carlson & Hartman 2001). It is therefore important to decouple the effects of habitat change and predation on breeding success and mortality. Conclusions should be drawn cautiously, as they may profoundly influence management options. To illustrate this point, an increase in avian predators (namely carrion crows and magpies) coincided with a decline in wader populations in the UK (Bolton *et al.* 2007). However, this decline was ultimately attributed to changes in land-use practices and not to increased predation (Bolton *et al.* 2007).

Increasing populations & range expansion

The impacts that predatory species have on prey species is influenced by the numbers of predators in the environment. Therefore, to understand fully if a predator is likely to have an impact, it is important to understand what factors influence its abundance, particularly when populations increase or when their ranges shift or expand. Range shifts, i.e.

the expansion and contraction of species' distributions, have been documented for several avian species (see La Sorte 2006; Anderson & Otter 2007; Li *et al.* 2010). These movements include indigenous species gradually moving into novel environments (Hockey & Midgley 2009; Duckworth *et al.* 2011). Thus, changes in habitat quality may have consequences other than altered predator-prey interactions, and land use change has been identified as the primary driver of shifts in some species (Hockey & Midgley 2009), although climate change may also play a role (e.g Guisan & Thuiller 2005). Climate can limit the range of many species (Root 1988). The capacity for range shifts depends on habitat requirements and characteristics of species (van der Putten *et al.* 2010). Climate may be more restrictive in the range of habitat-generalists whereas habitat-specialists are more dependent on the habitat to provide all their resource requirements of specialised interactions (van der Putten *et al.* 2010). For example, climate previously restricted the range of the hadeda ibis (*Bostrychia hagedash*) in southern Africa. Soil moisture determined foraging efficiency and therefore energy uptake, confining this species to wetter parts of southern Africa (Duckworth *et al.* 2010). A considerable range expansion of this generalist species into drier areas has occurred over the last 40 years (MacDonald *et al.* 1986), due to increased irrigation and hence soil moisture (Duckworth *et al.* 2010). Hockey and Midgley (2009) found similar range shift dynamics in 18 regionally indigenous, habitat-generalist birds in South Africa, 17 showing directional south-west shifts.

Recently, concerns have been raised among public and conservation for a, that pied crows (*Corvus albus*) are showing similar range expansions in South Africa (BirdLife South Africa 2011). It is therefore necessary to understand species range limits and how these are changing in response to altered land use options, climate or other factors.

Climate change predicts that species will shift towards the poles or to higher latitudes, and changes in the distributions of many bird species across the northern hemisphere have supported these predictions (Hughes 2000; Huntley *et al.* 2007; Li *et al.* 2010). In their seminal paper on effect of climate change on birds, Thomas and Lennon (1999) suggested predicting avian range shift through repeat bird surveys. By reviewing 134 avian species in Great Britain, they found an average of 18.9 km northward migration of southerly species in response to 20 years of climatic warming. Species already occupying the northern regions of the UK did not show significant systematic northward shifts, suggesting that a northward shift is not a universal trend. However, overall empirical data do suggest that species are shifting towards favourable climatic regions (Huntley *et al.* 2007.

The negative consequences of climate change on endemic and specialised species have received far more attention than climate change-induced species expansion (Walther *et al.* 2005a). Interestingly, climate-change driven range expansion is apparently more common than species contractions (Walther *et al.* 2005b). However, this may be due to difficulties in detecting range contractions as opposed to more noticeable expansions (Dawson *et al.* 2011). Despite this, our aesthetic and scientific fascination with endemism and rare biodiversity has diverted attention from distribution and population changes of more common and widespread species. Gaston and Fuller (2008) highlight the need to carefully monitor common and widespread species populations, as they are fundamental to ecosystem processes, as a small change in their populations can result in a large change in ecosystem biomass (Ellison *et al.* 2005). One exception to this gap is the close monitoring of American crow (*Corvus brachyrhynchos*) populations, an excellent proxy for the presence of West Nile Virus (WNV) (LaDeau *et al.* 2010). Thus, American crow declines or high mortality events alert authorities to this infectious virus (LaDeau *et al.* 2010). Generally, however, too often common species have fallen under the radar of scientific investigation, and when they are studied, their rapid decline from common to threatened is highlighted (see Gaston & Fuller 2008). Less attention has been paid to common species shifting in range and expanding, what has driven these changes, and what the ecological consequences from this may be.

Anthropogenic changes in resource availability have had a profound influence on species (Møller *et al.* 2008). For example, supplementary feeding can increase overall winter survival, enhance breeding success and promote residency in urban areas where anthropogenic food substitution is commonplace (Robb *et al.* 2008). Backyard feeding was associated with the range expansion of the northern cardinal (*Cardinalis cardinalis*) and American goldfinch (*Carduelis tristis*) in the USA (Robb *et al.* 2008). Additional food provisioning in winter promoted overwintering of at least five birds species in Finland, reducing southward winter migrations and thus promoting urban residency (Jokimäki & Kaisanlahti-Jokimäki 2012). Changes in range and movements have thus occurred through artificial food supplementation and can lead to population growth, especially in an urban environment. Thus, given that crows are often associated with humans it is likely that they have the potential to also benefit from increases in supplementary foods. For example, breeding crows and ravens within 5km of campgrounds and human settlements enjoyed increased reproductive output, reduced home ranges, increased adult survival, and therefore increased abundance, in association with people (Marzluff & Neatherlin 2006).

Urbanisation has fragmented habitats (Schmiegelow & Monkkonen 2002), introduced edge-effects (Andrén 1994), altered gene flow and residency (Allen & O'Connor 2000), promoted exotic and generalist species (Cam *et al.* 2000), and modified population and resource distributions (Grimm *et al.* 2000). In addition, certain guilds are consistently favoured by urbanisation, leading to dramatic shifts in community composition (Chace & Walsh 2006). To illustrate, gleaners are often missing from urban environments due to the lack of tall trees, whereas granivores and insectivores thrive (Allen & O'Connor 2000). In addition, positive population responses can develop in those species that meet their food requirements in an urban setting (Chace & Walsh 2006). Urbanisation thus favours a few synanthropic species, stimulating their population growth, which ultimately results in urban biotic homogenisation (McKinney 2006).

One taxonomic group that has received attention in urban environments is corvids. Several corvid species are infamous for adapting their behaviour and biology to exploit features of the urban environment to optimise resources, avoid predators, and select innovative nest sites (Everding & Jones 2004; Marzluff & Angell 2005). The natural plasticity of a species can influence its ability to adapt to an urban environment (Luniak 2004). Corvids possess advanced cognitive capacities, including spatial and temporal memory, learning, and advanced behavioural adaptability (Bednekoff & Balda 1996; Emery & Clayton 2004). It is therefore unsurprising that corvids thrive in association with humans. Indeed, corvid populations are generally increasing world-wide in urban areas (Marzluff & Neatherlin 2006). Carrion crow (*C. corone*) populations have increased by 80% in the UK within 30 years and expanded their range (Gregory & Marchant 1995; Hudson 1992; Gibbons *et al.* 2007), hooded crows (*C. cornix*) increased by 80% in Orkney islands in the UK between 1983 – 2002 (Amar & Redpath 2002), American crows (*C. brachyrhynchos*) have expanded in their range and abundance in 27 states in the USA and Mexico (Gorenzel *et al.* 2000; Marzluff *et al.* 2001), common raven (*C. corax*) and Stellar jay (*Cyanocitta stelleri*) have increased in America (Peery & Henry 2010), and anecdotal evidence suggests pied crows (*Corvus albus*) are increasing and potentially expanding in South Africa (BirdLife South Africa 2012). General trends of corvids from several continents therefore show not only increases in numbers, but also in range - especially in urban settings.

These increase in corvid numbers and changes in distribution could potentially impact local biodiversity. A common result of urbanisation is the increased density of synanthropic species compared to natural settings (Luniak 2004). For example, the American crow has a smaller home range in urban (<15 ha) than in wild (30-40 ha) environments, which inflates their numbers in urban areas (Marzluff *et al.* 2001). Several studies have expressed concerns over inflated corvid populations and their impacts on target species (see Parker 1984; Summers *et al.* 2004; Opermanis *et al.* 2005; MacDonald & Bolton 2008; Amar *et al.* 2010). Corvids, being conspicuous and diurnal are one of the most obvious nest predators and hence have been labelled as notorious thieves and nest robbers. The assumption that corvids have an inherently negative impact on bird species has resulted in several corvid culling programmes to promote target-species population growth. Caution must be exercised as management decisions based on these assumptions are fraught with the complexities described earlier in this chapter, ethical issues, and can give rise to potentially ineffective strategies. Increased corvid densities do not necessarily have a negative impact on bird populations (Marzluff *et al.* 2001). However, although there has been a great deal of research on the potential impacts of corvids on biodiversity, a synthesis of this information to understand overall trends is lacking. Thus, a rigorous systematic review is urgently needed to better inform whether and in what circumstances corvids are likely to impact on biodiversity.

The benefits of systematic reviews

Systematic literature reviews have been used to concisely summarise research evidence. One of the disadvantages of the 21st century in terms of technology and media sharing is that the wealth of knowledge and constant influx of new information is often overwhelming. People simply cannot spend hours sifting through research papers on a specific question to draw evidence-based conclusions of the effectiveness and legitimacy of the assumption, treatment or management in question. Scientifically based experiments on specific topics are often rare or inconclusive, and the potential for opinion and anecdote to trump science is ever increasing. Additionally, studies often use different experimental approaches and explore different aspects of the same question, making solid and uniform conclusions rare (Lau *et al.* 1992). Thus, condensing all known literature into a single source as a review allows trends to be drawn from a larger sample of peer-reviewed studies, thus increasing its robustness (Pullin & Stewart 2006). Collating all known literature on a specific, problem-oriented question enables the efficacy of a treatment or management plan to be evaluated (Lau *et al.* 1992).

The main attraction of a systematic literature review, as opposed to a traditional one, is the rigorous scientific protocol applied to data gathering. The power of a systematic review lies in the elimination of bias via the selective “cherry-picking” of studies. Here, all information related to the defined research question is gathered through systematic searches, thereby minimising selection bias and allowing firm and informative conclusions to be drawn (Lau *et al.* 1992). Importantly, studies undergo a rigorous eligibility process before inclusion is considered (Pullin & Stewart 2006). The evaluation of data is methodically undertaken, by specifying what information is required and eliminating all studies that do not meet these requirements. Coupled with this, the validity of different studies is identified and categorised according to different degrees of quality (Pullin & Stewart 2006). Misleading and biased findings are eliminated if all known literature is collected and a stringent study quality protocol is used. Systematic reviews are particularly important when the outcomes may influence controversial management decisions, such as the lethal control of corvids to reduce predation pressure on target species.

Systematic reviews have been used to explore the likely effects of predator control on target species’ breeding parameters and population growth. General trends from Côté and Sutherland's (1997) review suggest that predator control has a positive effect on nest survival and post-breeding population size of prey; however, significant increases in the breeding population size did not follow predator control. Côté and Sutherland's example shows that predator control has no overall effect on prey population growth since numbers of breeding birds are, essentially, drivers of population increases and the breeding population sizes were not enhanced with predator control (Bolton *et al.* 2007). Demonstrating the lack of population increases shows that management options can be misinformed by assumptions. Reviews need to establish general trends, and if an impact of predators is found, should case-specific studies be conducted to further explore the relationship between predator and prey species, or biodiversity in general. If predator control is carried out with little benefit to target species, then funds and effort have been wasted (Amar *et al.* 2010). Systematic reviews can therefore help generate a clearer picture of a common research question and clarify assumptions.

Corvid control

Raptors and corvids are among the most commonly persecuted bird species (Etheridge *et al.* 1997). Corvids are efficient nest predators and typically take all eggs from a predator-destroyed nest (Angelstam 1986; Marzluff & Balda 1992). As such, these species are targeted for removal to promote breeding success and reverse population declines of target species like gamebirds, ground-nesting birds and species of conservation concern (Luginbuhl *et al.* 2001; Bodey *et al.* 2011). In the Faroe Islands predatory birds were controlled by imposing a compulsory ‘beak tax’ for men between the ages 15-50 who had to produce the beaks of ravens, crows, great skuas and black-backed gulls as tax from 1742 until 1881 (Bloch 2012). Public concerns about predators are often raised, putting pressure on authorities to implement control schemes (Newton 1998; Summers *et al.* 2004; Valkama *et al.* 2005, Amar *et al.* 2010). Lethal measures are frequently employed to control predators such as foxes and crows, which are believed to be the most significant predators of red grouse, an economically important gamebird in the UK (Redpath & Thirgood 1997). However, the effectiveness of predator control in promoting positive population growth of target species is still debated (Valkama *et al.* 2005).

Several studies have found no impact of predator control, most likely because of compensatory predation operating, whereby predation of the controlled species is substituted by another species (Opermanis *et al.* 2005; Bodey *et al.* 2009; Stien *et al.* 2010). For example, black grouse populations did not increase after corvids were removed because other predators stepped in, and therefore predation pressure was not reduced (Parker 1984). Smith *et al.'s* (2010) recent review on predator control found that removing all predators (rather than a select few) did, on average, achieved increases in target species' populations. However, removing all predators will often be an unrealistic and undesirable management option. This highlights the need to identify which predators are responsible for limiting target species populations. Only then can adequate species and context specific management options be developed to address this conflicting issue of predation and desired target species population growth.

Being generalist and opportunistic predators has raised concerns as to how corvid increases may potentially impact biodiversity. Yet, despite wide-spread attention and sometimes negative predictions of corvid impacts on biodiversity, studies appear inconsistent (Marzluff & Neatherlin 2006). If corvids have an inherently negative impact on biodiversity and respond positively to anthropogenic environmental alterations, then this added predation pressure may accelerate species declines and present another anthropogenic threat to biodiversity. A systematic literature review will explore whether corvids have consistently negative effects on biodiversity.

These concerns of increasing corvid abundance and biodiversity have also been seen within South Africa, where considerable concern has been expressed over the impact that pied crows may be having on biodiversity. Pied crows are the most widespread corvid in Africa, occurring in most of sub-Saharan Africa except for the central African rainforest and Namibian deserts (Londei 2010). This species is often associated with people (Carlson & Hartman 2001; Mwinyi & Said 2009) and is increasingly a prominent feature of urban environments (Marzluff & Angell 2005). Evidence suggests pied crows are becoming more frequent along roads and urban areas, especially in the Karoo where their numbers were previously low or absent (Dean *et al.* 2006). Pied crows have potentially high breeding rates (average 4 eggs per pair) (Maclean 1993), are opportunistic, aggressive and show great potential to not only survive, but thrive in new environments. Concerns have been especially raised in the Western Cape province, about their rapid population increase and potential threat to passerines, reptiles and raptors (Simmons & Barnard 2011; Lambrechts 2011).

To summarise, in this thesis I undertake a systematic review to examine general trends in the negative impacts that corvids, specifically members of the genus *Corvus*, have on biodiversity. Additionally, I undertake a more focused analysis exploring population changes of pied crows in South Africa, to investigate the drivers of changes in abundance. Descriptive and correlative analyses will be conducted to examine which habitat types or landscape attributes are associated with pied crow abundance changes. Finally, conclusions of the impacts of corvids and future research recommendations to deal with pied crows in a South African context will be briefly outlined.

CHAPTER 2

THE IMPACTS OF CORVIDS ON BIODIVERSITY: A REVIEW

Introduction

Predation can have a substantial impact on prey populations (Smith *et al.* 2010), limiting breeding success (Newton 1998; Stien *et al.* 2010; Luginbuhl *et al.* 2012) and suppressing population growth. Predation has shaped the life history strategies and behaviour of prey species, such as changing brood size, foraging behaviour and timing of breeding (Tryjanowski 2001; Brambilla *et al.* 2004). Predators can only impact prey population size when predation adds to other forms of mortality, beyond that which would have otherwise occurred naturally (Redpath & Thirgood 1997). This 'doomed surplus' concept (Errington 1946) underlies the essence of predation theory, since exceeding this mortality rate will ultimately have a negative impact on prey populations. Additionally, rare and sensitive species may be especially susceptible to increased predation, particularly if predation rates increase or remain high while prey populations decline, thus inflating predation pressure (a phenomenon known as 'hyperpredation') (Bui *et al.* 2010). Changes in predation pressure due to fluctuations in predator and prey densities can exacerbate predation to unsustainable levels where predation can cause decreased productivity and a resulting decline in population size (Stoate & Szczur 2001; Summers *et al.* 2004; Baláž *et al.* 2007; Dunn *et al.* 2010). This is of particular concern when prey species are of socio-economic (e.g. gamebirds) or of conservation importance (Valkama *et al.* 2005; Baines *et al.* 2008). To effectively inform management decisions, predation levels and the impact of predators needs to be accurately assessed.

In an attempt to boost breeding performance and population densities of target species, predator control has often been implemented (Butchko & Small 1992; Meckstroth & Miles 2005). This is based on the assumption that predation is a limiting factor in prey populations, and that predator control results in population increases (Holt *et al.* 2008). However, despite a wealth of cases employing predator control, the efficacy of predator control in enhancing species' populations is still contentious (Park *et al.* 2008). One reason is that the impacts of predator removal may be complicated by compensatory predation, where one predator is replaced by another, or by mesopredator release, when removal of one predator leads to increased abundances of another (Bodey *et al.* 2009). Coupled with this, experiments involving predator control through lethal removal of a particular predator, or a subset, is controversial, potentially socially unacceptable, time-consuming, difficult, and expensive (Ivan *et al.* 2005; Valkama *et al.* 2005; Smith *et al.* 2010). The objective of predator control needs to be defined and goals clearly stated. Scarce conservation resources for species of conservation concern need to be allocated to management options that produce desired results (O'Connor 1991). Several reviews have explored whether predator control is effective in reducing predation or increasing breeding populations of target species (Côté & Sutherland 1997; Valkama *et al.* 2005; Gibbons *et al.* 2007; Holt *et al.* 2008; Smith *et al.* 2010). It is important to identify where the interests in the outcomes of the systematic review lie, as the goals and objectives of predator control may differ depending on the management objectives. For example, game management is primarily concerned with post-breeding abundance before the hunting season, whereas biodiversity conservation is more interested in enhancing breeding population densities (Gibbons *et al.* 2007). Given widespread interest in whether predation can limit prey populations, cost-effective intervention is needed. Systematic reviews are of particular value when uncertainty remains in the conclusions drawn from several sources. They are particularly useful when these conclusions influence controversial management and policy changes, such as policies on lethal control of predators.

Côté & Sutherland (1997) conducted a meta-analysis from 20 published papers on the effectiveness of predator removal on enhancing bird populations, and concluded that predator removal significantly enhanced hatching success by 75% as well as post-breeding population sizes. However, predator removal did not generally result in subsequent increases in breeding population sizes. Thus, the general finding from that review was that although it might be useful for game-managers, it was unlikely to be effective for the conservation of declining species. Smith *et al.* (2010) updated Côté & Sutherland's (1997) review by analysing 83 published studies and also concluded that predator removal enhanced hatching and fledging success, but this time found that although the impact on post-breeding population size was not clear cut, predator removal did enhance breeding population size. Nordström's (2003) review focussed on 38 studies of ground-nesting birds in the Baltic and again found a general increase in nest success, post-breeding population size and breeding population size with predator removal. Holt *et al.* (2008) also conducted a similar meta-analysis and found an average 1.6-fold increase in prey population size following predator removal. The authors also found that removing multiple predator species was 3 times more effective than removing a single species. Newton (1998) drew similar conclusions and suggested that removing one predator was less effective due to compensatory predation. Newton (1998) also highlighted that most papers focused on generalist predators and ground-nesting birds.

Ground-nesting birds may be particularly prone to predation, and may therefore be more likely to respond to predator control. While Newton (1998) reviews predator removal studies, Valkama *et al.'s* (2005) more traditional review assessed dietary composition and correlative studies. Valkama *et al.* (2005) concluded that only very few raptor species regularly prey on gamebirds, and even for these there was little evidence that they reduced prey population densities. They did, however, conclude that certain raptor species (e.g. hen harriers (*Circus cyaneus)*) did have the capacity to limit prey population sizes. These reviews therefore drew overall trends and conclusions from a wealth of information on predator impacts on prey populations.

Management of common generalist predators often takes place for game management or for conservation purposes. Within the northern hemisphere, and particularly northern Europe, this most commonly involve the control of foxes and corvids, both of which are common and usually unprotected (Parker 1984; Tapper *et al.* 1996; Draycott *et al.* 2008; Bodey *et al.* 2009). Corvid species are also frequently identified as major nest predators of bird species of conservation concern (Andrén 1992; Soderstrom *et al.* 1998; Baláž *et al.* 2007; Klausen *et al.* 2009). Yet, despite a plethora of studies and experiments on corvid predation their overall impacts on biodiversity remain unassessed. Because corvids are diurnal and conspicuous nest predators, their importance in prey population regulation is often assumed prior to any assessment of the evidence. There are several biological reasons for why corvids may be a conservation management problem. They are an adaptable, opportunistic, generalist predator with high cognitive abilities. Yet, further problems will result if corvid management decisions are based on mis-conceptions or poorly substantiated conclusions about their ecological impact on prey populations. Pied crows are believed to be increasing in South Africa which has heightened concerns about their potential threat to local biodiversity. BirdLife South Africa has come under pressure from the public to tackle this crow ‘problem’. This is a contentious issue, since this species is indigenous and so management decisions need to consider the conservation of all aspects of biodiversity, including pied crows. However, although this species is indigenous on a national-scale, there are regions where it is locally absent and hence not indigenous. It is also important to distinguish pied crow management from that of the Indian house crow (*Corvus spelendens*), which is an exotic, invasive species. Furthermore, management is expensive and can cause further conservation issues if not implemented correctly. A systematic literature review is therefore appropriate to explore the relationships between corvids and populations of their prey species, and investigate if the causes for concern are established within the scientific literature.

Methods

Literature survey

To ensure robustness and repeatability, a formal process was employed to obtain all relevant studies for this systematic review. The scope of the study included species of the genus *Corvus* only. This is sufficiently broad enough to justify a review, since *Corvus* genera make up a third of all corvids, are notorious nest predators, and a considerable number of studies exist (dos Anjos 2009). 'Corvid' is used here to mean species of *Corvus*, unless otherwise stated. Corvid impacts were investigated by obtaining all relevant information regarding corvid predation. The question of concern has practical uses, as suggested by Smith *et al.* (2010), as the outcomes of the literature review will influence management decisions about corvid control and intervention.

Comprehensive literature searches were generated through Web of Science (apps.webofknowledge.com) to obtain relevant studies using the following keywords and combinations: (corvid* OR crow* OR raven* OR corvus) AND (predat* OR experiment*). The search was refined to studies included within the Science and Technology research domain only. The search was refined further, to include studies under the following topics only: environmental science, ecology, zoology, and biodiversity conservation.

Non-English studies were included if the abstract was in English, and provided sufficient information about which breeding parameters were used, outlined the study design, and gave the statistical significance of the outcomes. Additional references were obtained through reference lists of these studies. A separate systematic search was conducted in Google Scholar to evaluate the robustness of the Web of Science search. It was found that Web of Science was more robust and included several references missed through Google Scholar.

An “inclusive approach” was used to extract relevant studies (Reijnders *et al.* 2008). Titles of the studies obtained were scanned for relevance based on the abovementioned criteria and any parameter that measured their effect on prey species’ breeding parameters or population sizes. Abstracts were scanned for relevance of studies with ambiguous titles. All gathered literature was divided into two types of studies: experimental and correlative. Experimental studies were investigated, looking specifically at the impacts of experimentally removing corvids on the productivity, breeding population sizes, and post-breeding population sizes of target species. Then, for correlative studies, I investigated the direction of relationships between corvid increases and the responses of target species in terms of population size, breeding performance and behavioural changes. I also examined relationships of corvid predation pressure on artificial nests. Lastly, I explored the overall impacts of corvids on biodiversity by combining both experimental and correlative studies to provide a more holistic view.

Location of study (country), target species, and broad species group (e.g. passerine, wader, raptor, mammal etc.) was additionally extracted, with relevant breeding parameters or population size changes in response to predator control (for experimental studies), or changes in corvid abundances (for correlative studies). For the sake of succinctness, henceforth, when

I describe an impact, it is statistically significant; for example when stated "productivity *increased"*, it means it increased *significantly*.

Lastly, several different studies investigated more than one species, or more than one population or breeding parameter. Therefore, in this thesis, there is a distinction between the terms 'study' and 'case'; where the case is a response (e.g. breeding population size, clutch survival etc.) of a single species. Hence, there can be several cases for a single species in a single study.

Parameter & family groups

One of the challenges of a systematic review is to collate all response parameters and condense them into biologically meaningful groups. Factors affecting breeding parameters and population sizes were therefore explored (Gibbons *et al.* 2007). For the experimental studies, three dominant response groups were used to condense the different study parameters: 1) productivity, 2) breeding population size, and 3) post-breeding population size. Terminology varied between studies, however, all study parameters were condensed to relate to one of the three abovementioned parameters (Table 1).

Table 1: Response parameters of target species (terminology) condensed into three dominant response groups (parameter group) used for the analysis of the impacts of corvids on biodiversity in the experimental studies. PS = population size.

Terminology	**Parameter Group**	**Terminology (*continued*)**	**Parameter Group (*continued*)**
breeding pair counts	breeding PS	chick survival	productivity
nest densities	breeding PS	clutch success	productivity
counts[1]	post-breeding PS	clutch survival	productivity
population size[1]	post-breeding PS	fledgling success	productivity
breeding success	productivity	hatching success	productivity
brood failure	productivity	nest loss	productivity
chick mortality	productivity	nest success	productivity
chick production	productivity	nest survival	productivity

[1] Papers specified the timing of year as being post-breeding.

Some parameters did not fall into these categories and were mentioned separately (such as lay date and clutch size). Parameters were also condensed for the correlative studies. For example, abundance measures included density, presence, numbers, and proximity.

To explore any pattern of impact, prey species were condensed into several family groups. Prey species of experimental studies were classified into five groups – galliforms (gamebirds), gruiforms (crane-like birds), passerines, waders, and raptors. Only one study reported on waterfowl (ducks), and these were placed into the wader category for convenience. Prey species reported in correlative studies were condensed into eight groups – ciconiiforms (ibises, storks, herons etc.), galliforms, mammals, passerines, pelicaniforms (birds with four webbed toes e.g. pelicans), raptors, seabirds and waders. These family groups were kept consistent throughout this review where possible.

Types of studies investigated

Experimental studies - Studies were classified as experimental when a) corvids were removed together, b) there were controls in either space or time, and c) specific population parameters of prey species were measured. Studies that removed corvids alongside other predators (e.g. foxes and raptors) were also included, and identified as multiple-species predator removal. Artificial nest experimental studies were included but were reported separately, as although they provide a measure of predation pressure by corvids, they are known not to be directly equivalent to natural nests (Zanette 2002). Some quasi-experimental studies that removed corvids, but did not have controls, were included with the correlative studies.

Experimental corvid removal could either significantly increase (+), decrease (-) or have no effect (none) on the prey parameters measured. For some terms, when breeding or population parameters increased with corvid removal, this suggests a negative effect of corvids. Therefore, a finding suggesting a negative impact of corvids would be revealed as a positive response. For ease of communication, a negative symbol (-) depicted in this review represents studies which found a negative impact of corvids on prey populations.

Correlative studies – These studies explore the relationships between various parameters of corvid and potential target species populations to draw inferences on impacts. Since these studies examine the influences of corvids, and not specifically predation rates, the term ‘target’ species is more suitable than ‘prey’ species. Different correlative approaches have been used to explore impacts of corvids. For example, Newson *et al.* (2010) used temporal correlations in bird survey data from annual national monitoring schemes to explore whether the population trends of 29 British bird populations were associated with increases in avian predator abundance. The directional responses of target species’ trends (increasing, decreasing, and stable) are related to predator abundances, allowing inferences to be drawn. Others studies use only spatial correlations, for example, Baláž *et al.* (2007) compared nest success in habitats with low or high corvid abundance. Others use a combination and explore the relationships between corvid and target species abundance, together with population trends (e.g. Amar *et al.* 2010). Target species’ population and/or breeding parameters either increased (+), decreased (-) or showed no response (none) in response to increases in corvids. A few studies described changes in predator populations of *Corvus* species grouped together with other predators into a single variable. Quasi-experimental studies were included in this section when the authors did not provide adequate temporal (i.e. before-after values) or spatial controls. These studies included Stoate and Szczur (2001); Baines *et al.* (2004) and Baines *et al.* (2008). Two studies (Sims *et al.* 2008; Tryjanowski 2001) measured the relationships of corvid abundance on several species which were combined into one metric, and therefore species-specific relationships with corvid abundance cannot be explored. These were therefore reported as ‘several species’ or ’27 different birds’. The correlative studies measured prey species parameters which were condensed into one of the seven following groups: productivity (brood size, breeding success, and clutch survival), chick condition and growth, parental provisioning, adult survival, abundance, predation rate, or species richness.

The most commonly reported corvid parameter in these correlation studies was corvid abundance and was analysed separately. Studies that measured clutch survival of artificial nests in relation to fluctuations with corvid abundance were again assessed separately.

Contingency tests were used to assess whether one aspect examined was disproportionately affected depending on corvid species or type of study. One such exploration assessed whether the impacts of corvids and predators were greater for ground-nesting species. Correlative studies described in artificial nest experiments were not included, as they only show predation pressure and may not represent true corvid predation.

Results

Literature search

A total of 2031 studies were identified by the search by December 2012 in the fields of environmental science, ecology, zoology, and biodiversity conservation. All studies were assessed for relevance by reviewing the title. From this, 285 studies remained and I read the abstract from each of these to ensure they met the abovementioned criteria for inclusion. One-hundred and five studies were eliminated based on the abstract. A total of 180 papers were further assessed for relevance, of which, 46 studies were finally selected for use in this review. Of these, 19 were categorised as experimental studies and 27 as correlative studies.

Table 2: Number of cases for each corvid species and country for both experimental and correlative studies. Number of studies are indicated in brackets (n). Some studies investigated the impacts of more than one corvid species. One study did not specify the corvid species and was hence noted as 'corvids'. Another study (Summers *et al.* 2009) investigated the relationship of two corvid species (hooded and carrion) and were therefore included twice, hence n=117.

	Study type	
Corvid species	**Experimental**	**Correlative**
American crow	6 (3)	6 (4)
Carrion crow	35 (8)	95 (12)
Common raven	6 (5)	11 (7)
Fish crow	-	1 (1)
Hooded crow	10 (7)	2 (2)
Jungle crow	-	1 (1)
Corvids	-	1 (1)
Total	57 (19)	117 (27)

	Study type	
Corvid species	**Experimental**	**Correlative**
Canada	-	1 (1)
Japan	-	1 (1)
Norway	7 (4)	1 (1)
Poland	-	1 (1)
Portugal	-	3 (1)
Slovakia	-	1 (1)
Sweden	1 (1)	-
Switzerland	-	1 (1)
UK	39 (10)	98 (12)
USA	7 (4)	10 (8)
Total	54 (19)	116 (27)

Experimental studies

A total of 23 species were included in the 19 studies meeting the quality criteria. The most studied avian group were waders (n=9), passerines (n=6) and galliforms (n=6), and a single study each on one gruiform and a raptor. A total of 54 cases were found. The most reported parameter from the 23 species studied was productivity (31 cases), breeding population size (16 cases), post-breeding numbers (3 cases), clutch success (3 cases) and lay date (1 case) (Appendix A, Table A). In no cases did predator removal have a negative effect on the target species (where predators were associated with positive population parameters), and so I did not list numbers of positive relationships any further in this section. Results for the two parameters with sufficient sample sizes (productivity and breeding population size) found that the majority of species showed no response to corvid removal (Table 3). Contingency tests between productivity and breeding population size suggested that both parameters showed similar responses to predator control (Table 3).

Table 3: Effect of experimental predator removal on target species populations: percentage of experimental studies having a negative or no impact on breeding parameters when corvids and other predators were removed. Parameters from 23 species from corvid (and other predators) removal studies (n=19) are shown. Number of cases is given in brackets. No studies found a positive effect on population parameters (i.e. that predators were beneficial). For all studies used see Appendix A.

Response	Productivity	Breeding Pop. Size	χ^2	DF	P-value
-	39% (12)	25% (4)	1.815	1	0.177
none	61% (20)	75% (12)			
Total (n)	32	16			

Combining all five abovementioned parameters, removing corvids, and in some cases other predators, improved productivity and/or population size parameters of the target species on 39% (13 species, 21 cases) of occasions. This shows that these predators had a negative impact on these parameters. However, the majority of species (61%, 18 species, 33 cases) showed no measureable effect of removing corvids and predators on any parameters measured.

Four corvid species were studied in the experimental studies found. The majority of cases focussed on carrion crows (65%, n=35), followed by the hooded crow (18%, n=10). Both the American crow and common raven were investigated in six cases (11%), with one case study investigating unknown corvids (1%). A contingency test comparing carrion crows with hooded crows revealed more negative impacts of carrion crows than expected, however this was marginally non-significant (χ^2=3.19,DF=1, p=0.074).

Impacts of experimental removal on productivity

Productivity before and after experimental predator removal for four avian groups was examined; waders (n=7), galliforms (n=3), gruiforms (n=1) and passerines (n=1). From all studies that found predator removal to benefit productivity (n=12), only one study (Erikstad *et al.* 1982) removed only *Corvus* species. All other studies demonstrating a negative effect on productivity removed other predators along with corvids. Productivity increased when carrion crows were removed alongside gulls (Parr 1993), foxes (Bolton *et al.* 2007; Fletcher *et al.* 2010), and other corvids and mammals (Stoate & Szczur 2006; White *et al.* 2008). The removal of common ravens and coyotes improved productivity of sandhill cranes (Littlefield 2003), while removing American crows with skunks and racoons improved pheasant productivity (Chesness *et al.* 1968).

Impacts of experimental removal on breeding population size

The effect of experimental removal on breeding population size was examined for three avian groups: waders (n=9), galliforms (n=4), and passerines (n=3). Of the 9 waders, golden plover (*Pluvialis apricaria*), lapwing (*Vanellus vanellus*) and curlew (*Numenius arquata*) were reported twice, giving a total of 16 studies (as mentioned in the total line for Table 3). The experimental studies measuring this parameter only involved three corvid species; American crow, carrion crow and hooded crow (see Appendix A). Chesness *et al.* (1968) found no effect of American crow removal (alongside skunks and racoons) on pheasant breeding population size. In contrast, Tapper *et al.* (1996), Fletcher *et al.* (2010), and Slagsvold (1980) found that breeding populations increased with predator control. In these three cases, carrion crows were removed alongside other predators, specifically corvids and other mammalian predators (Fletcher *et al.* 2010) and gulls (Parr 1993). Slagsvold (1980) was the only study which removed only corvids and examined breeding population size; he found that removal of hooded crows increased the breeding population size of fieldfares

(*Turdus pilaris*). The majority of cases (12 of 16) found no effect of predator removal on breeding population size..

Impacts of experimental removal on post-breeding population size

Post-breeding population size (i.e. population size directly after the breeding season) was reported for three species (grey partridge, lapwing and blackbird) in three separate studies (Tapper *et al.* 1996; Bolton *et al.* 2007; White *et al.* 2008). In all studies, corvids were removed alongside mammalian predators (including stoat, foxes and small mammals). In only one case did predator removal have a positive effect; on grey partridges (Tapper *et al.* 1996). No statistically significant effect was found for the other two cases (lapwings and blackbirds; see Appendix A), however, there was a marginally non-significant tendency for predator removal to increase post-breeding population size (p=0.075) overall.

Impacts of experimental removal on lay date & clutch size

Amar & Redpath (2002) found no effect of hooded crow removal (only species removed) on the lay date or clutch size for hen harriers. Clutch size increased when predators were removed in two (67%) of three studies (Chesness *et al.* 1968; Tapper *et al.* 1996), although in both these studies, mammalian predators were also removed.

Experimental studies removing corvids only

Eight experimental studies removed only corvids (Slagsvold 1980; Erikstad *et al.* 1982; Parker 1984; Stoate & Szczur 2005; Clark *et al.* 1995; Amar & Redpath 2002; Summers *et al.* 2004; Stien *et al.* 2010). For these studies, in the majority of cases (88%) corvid removal had no measureable impact on breeding parameters or population sizes (Table 4). Parker (1984) found no effect of corvid removal on willow ptarmigan (*Lagopus lagopus*) productivity. Only two studies (12%) showed a significant benefit of removing corvids (Slagsvold 1980; Erikstad *et al.* 1982). Fieldfare (*Turdus pilaris*) breeding population size increased significantly when hooded crows were removed in Norway (Slagsvold 1980), although this was attributed to interspecific competition rather than predation. Erikstad *et al.* (1982) found that willow ptarmigan productivity increased in the absence of hooded and carrion crows, and specifically concluded that territorial crows rather than the non-breeding floater population were the major predators.

Table 4: Outcomes (negative or none) of eight experimental studies in which only *Corvus* species were removed.

Parameter	-	None	Source
Breeding pop. size	1	1	Slagsvold 1980; Parker 1984
Productivity	1	12	Parker 1984; Erikstad *et al.* 1982; Clark *et al.* 1995; Amar & Redpath 2002; Stoate & Szczur 2005; Summers *et al.* 2004; Stein *et al.* 2010
Lay date	-	1	Amar & Redpath 2002
Clutch size	-	1	Parker 1984
Total (n)	12% (2)	88% (15)	

Although kleptoparasitism by corvids was observed by Amar & Redpath (2002), and food shortages were hypothesised to limit hen harrier productivity, there was no effect of hooded crow removal on productivity, lay date or clutch size.

Effect of corvid removal on different avian groups

Productivity of galliforms was the most commonly reported parameter (n=12), possibly because of the economic importance of these species for hunting. Most cases analysing the impacts of corvid removal on breeding population size were done on waders, and these generally found no impact (Table 5).

Table 5: Distribution of the impacts (% of change in population parameters) of predator control on different avian groups on various breeding parameters from 19 experimental studies. Number of cases (sample sizes) are indicated in brackets. Eight studies removed corvids only, while 11 studies removed corvids alongside other predators. Predator removal improved breeding and population parameters (indicated here as corvids having a negative (-) impact) or showed no effect (none). Population (pop.) and breeding parameters were sourced from all known literature, which were divided into five avian groups. Only one study measured duck breeding and population parameters, which was grouped with 'waders'.

Avian group	Impact	Productivity	Breeding pop. size
Galliforms	-	25% (3)	50% (2)
	none	75% (9)	50% (2)
Waders	-	47% (7)	20% (2)
	none	43% (8)	80% (8)
Passerines	-	33% (1)	33% (1)
	none	66% (2)	66% (2)
Gruiforms	-	100% (1)	-
	none	-	-
Raptors	-	-	-
	none	100% (1)	-

Predator removal influenced avian groups differently (Figure 1). Due to sample size, a contingency test could only be conducted on the impacts on productivity by corvids between galliforms and waders. This showed no difference in the impacts of corvids on the productivity of these groups (χ^2=1.34,DF=2, p=0.511). Corvids and other predators therefore had a similar effect on different groups of birds.

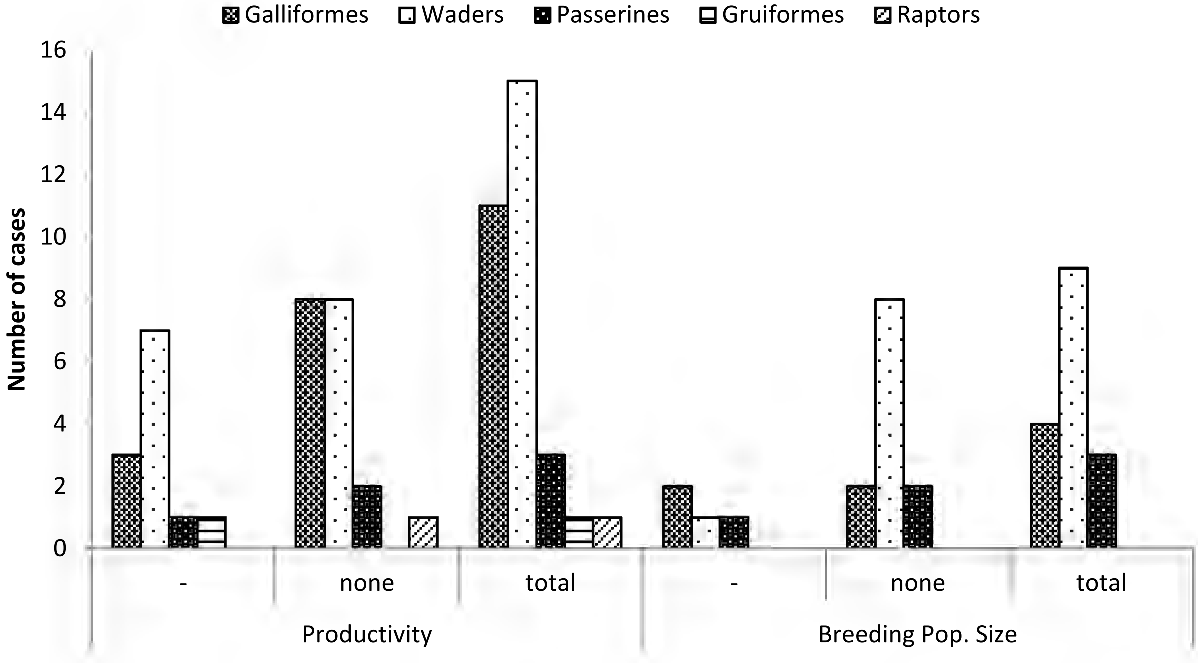

Figure 1: Response of several avian groups (23 species) where relationships between species *Corvus* and productivity or breeding population size of avian groups were examined in experimental studies. Corvids either had a negative influence (-) or no influence on the parameters measured. Productivity parameters included hatching success, fledging success, and chick mortality.

Correlative studies

Twenty-seven studies reported correlations between corvid abundance and its influence on the population size, breeding performance or behaviour of >59 target species (see Appendix B, Table B). Thus, a total of 116 relationships were examined. The explanatory variable in these relationships was a measure of corvid pressure being represented in three different ways: abundance, activity, and levels of predation. Abundance was the most commonly used measure and included the presence or density of corvids (see Appendix B).

The majority of cases (63%, n=74) found no influence of corvids (Figure 2; Table 6). Only in 26% (n=30; Summers *et al.* (2004) investigated hooded and carrion crow simultaneously and was therefore reported twice) of cases was a negative association found. Interestingly, in

11% of cases (n=13) a positive association was found, indicating that both corvid abundance and target species' abundance simultaneously increased. Passerines were the most commonly reported group (n=78), followed by waders (n=21), galliforms (n=7), pelicaniforms (n=3), mammals (n=2), seabirds (n=2), ciconiiforms (n=2), and one raptor.

In the correlative studies found, seven corvid species were studied (Table 6). The vast majority of studies (81%, n=95) focused on carrion crows, with only 9% (n=11) on common ravens, 5% (n=6) on American crows, 2% (n=2) on the hooded crow, and fish crow, jungle crow and unknown corvids 1% (n=1) each (see Appendix B). A contingency test comparing the impacts of carrion crows with common ravens (those with sufficient sample sizes) revealed that neither corvid species had a disproportionate impact on target species' (χ^2=2.45, DF=2, p=0.293).

Table 6: Varied impacts (%) for each corvid species' change in abundance on target species derived from the 27 correlative studies. Corvid abundances could either have a positive (+, benefit), negative (-), or no (none) influence on target species' breeding or population parameters. One study did not specify the species of corvid, and is classified here as Unknown (Baláž *et al.* 2007). Although 116 cases were examined, one study by Summers *et al.* (2004) investigated hooded and carrion crow simultaneously and was therefore reported twice, hence n= 30 for negative influences.

Corvid species	+	-	None
American crow	-	100% (6)	-
Carrion crow	12% (11)	17% (16)	72% (68)
Hooded crow	50% (1)	50% (1)	-
Common raven	9% (1)	36% (4)	55% (6)
Fish crow	-	100% (1)	-
Jungle crow	-	100% (1)	-
Unknown	-	100% (1)	-
Total	11% (13)	26% (30)	63% (74)

Influences of corvid abundance on different avian groups

Exploring these correlative studies revealed that certain groups of target birds are studied more than others, and that corvid impacts are not always consistent between these groups (Figure 2). Differences do exist between all the avian groups (χ^2=33.29, DF=14, p=0.002). Passerines were the most commonly studied target group (perhaps unsurprising given that they are the most common avian family) and in the majority of cases (70%, n=53) were uninfluenced by corvid abundance (Figure 2; Table 7). Similarly, the majority of waders, mammals and galliforms showed no response to increases in corvid abundance (Table 7). A contingency test comparing passerines and waders (those with sufficient sample sizes) was statistically not significant (χ^2=3.52, DF=2, p=0.172). Results in other avian groups tended to be more frequently negative, but these need to be regarded as examples only and not overall trends of those groups, given the low sample size.pelicaniforms

Table 7: Summarised findings from correlative studies showing the direction and frequency of different avian groups' response to increasing corvid abundances.

Group	+	-	none	Total
Ciconiiforms	-	100% (2)	-	2% (2)
Galliforms	-	43% (3)	57% (4)	6% (7)
Mammals	-	-	100% (2)	2% (2)
Passerines	16% (12)	14% (11)	70% (53)	67% (76)
Pelicaniforms	-	100% (1)	-	3% (3)
Raptors	-	100% (1)	-	1% (1)
Seabirds	**-**	100% (2)	-	2% (2)
Waders	4% (1)	30% (7)	65% (15)	19% (23)
Total	11% (13)	26% (29)	63% (74)	116

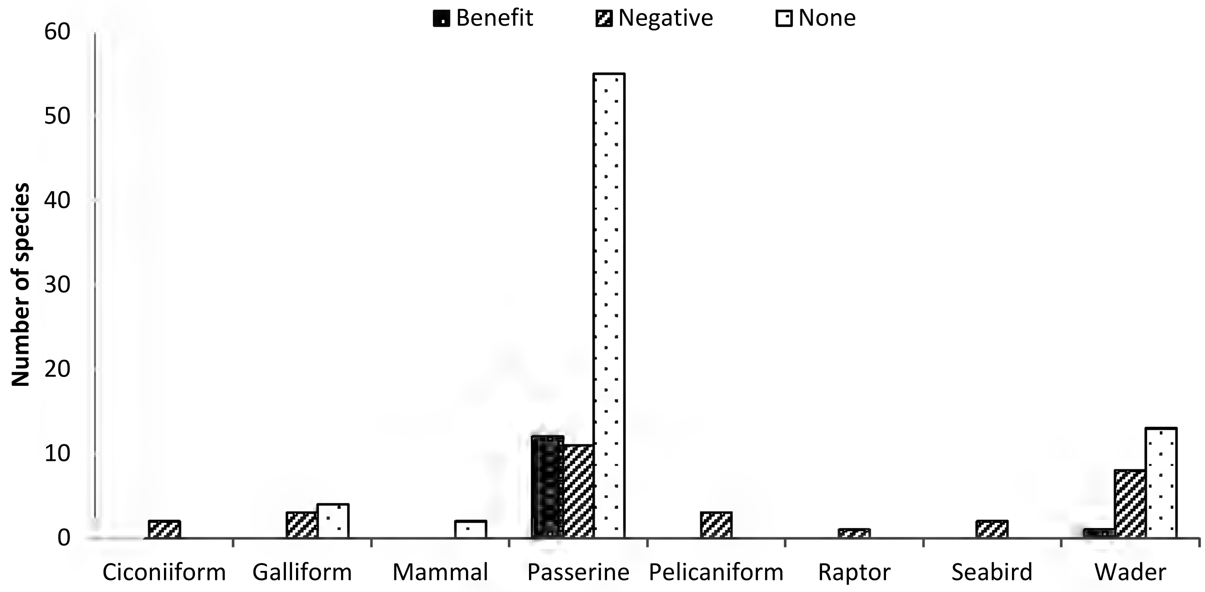

Figure 2: Graph showing the frequency of relationships (+/-/none) from 27 correlative studies between of corvids and target species (n=116 cases) categorised into different family groups. A contingency test comparing passerines and waders revealed that observed negative impacts on waders was higher than expected, however this was not significant (χ^2=3.52,DF=2, p=0.172).

Correlations between corvids and clutch survival

Ten studies reported on correlative studies between clutch survival and corvid abundance or predation pressure (Appendix B). All species show a negative relationship with clutch survival, except for some passerines (Figure 3). A negative association with clutch survival was found for the majority of species studied (77%, n=14) suggesting that increases in corvid abundance and the accompanying predation could limit breeding success of these species (Figure 3). Only 4 species (blackbirds (*Turdus merula*), whitethroats (*Sylvia communis*), yellowhammers (*Emberiza citronella*) and chaffinches (*Fringilla coelebs*)), all part of a single study in the UK, showed no response to increases in corvids (Stoate & Szczur 2001, 2005). Thus, there is quite strong evidence that clutch survival is negatively affected by corvids.

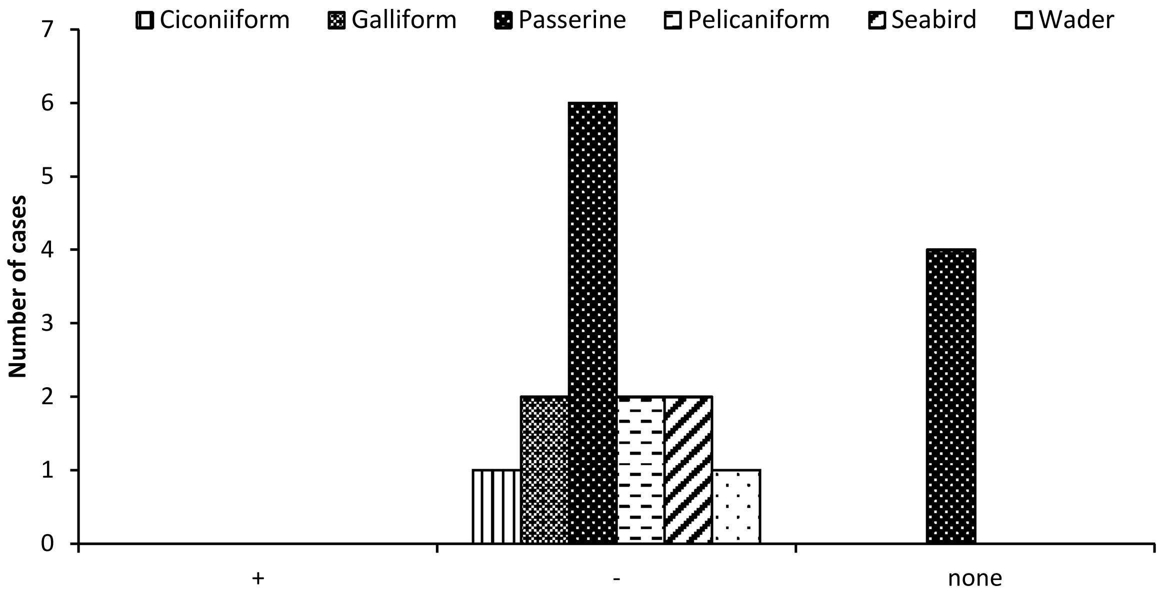

Figure 3: Number of cases that showed an association with corvid abundance and clutch survival for each avian group. A total of 18 cases (from 10 studies) reported on changes in clutch survival in response to changes in corvid abundances. A total of 16 species were reported that were condensed into the six avian groups shown in the graph.

Correlative studies with artificial nests

Of the seven cases that investigated the impacts of corvid abundance and predation on artificial nests, four cases (57%) showed a negative relationship (Appendix B, Table C). Only three cases (43%) reported no association between artificial clutch survival with increasing corvid abundance (Luginbuhl *et al.* 2001; Jokimäki *et al.* 2005). However, with such small sample sizes it is hard to draw conclusions.

Exploring impacts by combining experimental and correlative studies

Combining experimental and correlative studies, I found that the majority of results (63%, n=107) detected no impact of corvids on their target species (Figure 4; Appendix C). In total, a negative impact was detected 50 times (29% of results), with 29 of these 50 being found through correlative studies. Several of the correlative studies detected positive influences (benefits) of corvids on target species (8%, n=13), whereas no positive effects were detected in the experimental studies. A contingency test comparing the impacts of waders and passerines suggested that waders are being significantly more negatively affected by corvids than expected, and also show significantly fewer beneficial relationships compared to passerines (χ^2=7.15,DF=2, p=0.027). Furthermore, experimentally removing only corvids (n=8) and those also removing other predators (n=11) showed that crow-only removals found significantly fewer negative impacts than expected (χ^2=5.7, DF=1, p=0.01).

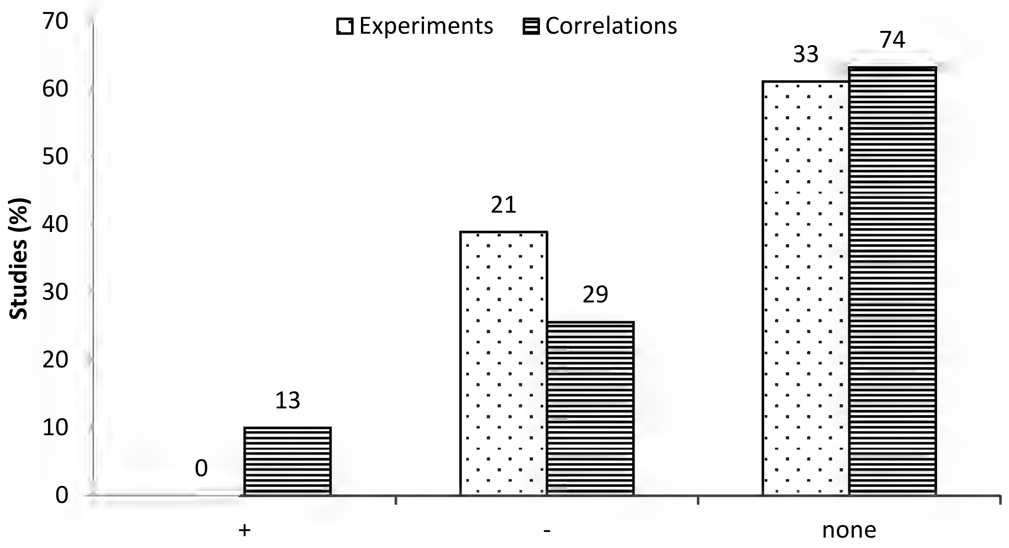

Figure 4: Comparing the different impacts (positive (+), negative (-), or no effect (none)) of corvids on target species' (%) between experimental and correlative studies. A total of 170 cases from 46 studies were used. The number of cases (sample size) from each study type and each effect is indicated on the graph.

Examining the different avian groups studied in these different studies (correlative and experimental combined), I found that waders were the most frequently investigated (n=47). Around half (52%) of these studies showed no relationship with corvids. Negative impacts of corvids were reported for all species groups, except for two mammals (Iberian hare and European rabbit), which were unaffected by corvid population changes (Beja *et al.* 2009). The impacts of corvids were not distributed equally among avian groups (Table 8).

Table 8: Number of cases showing the impacts of corvids on different avian groups from experimental and correlative studies. Percentage of impacts were only displayed when n >20, as these show meaningful differences in the impacts of corvids within one avian group, and are shown in brackets. Waders and passerines were the most negatively affected avian groups.

Avian Group	+	-	none
Ciconiiform	-	2	-
Galliform	-	11 (46%)	13 (54%)
Gruiform	2	-	-
Mammal	-	-	2
Passerine	11 (18%)	16 (26%)	34 (56%)
Pelicaniform	-	3	-
Raptor	-	2	3
Seabird	-	1% (2)	-
Wader	2 (4%)	15 (31%)	31 (65%)

To explore whether ground-nesting species might be more vulnerable to predation by corvids, I tested whether there was a significant difference in the proportion of impacts on ground-nesting and non-ground-nesting species. No such difference was found (χ^2=3.38, DF=2, p=0.184) (Figure 5).

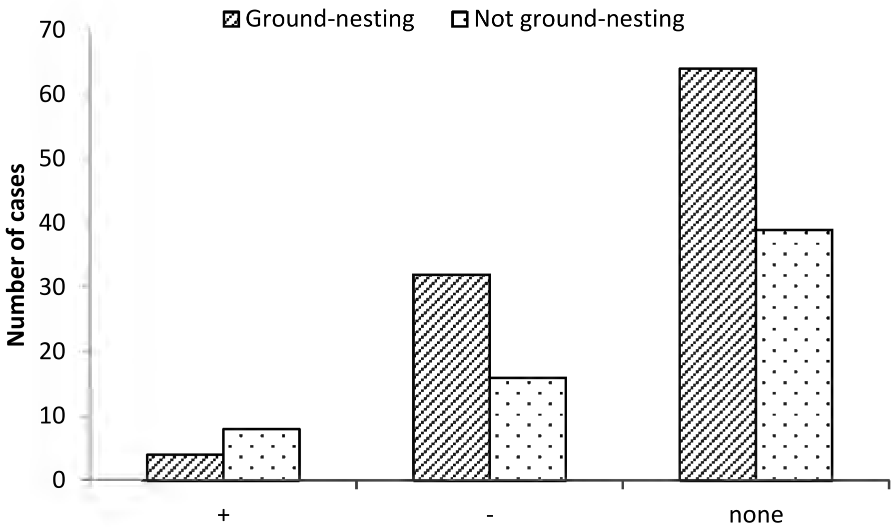

Figure 5: Distribution of the impacts of corvids (positive (+), negative (-), or none) on ground-nesting and non-ground-nesting bird species found in experimental and correlative studies. There was no difference in the impacts between the two categories (χ^2=3.38, DF=2, p=0.184).

Discussion

There is no consistent pattern with regards to corvid impacts on biodiversity; in fact, no impact is most commonly reported. The range of responses found demonstrates a diversity of relationships between the different avian groups, target species, and corvid species. When combining experimental and correlative studies, the majority showed no influences (63%), with some negative (29%) and apparently beneficial (8%) relationships. Furthermore, only correlative studies found positive statistical relationships between corvids and target species, suggesting that different study types may have the capacity to detect impacts differently. The vast majority of cases in both experimental and correlative studies revealed no impacts. It therefore appears that corvids, in general, are not solely responsible for limiting target species' productivity or population size.

Influences of corvid predation vary between species and studies. For example, both Parker (1984) and Erikstad *et al.* (1982) removed hooded crows and common ravens, and measured the effect on willow ptarmigan, but drew opposite conclusions about corvid predation. Thus, the impact of the same corvid species (hooded crow and common raven) may differ considerably between studies. Erikstad *et al.* (1982) noted, however, that the negative impacts of crows were attributed to territorial crows learning the location of ptarmigan nests. This therefore demonstrates the intricacies involved in drawing general conclusions on the impacts of corvids.

Despite the inconsistent findings of corvid impacts from these studies, negative impacts have been detected. Of the 46 experimental and correlative studies, 30 studies showed evidence of a negative impact of corvids on target species' breeding performance or population size. Within these two types of studies, 67 species were studied, of which 35 species were negatively impacted by corvids and other predators. Lapwings (*Vanellus vanellus*) were the most frequently studied species, with 16 different parameters being examined in 10 different studies (Parr 1993; Tharme *et al.* 2001; Bolton *et al.* 2007; Baines *et al.* 2008; MacDonald & Bolton 2008; Amar *et al.* 2010, 2011; Fletcher *et al.* 2010; Newson *et al.* 2010; Bodey *et al.* 2011). There was an interesting distribution in the types of species that were the focus of study. The top three species are all waders (lapwing n=16, curlew n=8, golden plover n=8) followed by two passerine species (blackbird n=7 and yellowhammer n=6). This suggests that there may have been particular concern that corvids and other predators may have a disproportionate impact on them. This suggests that most studies are being done because anecdotal evidence suggests that they are potentially affected by predators, and also suggests an inherent species sampling bias.

Waders were found to be more affected by predation than passerines, but, only when both experimental and correlative studies were considered. There is therefore a statistical tendency for waders to be impacted more negatively from corvids and other predators, which warrants further investigation. Previous research has suggested that ground-nesting birds, such as waders, are particularly prone to be negatively influenced by predation (Newton 1993; Nordström 2003). Gibbons *et al.* (2007) conclude that populations of ground-nesting species, especially waders and some gamebirds, are likely to be limited by predation as their nests and young are likely to be more vulnerable to predation. However, in this study I found that ground-nesting species were not disproportionately affected by predation. The opposite is often claimed to justify predator control to enhance wader populations of conservation concern (see Bolton *et al.* 2007; Evans *et al.* 2009; Bodey *et al.* 2011). This study therefore suggests that although waders can be influenced by predators, not all ground-nesting birds are equally affected by corvids and other predators.

From all studies examined in this study, there were far fewer negative impacts compared with positive or no impacts. It thus appears that in the majority of cases, corvids do not negatively effect on target species (see Appendix C). However, it is useful to investigate which method is more suitable to examine the impacts of corvids on biodiversity. Experimental studies are often favoured as they manipulate the variable of interest (in this case corvids), and allow for causative relationships to be drawn (Nicoll & Norris 2010). Correlative studies, on the other hand, often make use of existing datasets on species abundances by collecting data either temporally (e.g. Newson *et al.* 2010) or spatially (e.g. Tharme *et al.* 2001). They are therefore often less expensive and can be done opportunistically (e.g. Amar *et al.* 2011, Newson *et al.* 2010). It is therefore important to utilise existing datasets to explore correlative trends, and then further investigate interesting findings through rigorous experimental studies of crow removals.

The best method to detect the real impact of corvids on biodiversity is through experiments that only remove corvids and no other predators. I found only 8 experimental studies which removed only corvids. From these studies, Parker (1984), Clark *et al.* (1995), Stoate and Szczur (2005), and Stien *et al.* (2010) found no impact on their target species, which they believed was due to compensatory predation by other predator species. Summers *et al.* (2004) results were confounded by climate, where increased rains obscured patterns of corvid impacts. Amar and Redpath (2002) concluded that food supply was the ultimate limiting factor of hen harriers. Only two of these experimental studies showed an impact of corvids on nest survival and bird diversity; Erikstad *et al.* (1982) and Slagsvold (1980). Slagsvold (1980) showed that carrion crows had different effects depending on the target species. In line with the overall results found in this study, some species increased due to reduced predation pressure from carrion crows, while others decreased due to increased interspecific competition. However, the significant increase in fieldfare (*Turdus pilaris*) numbers following carrion crow removal was due to preferred habitat being utilised during winter migrations, and increases began prior to crow removal (Slagsvold 1980). Thus, the seemingly negative impact of crows was apparently confounded by the fieldfare’s habitat preference. It is therefore essential to use corvid-only removal experiments to detect impact, and when an impact is found, investigate it further to understand the mechanisms of impact.

Experiments removing only corvids (n=8) found significantly fewer negative impacts than expected . Compensatory predation or mesopredator release may play a role here. The biggest predators of corvids are corvids themselves, and culling one species of corvid could result in the higher predation rates by others. For example, Bodey *et al.* (2009) detected the competitive release of common ravens when hooded crows were culled. Predation by common ravens potentially obscured changes in predation rates when hooded crows were removed, which meant the impacts of hooded crows could not be detected. To detect the impacts of corvids in general, future studies are needed on species specific responses to corvids. In addition, studies are needed where all corvids are experimentally removed in order to properly quantify the impacts of *corvids* (in general) on target species. However, a well-designed experiment needs to be thoughtfully implemented, as several factors (e.g. compensatory predation) could potentially make corvid predation events difficult to detect. Nevertheless, the fact that less negative impacts were detected from the corvid-only removal experiments does provide some support for the notion that corvids do not necessarily have a large negative impact, particularly in comparison with some other predators.

An unexpected yet interesting finding was that correlative studies detected several positive relationships, suggesting the possibility of beneficial impacts from corvids on the target species. Passerines were positively correlated with corvid abundance 12 times (11%), while only one wader (a snipe) showed an apparent benefit of corvids. However, interpretations of these results, as with all correlations, must be approached with caution as they may not be causative, but may have arisen simply by chance. Also, a positive relationship could arise from behavioural changes of target species’ in the presence of predators like corvids, or correlated with a third unknown environmental variable. In these cases, the presence of the corvid does not benefit the target species, but the initial negative impact has driven behavioural changes to cope with increased predation pressure. In a more in-depth behavioural study, Dunn *et al.* (2010) found that yellowhammer chick condition and growth was positively associated with carrion crow abundance. This was attributed to increased parent provisioning load with increasing predation risk. Importantly, chick condition and growth improvements were only found in habitats with high food abundance, and in fact the opposite is true for poor habitat quality regions (Dunn *et al.* 2010). The interpretation that corvid presence increases chick provisioning rate is therefore misleading, because this behavioural coping-strategy in the presence of corvids will yield different impacts depending on the habitat condition. Conclusions cannot be drawn that corvids improve the condition of yellowhammer chicks. However, this does demonstrate interesting behavioural adaptations of target species to increased predation risk, and also shows that habitat condition can determine whether non-lethal impacts of corvids are beneficial or harmful.

The possibility of inferring misleading trends needs to be acknowledged. Spurious relationships need to be identified and separated from causative ones. For example, Tryjanowski (2001) found an apparent benefit of corvids on species diversity, where species richness increased with proximity to raven nests. This was attributed to increased predator protection by aggressive ravens, which indirectly increased nest survival of species. This finding differs from the associated benefits of several passerine species from Newson's *et al.* (2010) study, which are potentially not causative, but where corvids and the species in question both happen to benefit in the same region at the same time. Still, these correlative trends are useful in highlighting relationships that would otherwise be missed.

In conclusion, this study highlights that there is little consistency in the impacts of corvids on other bird species. These impacts are by no means as clearly negative as suggested by public or landowner perception. Further research on species specific impacts needs to be conducted in order to draw meaningful conclusions. Although this study describes few conclusive reports that corvids impact biodiversity, there is still a potential for corvid species to cause excess mortality, or alter behavioural or reproductive patterns in other species. For example, Kristan and Boarman (2003) found that common ravens in the Mojave desert can reach unnaturally large numbers, due to supplementary food from anthropogenic sources, which has resulted in hyper-predation on the native desert tortoise (*Gopherus agassizii*). They concluded that this increase in predation pressure is impacting the tortoise population, and could potentially result in the extinction of this reptile. Monitoring of corvid populations and experimental studies quantifying their impacts on specific species should therefore be continued.

Thus, from the evidence presented in this study, biodiversity is not consistently negatively impacted by corvids, and in fact are most often unaffected by them. However, negative impacts exist and those cases require further investigation to assess the impacts of corvids, and develop management tools to mitigate their impact.

CHAPTER 3

AS THE CROW FLIES: PIED CROW CHANGES IN ABUNDANCE AND RANGE EXPANSION

Introduction

Monitoring changes in bird distribution and abundances is often viewed as a conservation priority since these changes can draw attention to population declines or local extinctions (Fuller *et al.* 1995; Sax & Gaines 2003; Lesinski 2009), expanding ranges of potentially invasive species (La Sorte & McKinney 2006; Fleischer *et al.* 2008), and changes in species assemblages (Thomas *et al.* 2004; Sims *et al.* 2007). Population changes may also provide important insights into fundamental ecological processes such as fluctuating predation pressure, and can be indicative of larger scale changes in habitat quality (Evans 2004; Robinson & Sherry 2012), land cover (Sugden & Beyersbergen 1986; Amar *et al.* 2011), or climate (Rutherford *et al.* 1999; Beans *et al.* 2012).

At any given time, populations are subjected to pressures from predation, disease, or changes in resources. Avian species respond differently to such pressures which potentially alter population numbers and drive range shifts depending on their behavioural and physiological plasticity and adaptability (Yeh & Price 2004).

Research is most often preoccupied with declines of highly specialised, endemic or rare species (Peery & Henry 2010; Salmona *et al.* 2012; Herzog *et al.* 2012) and when population expansions are explored, they are most typically concerned with exotic invasive species (Hulme 2009; Fennell *et al.* 2012). Surprisingly much less attention has been paid to those common species that may benefit from altered landscapes (Gaston & Fuller 2008). Common species can exhibit disproportionate impacts on ecosystems due to their sheer numbers, highlighting the importance of monitoring and understanding the mechanisms for such population changes (Gaston & Fuller 2008). It is therefore essential to understand changes and mechanisms driving population sizes, as lack of such understanding presents immense challenges for conservation of biodiversity, particularly if predatory species are increasing. The importance of these changes and their impacts on species may intensify as the impacts of climate change further emerge.

Several crow species have shown stark increases in their numbers and range in the last 50 years (Marzluff & Angell 2005). This appears to be a global phenomenon, with crow populations expanding in North America (Chamberlain-Auger *et al.* 1990; Marzluff *et al.* 2001), Europe (Luniak 2004; Lesinski 2009; Jokimäki & Kaisanlahti-Jokimäki 2012), the UK (Amar & Redpath 2002; Gibbons *et al.* 2007), Australia (Stevenson 2011) and Asia (Kale *et al.* 2012). Surprisingly little information has been published on crow population increases in South America and Africa. Carlson & Hartman (2001) assessed pied crow densities in Tanzania and noted their increase in association with certain human settlements. A crow eradication programme in Zanzibar described the pied crow population to be low in 1990 and not considered a pest, however the authors note that pied crows are socio-economically destructive and are increasing in some areas (Mwinyi & Said 2009). Anecdotal observations in South Africa suggest similar trends. In the western USA, American crows have increased by 300% since the 1980s (Sauer *et al.* 2008), the Indian House crow showed a 30-fold population increase in recently invaded Singapore (Lauro & Tanacredi 2012), hooded crows have increased by 80% in some regions in the UK (Amar & Redpath 2002) and the common raven has increased by 1500% in urbanised areas in the Mojave Desert (USA) over the last 30 years (Boarman 1993). These unprecedented rates of corvid increases have drawn attention to potential issues that may occur from population booms of these predatory and scavenging species. It has become clear that global increases in crow and raven populations are of conservation relevance and need to be further explored.

Many of the changes in crow abundances have occurred in urban areas (Marzluff *et al.* 2001). Many crow and raven species are synanthropic (human-commensal) species; in the USA over 75% of American crows occur within 5km of urban centres and are thus closely associated with people (Marzluff & Neatherlin 2006). Urban centres promote residency (Chace & Walsh 2006), provide ample nest-sites (Mills *et al.* 1989), offer high food predictability through feeders, rubbish-dumps and road-kill (Kristan & Boarman 2003; Chace & Walsh 2006; Function 2009; Kale *et al.* 2012), and protection from predators including from human persecution (Vuorisalo *et al.* 2003; Luniak 2004). Nest densities also tend to be higher and territory size tends to be reduced in urban areas as resources are ample and therefore allow for greater abundance (Luniak 2004; Chace & Walsh 2006). This is supported by Luniak (2004) who found a positive relationship between corvid densities and buildings. It is therefore unsurprising that urban areas potentially boost crow breeding performance, through improved chick condition and lower mortality and thus provide the perfect conditions enabling population expansions (Bui *et al.* 2010; Kale *et al.* 2012).

Anecdotal evidence of negative impacts on biodiversity caused by increasing pied crow populations in southern Africa resulted in BirdLife South Africa (2012) producing a position statement on the issue, calling for conclusive evidence with which to evaluate public claims. Pied crows are generalist, aggressively territorial, fast breeding (3-7 eggs), and highly adaptable, which allows them to respond positively to anthropogenic expansion and development. It is therefore necessary to quantify changes in pied crow abundance and investigate which habitat types or regions are showing increases in abundance. Concerns have also been raised that pied crows are establishing populations in the Karoo and other parts of western South Africa (Simmons & Barnard 2011). This region has few trees, and the presence of electricity and telephone transmission lines in these areas may potentially facilitate crow expansion by providing nest and perch sites (Lammers & Collopy 2007).

Knight and Kawashima (1993) found that common ravens in North America were more abundant along transmission lines, especially those along highways, as road-kill generates carrion. This is supported by Dean *et al.* (2006) who also found an association of pied crows with roads in South Africa, where pied crows were often seen feeding on road-kill in the Nama Karoo. Dean and Milton (2000) also noted a preference for pied crows to nest in transmission lines along roads. Londei (2010) found that pied crows favour artificial pastures for livestock rather than cultivated lands or natural reserves. Understanding the associations between pied crows and habitat use variables can provide essential insights into causes for their increase and spread.

When corvid numbers increase, concerns are often raised about threats they may pose to biodiversity (Birdlife South Africa 2012). Pied crows have been negatively portrayed in the media for preying upon and harassing other species, such as mobbing raptors, raiding passerine nests, and predating on juvenile tortoises (Simmons & Barnard 2011; Lambrechts 2011). Birdlife SA has recently come under increasing pressure to deal with the pied crow problem. Several farmers have expressed frustration with increasing crow populations as both pied and cape crows (*Corvus capensis*) are known to remove the eyes of lambs and sickly adults, steal hens' eggs and forage on seeds in arable land and on foodstuff for livestock (Rowley 1969). Additionally, there are concerns that land owners may use poison to control crows, which can have dire conservation impacts on non-target species (Davidson & Armstrong 2002). Pied crows are indigenous to South Africa, so culling would add further ethical and conservation dimension to this issue. Some corvid species are associated with predation of sensitive species (Chapter 2) and behaviour (such as mobbing, kleptoparasitism (e.g. Sordahl 1990; Amar & Redpath 2002). However, surprisingly no studies have been published on pied crows to quantify their impacts on any aspect of biodiversity. Changes in pied crow range and abundance, although suspected, have not yet been quantified (Mclean

1993). It is therefore essential to assess first, whether there is indeed an increase in the pied crow population size, and if so, where and why these changes have occurred.

Fortunately, the Southern African Bird Atlas Project (SABAP) allows comparisons of pied crow changes to be made over the last 25 years. In this study I compare reporting rates of SABAP1 (1987-1991) with SABAP2 (2007-2012) and describe changes in relative abundance of pied crows (as measured by reporting rate), across South African and within each province. Analysing each province separately was aimed at providing the provincial conservation authorities with information aimed at management on a provincial scale. I then explore changes inside or outside of protected areas, and in different biomes. In addition, I explore the evidence for four key explanations for their increase and range expansion: (1) changes in temperature; (2) changes in rainfall; (3) presence of transmission lines; and (4) urbanisation (i.e. areas dominated by human settlements). To explore these hypotheses, I tested whether changes in pied crow reporting rates in each quarter degree square are associated with 1) climate change (temperature and rainfall), 2) urban areas and 3) transmission lines over the last two decades, and infer which factors may be aiding pied crow expansion in South Africa.

Methods

Pied crow abundance & distribution

Data on pied crow abundance and distribution were obtained from the Southern African Bird Atlas Project (SABAP) including both SABAP1 (Harrison 1997) and the refined and updated SABAP2 (http://sabap2.adu.org.za/). SABAP is a citizen science initiative where areas are surveyed based on a card system recording the species of birds seen in the area for a given time (Harrison *et al.* 2008). SABAP1 and SABAP2 differ in both spatial and temporal resolution, with a higher resolution in SABAP2 to enable more rigorous analysis. On a spatial scale, SABAP1 used quarter-degree-grid cells (QDGC) on a latitude/longitude grid (QDGC; *ca.* 24 km x 24 km) with a temporal resolution in reporting rates used on a per month basis from 1987-1991. The spatial resolution of SABAP2 was based on a 5' x 5' grid cell, the 'pentad', where a pentad at this latitude is *ca.* 8 km x 8 km and nine pentads equal one QDGC. SABAP's temporal resolution relied on five-day reporting periods. In this study I used data from July 2007 – August 2012 (SABAP2 is an on-going project). These spatial and temporal differences introduce several difficulties in comparing SABAP1 with SABAP2 (see Bonnevie (2011) for more details). Nevertheless the best way to overcome these shortcomings was to generaliseSABAP2 pentad data to the QDGC level to make them spatially comparable with SABAP1.

For each QDGC (cell), I calculated the pied crow reporting rate, calculated as the number of cards recording pied crows divided by the total number of cards. . I assumed that there were no false positives i.e. that pied crows were always correctly identified. This is likely a safe assumption, as pied crows are a common, conspicuous, well-known and distinctive species. Reporting rate in each period (SABAP1 and 2) can then be used as a proxy for relative abundance.

The SABAP data, as a southern African regional project, included the political borders of South Africa. One issue with SABAP data is the discrepancies in survey effort in different areas throughout the country (e.g. mean number of cards per cell is 61, maximum 2297 for SABAP1). Different potential card thresholds in our subsequent analysis were explored to assess the extent of information lost in favour of robustly depicting actual change in reporting rates. A five card minimum for both SABAP1 and 2 was chosen to ensure confidence in the metric of change in pied crow abundance for each cell. This threshold required the exclusion of 751 (37%) of QDGC from the analysis.

Changes in pied crow abundance were illustrated with ArcGIS version 9.3 using changes in reporting rates between SABAP1 and SABAP2 for each cell. The categories described adhere to those used in SABAP maps (http://sabap2.adu.org.za/spp_summary.php?Spp=522&section=2) (Table 1). Overall trends were explored by the evaluating number of cells in each category described in.

Table 1: Description of the SABAP (South African Bird Atlas Project) categories derived from changes in reporting rates from SABAP1 and SABAP2.

SABAP categories	Description
SABAP1 only (no S2 cards)	No SABAP2 cards
SABAP1 only (has S2 cards)	Extinction
SABAP2 < SABAP1	Decline
SABAP1 = SABAP2	Stable
SABAP2 > SABAP1	Increase
SABAP2 only	Colonisation
Has SABAP2 cards	No pied crows

Environmental covariates

Relevant information was collated for the area in South Africa covered by the SABAP grid and extracted for every cell. The QDGC grid was re-projected to Albers Equal Area with the following parameters: central meridian at 24.00°E, standard parallel 1 at 18.00°S and standard parallel 2 at 32.00°S. This minimised distortion in South Africa. I extracted environmental covariates for all relevant layers. Layers included were provincial (geo-political) boundaries, biome, land cover, protected areas, transmission lines, co-ordinates (latitude and longitude), and reporting rates. Methods of processing and extraction for each cell are discussed in detail below.

Area for each cell was tabulated using zonal statistics, setting the processing cell size at 100 metres. All layers were spatially joined to the QDGC grid. The grid was clipped to encompass the land mass of South Africa only, excluding Swaziland, Lesotho and the ocean. The South African National Land Cover (NLC) (version 1.1, 2000) was used to obtain detailed information about the land cover across all QDGC (van den Berg *et al.* 2000). Cell size processing for this analysis was set at 30 metres. I used information from level I of the different land cover types used in the NLC, (see Table 2). This information was used in generalized linear models, which will be discussed later. For each cell the proportion of land cover relative to area was calculated. The dominant land cover type was determined by regarding the maximum type per cell as dominant. Due to low sample size, three cells classified as herbland were combined with shrubland, two cells classified as indigenous forests were combined with plantations, four cells classified as planted grasslands were combined with natural grasslands, and one cell classified as waterbodies was combined with cultivated lands as this cell was surrounded by cultivated lands. No QDGC was ever dominated by mines and this land use category was therefore omitted from the analysis. I tested to see if this method to minimise data lost by discarding non-dominant land cover types. The method proved to be justified as fewer than 16% of cells had a <50% land type dominance. This process was repeated for cells when classifying which biomes or provinces they were located in (i.e. dominant biome or province).

Table 2: Description of land cover types in the National Land Cover (NLC) 2000 project.

Land cover type	Description
Forest	Indigenous
Woodland/Bushland	Woodland, thicket, bushland, bush clumps & high fynbos
Shrubland	Shrubland & low fynbos
Herbland	Herbland
Natural Grassland	Unimproved grassland
Planted Grassland	Improved grassland
Plantations	Eucalyptus, pines, acacia, other, clear-felled
Waterbodies	Waterbodies
Wetlands	Wetlands
Bare rock & Soil	Natural surfaces, soil erosion surfaces, dongas/gullies, sheet erosion
Degraded	Degraded areas of any of the above mentioned categories
Cultivated	Cultivated, permanent, commercial, dryland/rainfed, sugarcane, irrigates, subsistence
Urban	Rural cluster, formal & informal townships, smallholdings, residential & industrial, transport

Land cover type	Description
Mines	Mines, quarries, mines, mine tailings & mine dumps

A cell was regarded as protected if more than 50% of its area fell within formal or informal protected areas. Information regarding protected areas was obtained from the following datasets; National Protected Area Expansion Strategy 2002 (updated in June 2006) (BGIS 2011); World Database of Protected Areas (www.protectedplanet.org); and the National Biodiversity Assessment (BGIS 2011). All spatial data on biomes was obtained from Mucina & Rutherford (2006). Each cell therefore had a single measure for land cover type, biome type, province and whether the cell was protected or not.

Climate related data were derived from the 1900-2010 Gridded Monthly (version 3.01) time series data on precipitation (mean annual rainfall) and temperature (mean annual temperature) from 1987-2010 (Matsuura & Willmott 2012). Climate data resolution was on half-degree-grid-cells and was therefore at a coarser resolution than our cells. Each cell was assigned a central point to which the climate values were extracted. The rate of change for rainfall and temperature for each cell was calculated as the slope of a linear regression line fitted through this time series for each cell and added as a single metric per cell. Information of rainfall and temperature trends were therefore provided for each cell, but this value was shared by four neighbouring QDGC.

Transmission line data were obtained from Eskom (2011). Only current existing (in 2011) transmission lines were included in the analysis. This included existing, commissioned and decommissioned lines because these represent the transmission lines that are physically present in South Africa, although not all still transport electricity. I excluded designed, dismantled, invalid, planned or surveyed transmission lines. Three categories of transmission lines were included (≤33 kV, 44-110 kV, ≥132 kV). The summed length (metres) of transmission lines for each cell was calculated using zonal statistics in ArcGIS. The proportion of transmission line length (m^2) relative to the cell area (km^2) was used as a single metric to describe transmission line density per cell.

Statistical analysis

I used two different Generalised Linear Models (GLMs) to explore the changes in reporting rates of pied crows between the two survey periods. Model 1 was used to quantify the percentage change between the two periods, and examined changes in and out of protected areas, between biomes, and land cover types. This model explicitly incorporated sample size during each survey period (i.e. the number of cards) into the analysis. The response variable for this model was the number of cards recording pied crows divided by the total number of cards for each cell in each period. To examine changes between the two time periods I fitted 'period' (1 or 2) as a categorical fixed effect in the model. Then to examine whether populations changed differently in 1) different provinces, 2) different biomes or 3) inside or outside of protected areas, I fitted the same model but included the main variable (province, or biome type, or protected area status) and the interaction with the period (e.g. period*biome) as explanatory variables. All models were run using the statistical package R (version RStudio-0.97.237; 2012).

For categorical variables used in model 1, differences by period (SABAP1 and SABAP2) within each term were derived by using the package LSmeans (least-squares means) which were back-transformed (to account for the logit link function used in the model, see later for distribution of response variables) to provide the mean abundance change and confidence limits for each level of factors. Differences between each level were evaluated through pairwise comparisons derived from the post-hoc LSmeans test.

To explore changes in relation to environmental correlates I used a slightly different model (model 2), which allowed for easier interpretation with multiple terms, including terms specified to account for spatial autocorrelation within the data. Model 2 used a change metric as the response variable, which was the percentage reporting rate from SABAP2 divided by the sum of reporting rates from both SABAP periods. A similar approach was used to examine population changes in other studies (Amar *et al.* 2010, 2011). The model was weighted by the minimum sample size of cards for either of the two periods to account, at least to some degree (although not to the same degree as model 1), for differences in sample size between cells. Four variables were analysed that were proposed for the increase in pied crows: temperature (°C), rainfall (mm), transmission lines (m^2/km^2) and urban areas (%).

Within this model (model 2) I attempted to account for spatial autocorrelation within the data by fitting latitude (X), longitude (Y) and the interaction between latitude* longitude (X*Y). The change response variable in model 2 produces an output measure which lies between 0-1, 0=extinction, 1=colonisation, 0.5=stability. However, we excluded all colonisation events, as recommended by Amar *et al.* (2011), as they have a disproportionately higher value in the response variable compared to cells showing large increases of pre-existing pied crow populations. This however only resulted in 81 cells (7%) being excluded. In my results, I translate this change measure into a real percentage change (increase or decline) through a logarithmic equation to allow for ease of interpretation. For example, a change value of 0.25 equates to a 68% decline and a change value of 0.75 equates to a 403% increase.

In model 2, I first ran the model exploring the univariate relationship between each of my four covariates and report on these outcomes. I then ran a full model, including all four covariates, to assess the significant effect of these variables on pied crow abundance changes while controlling for each variable.

In all models, cells where pied crows were never recorded were excluded. I used model 1 to describe population trends and to analyse categorical variables which were spatially grouped and where the need to account for spatial autocorrelation was therefore reduced (e.g. provinces, biomes, protected areas). Assessment of both models indicated overdispersion, and therefore to correct for overdispersion, a quasibinomial distribution was used. Use of this distribution, however, meant that I could not compare different model fit using an Information Theoretic approach (e.g. AIC) and instead used significance values (F tests) using a type III analysis, which gives the significance of each term after accounting for the variance explained by other terms in the model.

Results

Describing Pied crow changes in abundance & range expansion

The total number of QDGC (cells) covered by the original SABAP map in Southern Africa was 2024. Excluding oceans and cells that fell outside South Africa, a total of 1965 cards remained. After removing any cells that had less than 5 cards in any of the two periods, 37% of the cells were discarded (720 cells). Implementing a 10 card cut-off lost over 90% of the data. Therefore, the 5 card threshold produced sensible results, and increased the robustness of detection of changes in pied crows.

A total of 1245 cells remained after the 5 card cut-off and the clipped South African border. Pied crows were never reported in 90 cells (5%) during either period and these were excluded from any further analyses. Thus after processing, I had 1155 cells to explore change in pied crow abundance. Categorising these cells by change categories, the majority showed increases in reporting rates (51%, n=584), 34% declined (n=389), and less than 1% remained the same (n=4). Pied crows colonised 7% of cells (81 cells) and were lost from 8% of cells (n=97). I analysed cells that showed an increase in reporting rates at a finer scale

(Figure 1 A). Eight percent of cells (n=75) showed an increase in reporting rates between 0-10%, while 25% (n=245) showed an increase in pied crows greater than 100% (Figure 1 B.).

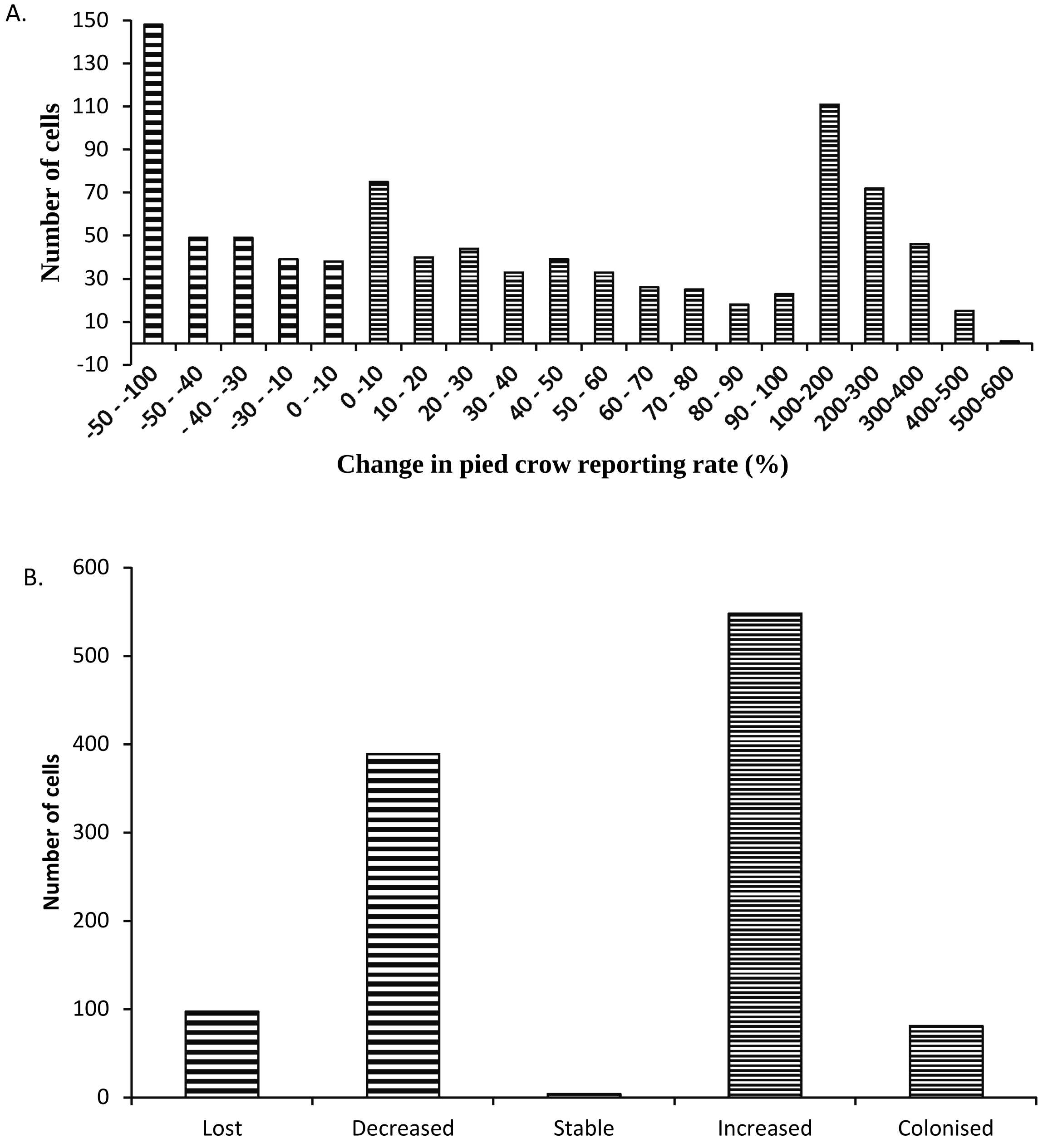

Figure 1: Distribution of changes in *Corvus albus* reporting rates per QDGC. A. Distribution of the magnitude of change in pied crow reporting rates. B. Distribution of changes in reporting rates by SABAP category. The majority of cells showed an increase in pied crow reporting rates across South Africa.

Analysis with model 1 suggested that overall there has been a significant increase in reporting rate between the two SABAP survey periods (χ^2=12.782, DF=1, p<0.001; Figure 2,

Table 3). Reporting rates increased from 35% in SABAP1 to nearly 40% in SABAP2 (+13% increase). Despite an overall increasing trend changes were not evenly spread across the country (Figure 4, A & B), with declines in the east and increase in the west.

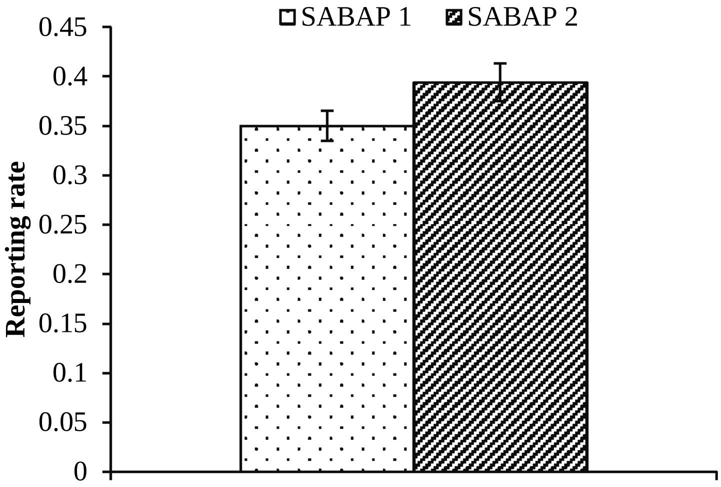

Figure 2: Differences in *Corvus* albus reporting rates between SABAP1 and SABAP2 in South Africa (mean±95% confidence limit; χ^2=12.782,DF=1, p<0.001). This is the output from the GLM model 1 which controls for sample size (number of cards) per cell.

Changes in reporting rates of pied crow differed between provinces, with a significant interaction between province and period (χ^2=160.43, DF=8, p<0.0001; Figure 3). Pairwise comparisons revealed significant increases in the Northern Cape (+72%, n=147; t=-4.216, p<0.01), Eastern Cape (+56%, n=166; t=-4.289, p<0.01), and Western Cape (+18%, n=198; t=-7.255, p<0.001; Figure 3). There were significant declines in the Northwest (-31%; n=117; t=4.781, p<0.01), and Limpopo provinces (-56%; n=140; t=5.736, p<0.001).

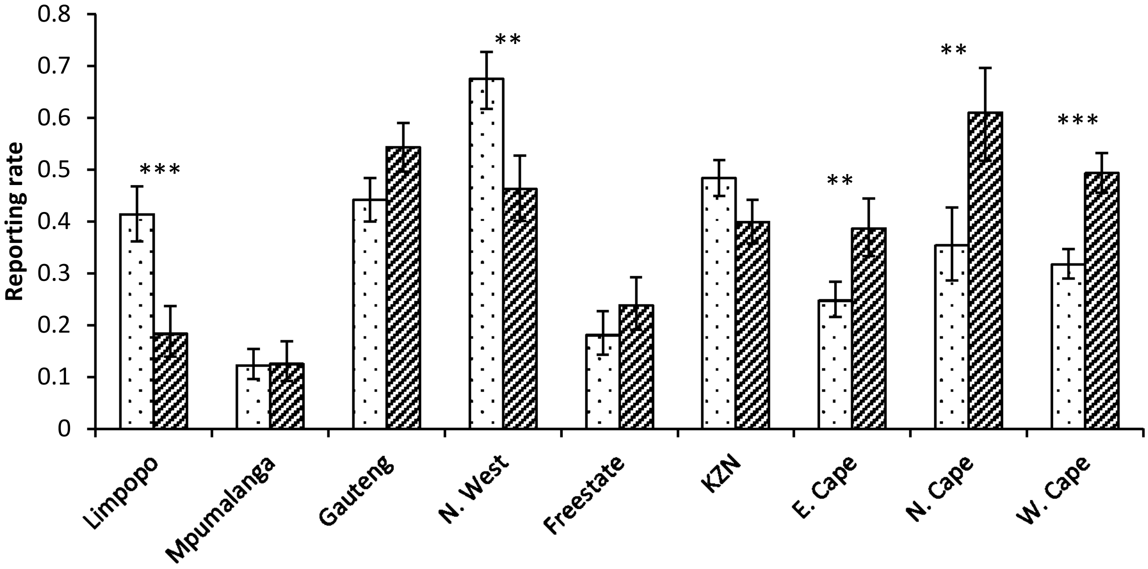

Figure 3: Reporting rates of *Corvus albus* across the nine South African provinces between SABAP1 (1987-1991) and SABAP2 (2007-2012). * p<0.05, **p<0.01, ***p<0.001. E = Eastern, N = Northern, W. = Western, KZN = Kwa-Zulu Natal.

Table 3: Outputs from Generalised Linear Models (main term, interaction, parameter estimates, χ^2, degrees of freedom (DF), and significance). The χ^2 values relate to the interaction between period and the main term, except for period only, which tested whether there was a significant change in reporting rates between periods (SABAP1 & SABAP2). Period only analysis was therefore shaded out as no information is available.

Main Term	Period	Main term	Period*main term	χ^2	DF	Intercept
Period	-	-	-	12.782	1	-0.61968
Province	***	***	***	160.43	8	-1.11046
Protected Areas	**	***	NS	0.491	1	-0.58747
Biomes	NS	***	***	84.434	7	-1.03889
Land cover	*	***	***	57.162	6	19.94335

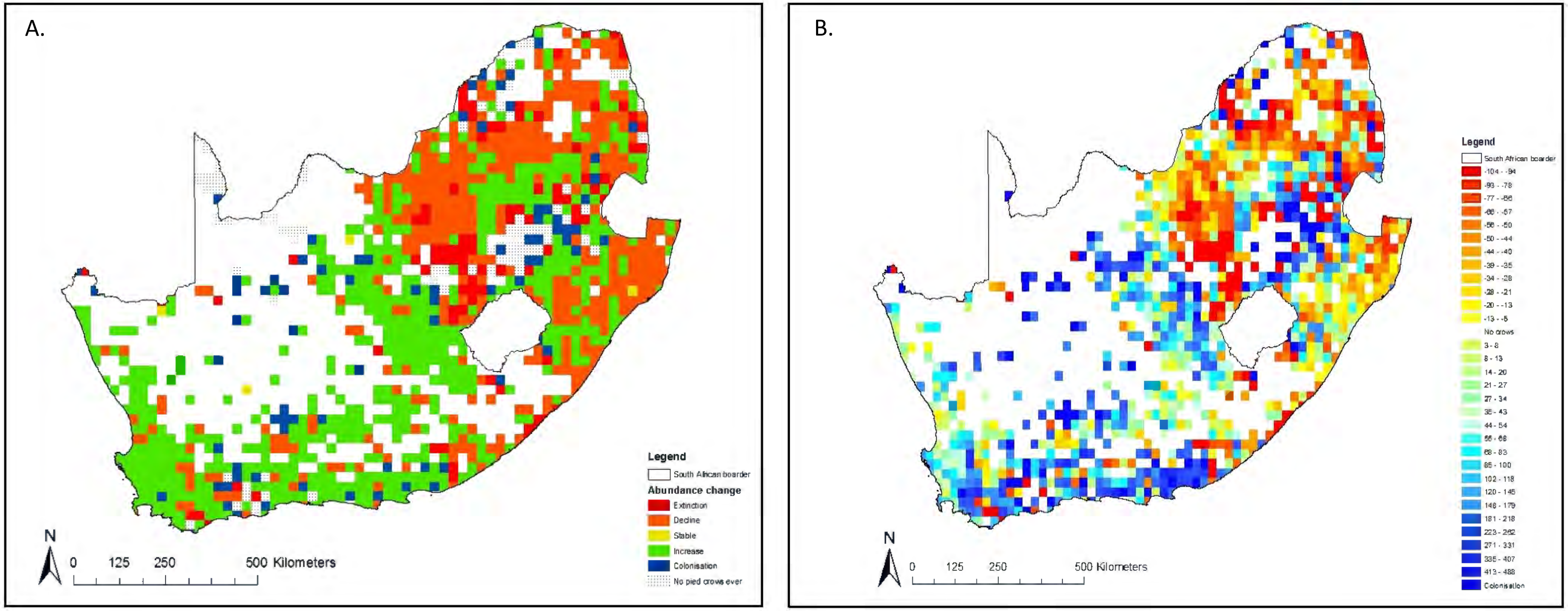

Figure 4: Changes in reporting rates (i.e. relative abundance) of *Corvus albus* in South Africa. A. Categorical changes as used by SABAP, showing higher declines and local extinctions in the east and higher increases in the west. B. Percentage change in each cell with hotter colours showing decreases or local extinctions, and cooler colours increases or local colonisations. Only cells with at least 5 cards in both periods were used for these maps. White areas indicate cells that had no information on pied crow abundance measures, or fewer than 5 cards per period.

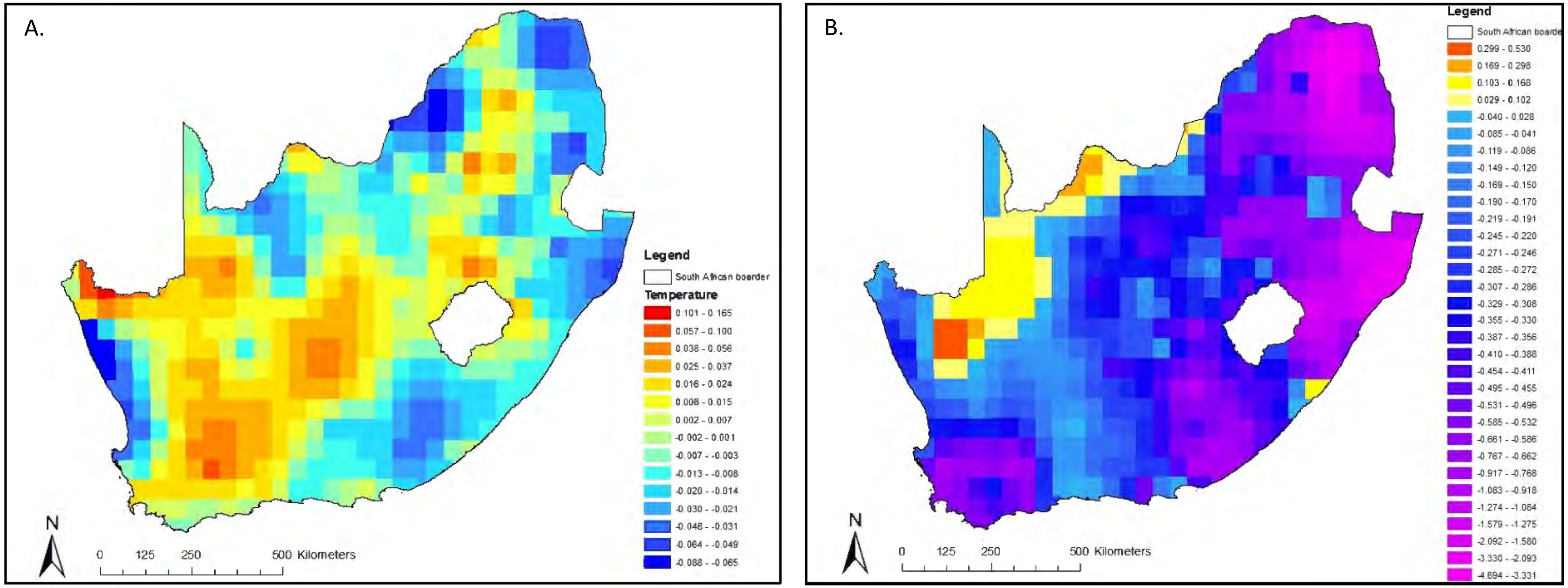

Figure 5: A. Temperature (°C) and B. rainfall (mm) trends in South Africa from 1987 to 2010. Values were derived from the slope of rainfall or temperature change over the 23 year period, the same timespan over which changes in reporting rates of pied crows were examined. The hot colours (red, orange, yellow) depict positive changes in temperature or rainfall (cooler purples indicated declines in rainfall). For temperature, the interior in the country shows greater rates of change than the coastline. For rainfall change, the Western Cape and eastern regions of the country are becoming drier.

Reporting rates of pied crows increased similarly in protected (+13%) and non-protected areas (+11%) (Figure 6, Table 3), although reporting rates were lower in protected areas

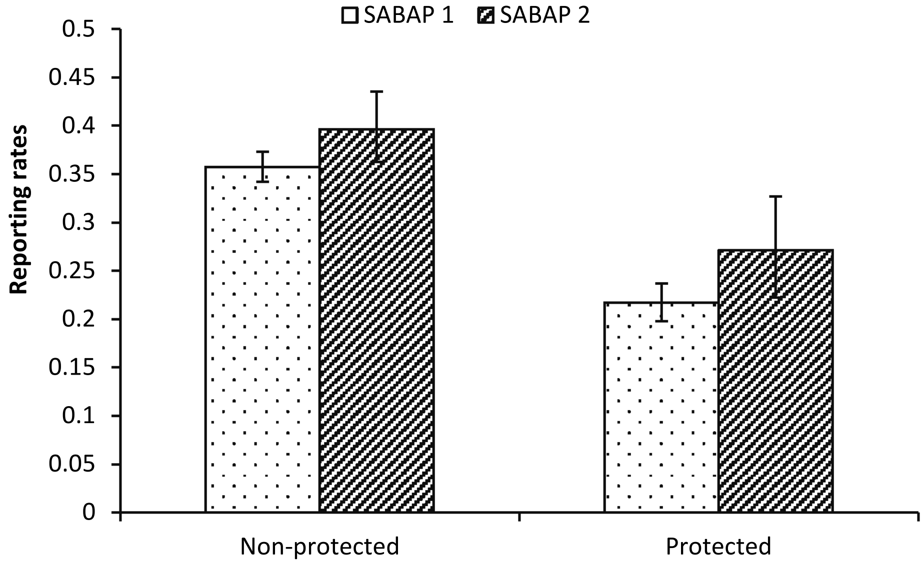

Figure 6: Reporting rates in protected and unprotected areas during the SABAP 1 and 2 periods (mean±95% confidence limit; χ^2=0.491, DF=1, p>0.05).

Unsurprisingly, given their spatial configuration (Appendix D, Figure C), reporting rates also differed significantly between the biomes (period*biomes χ^2=84.43;DF=7, p<0.0001; Figure 7) Pairwise comparisons revealed significant increases from SABAP1 to SABAP2 in the fynbos (+61%, n=294; t-value=-6.744, p<0.001) and Albany thicket (+130%, n=84; t=-4.226, p=0.003), and a significant decline in savanna (-21%, n=714; t=3.960, p=0.008) (Figure 7).

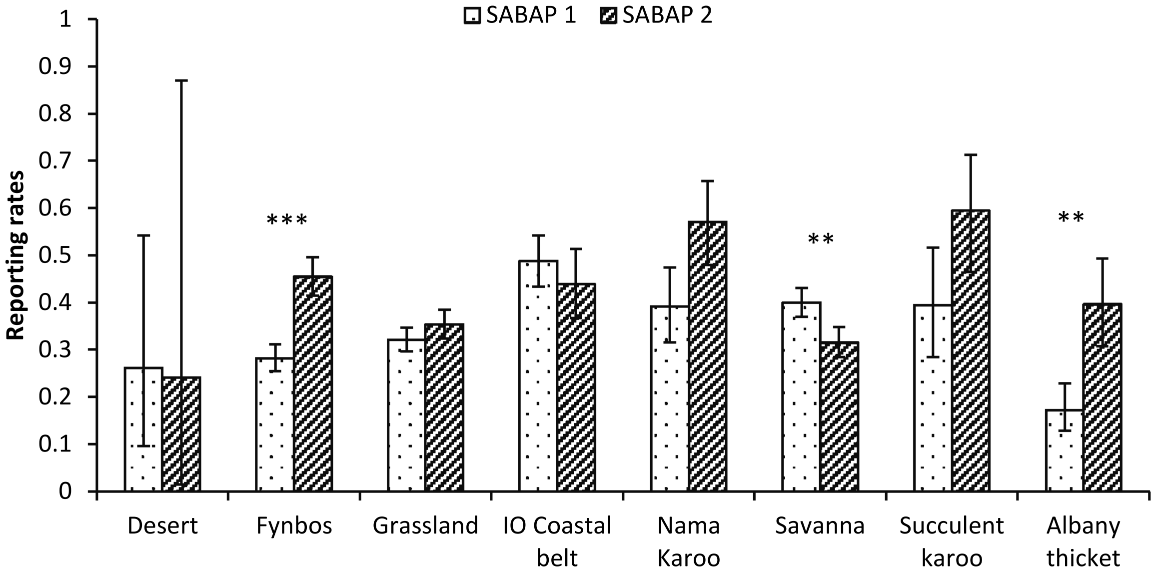

Figure 7: Reporting rates of pied crows (*Corvus albus*) across the eight dominant biomes in South Africa between SABAP1 (1987-1991) and SABAP2 (2007-2012) * $p<0.05$, **$p<0.01$, ***$p<0.001$. IO = Indian Ocean.

Similarly to the biomes, there were significant differences in changes in reporting rates between the different land cover types (period*landcover, $\chi^2=57.162$, DF=6, $p<0.001$) (Figure 8). This is perhaps unsurprising given the similarity in their spatial configuration to biomes (Appendix D, Figure C & D). The pairwise comparison tests revealed a significant increase in pied crow reporting rates in shrublands (+55%, n=334, t=-6.200, $p<0.001$) and urban areas (+28%, n=12, t=-4.687, $p<0.001$) between the two SABAP periods.

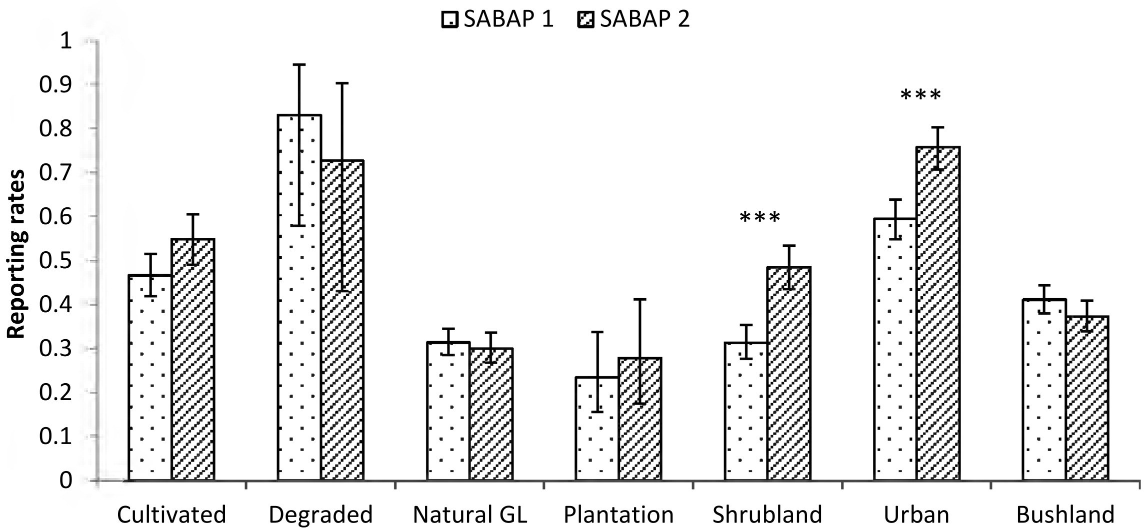

Figure 8: Reporting rates of *Corvus albus* across the seven dominant land cover types in South Africa between SABAP1 (1987-1991) and SABAP2 (2007-2012). The GLM depicted significant increases in reporting rates in shrubland (t=-6.200, p<0.001) and urban (t=-4.687, p<0.001). * p<0.05, **p<0.01, ***p<0.001. GL= grassland.

Exploring changes in reporting rates in relation to covariates

The next results use model 2, which included three spatial terms (X, Y and X*Y) in an attempt to control for potential spatial autocorrelation in these data.

Changes in pied crow reporting rates correlated with changes in climate in 1987-2010 (Table 4). Pied crows increased in areas that had become hotter and/or wetter (Figure 4, Figure 5, and Figure 9). Only temperature showed a significant positive relationship with changes in pied crow reporting rates in the univariate model (Table 4).Temperature and rainfall were significant when the full model was considered (Table 4). Thus, whilst not significant on its own, rainfall was a significant predictor of changes in reporting rates when temperature was controlled. The full model thus suggests that temperature and rainfall together explain the changes in pied crow reporting rates.

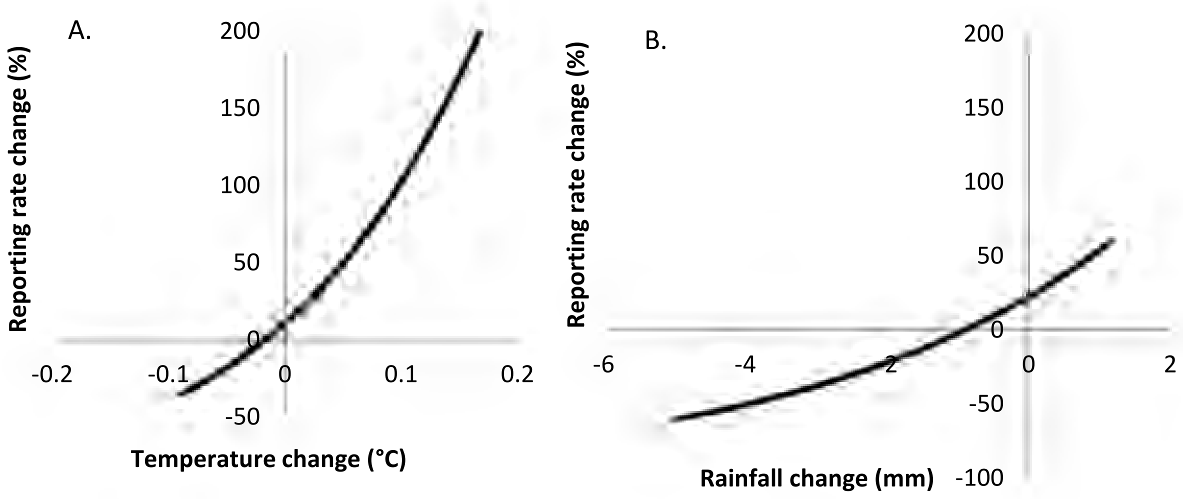

Figure 9: Relationships between temperature [A.] and rainfall [B.] and pied crow changes in reporting rates (%). Both variables show a significant positive relationship with pied crow abundance (i.e. reporting rate changes).

Table 4: Univariate and full model outputs (main term, significance, χ^2, degrees of freedom (DF), intercept, and parameter estimates) from the Generalised Linear Model 2 controlling for spatial autocorrelation. Shaded blocks indicate no information available.

	Main Term	Main term significance	χ^2	DF	Intercept	Parameter estimate
Univariate model	**Temperature**	**	9.5	1	1.882	4.332
	Rainfall	NS	0.241	1	1.844	0.036
	Transmission lines	NS	0.013	1	2.593	-0.00001
	Urban areas	NS	0.045	1	2.625	0.001
Full model	**Temperature**	**	10.602	1	1.31	4.112
	Rainfall	*	6.246	1	-0.621	1.559
	Transmission lines	NS	0.544	1	-	-4.23
	Urban areas	NS	1.927	1	-	0.0028

Discussion

This study found strong evidence of range changes in pied crows across South Africa over the last 25 years, with populations (as estimated by reporting rates) apparently decreasing in the north-eastern region of the country and increasing predominantly in the westerly interior (Figure 4). These broad-scale declines and extinctions in the north-east with simultaneous increases and colonisation to the west suggest that a large scale underlying driver of change might be responsible, as opposed to small-scale local factors which may influence avian abundances at a smaller scale such as persecution or land management change (Slagsvold 1980; Chace & Walsh 2006). Pied crows thus seem likely to be indicators of large-scale environmental change.

Expansion into the west of the country, especially the Western Cape, appears to be a common phenomenon (Hockey 2003; Hockey & Midgely 2009). Explanations for this recent westward colonisation include anthropogenic landscape changes, such as agriculture and urbanisation (Cowling *et al.* 1996; Hockey & Midgley 2009). Also, Hockey *et al.* (2011) found westward range expansion to reflect changes in land use rather than climate. All species showing westward migrations were habitat generalists, illustrating how such species are able to cope in a changing environment. Pied crows similarly are generalists expanding their range westwards seemingly due to climate.

During the data gathering period of SABAP1, pied crows mainly occupied the easterly regions (IO coastal belt, savanna, Karoo), with low abundances in the west (e.g. Albany thicket and fynbos). There appears to have been increases in the Karoo regions where pied crows previously existed, and an expansion in their range towards the interior, whereas crow abundance has decreased in the savanna. Temperature and rainfall explained most of the variation in the observed pied crow change patterns. This is in accordance with Williams and

Jackson (2007) who suggest that temperature change occurs first, inducing species range shifts earlier than rainfall changes. It appears that pied crows favour regions that are becoming hotter and wetter, and positive trends with transmission lines suggest that these structures have helped facilitate this expansion by providing nest sites in previously uninhabitable areas. Brook *et al.* (2003) illustrates how the Indian house crow (*Corvus splendens*) expanded its range into a region with more favourable climates, namely Singapore. They attributed this range expansion due to Singapore being hotter, with more dry months, climate conditions that were more favourable to this species

This is the first study to examine the response of pied crows to climate change. Not only are pied crows increasing in abundance, but they are *shifting* towards hotter and slightly wetter areas. This is a novel finding, with interesting implications for conservation and the first study to show this in a South African context. The synergistic effect of temperature and rainfall change may provide useful indicators to predict where pied crow increases are likely to be strongest in the future.

Climate change has been shown to alter not only species distributions, but also species interactions (van der Putten *et al.* 2010). Since climate change affects the distribution and abundance of species differently, adaptable species such as pied crows could become disproportionately abundant. This has given rise to novel community assemblages (so called ‘no analogue communities’) that potentially alter ecological functioning as species interactions, and the associated interspecific responses, change (Williams & Jackson 2007). This study has described such an event, where bird communities are being destabilised by a combination of climate and land-use change (such as transmission lines), and how this has contributed to the competitive advantage of an opportunistic predator like the pied crow. This raises the questions of how other species are being affected by climate change, and how those species will cope with the restructuring of trophic levels through altered abundances of opportunistic range-expanders such as crows.

One of the biomes showing substantial increases in pied crows – the fynbos - is a world biodiversity hotspot that is predicted to come under extensive pressure if predicted climate change occurs (Simmons *et al.* 2004). Endemic or threatened species (reptiles, birds, small mammals etc.) in these regions may succumb to further stresses alongside climate change; particularly if increased predation pressure results from the expansion of predatory species such as the pied crow. Novel climates through climatic shifts are predicted to be greatest in regions of high diversity, which increases the possibility of 'ecological surprises' – unexpected findings about natural ecosystems (Williams & Jackson 2007; Lindenmayer *et al.* 2010). Fundamental ecosystem changes can result from 'ecological surprises', with potentially devastating impacts on local communities (Lindenmayer *et al.* 2010). Ewel (1999) describes situations where a decline in environmental harshness gives rise to increased predation and competition, as certain species are disproportionately favoured in the absence of ecological limiting factors. In other words, as species communities shift (due to climate change, habitat transformation etc.), predation pressure can be inflated if one of the favoured species is a predator. A recently documented case illustrating pied crow predation pressures in the Karoo (which falls under the shrubland category) emphasises this point. One-hundred and sixty juvenile angulate tortoises (*Chersina angulata*) were collected under the nest of a single breeding pair of pied crows within 48 days (Lambrechts 2011). Although anecdotal, this finding highlights the need to consider the consequences for conservation strategy of shifting communities, such as growing predatory populations, in the face of climate change.

Findings from this study suggest that pied crows increased in regions dominated by urban areas. .Carlson and Hartman (2001) found a negative correlation between pied crow abundance and distance from human settlements in Tanzania. I did not find such a correlation in this study (model 2), however, the significant increase in pied crow abundance in urban areas (model 1) suggests that these regions are favourable conditions for pied crows. Anecdotal evidence supports this, as pied crows are often associated with larger cities and settlements, and are far scarcer in regions without man-made structures. Crows are efficient nest predators, and their increases in urban regions raise further concerns on their impacts in an already stressed and altered environment (Luginbuhl *et al.* 2012). Furthermore, several studies have demonstrated an increase in nest predation with increasing corvids (Chapter 2). Not only are we potentially aiding pied crow expansion and increase in abundance, but we are indirectly compromising the survival of open-nesting species that may already be under pressure from urbanisation and habitat transformation.

Reasons for corvid increases in urban regions have been attributed to increased concentration of additional food resources through feeders, waste sites and road-kill which reduces seasonal variability in food availability (Shochat *et al.* 2006; Robb *et al.* 2008). Additionally, corvids can reduce energy expenditures due to decreased foraging times and reduced nest defence as persecution (e.g. use of guns) is generally forbidden in urban areas (Chace & Walsh 2006; Robb *et al.* 2008). These factors, coupled with the potential reduction of large predators in urban areas, can result in increased survivorship of corvids (Chace & Walsh 2006). Local raven increases were associated with human activity that provided food resources and nest sites in the Mojave desert in the USA (Kristan & Boarman 2003). These increases resulted in 'hyperpredation' on the local tortoise population, causing concern for the longevity and sustainability of the tortoise population. Increases in a predatory species can therefore have dire consequences on local biodiversity and introduce difficult and complex conservation and land management issues when the underlying driving factor is human development.

In conclusion, the majority of cells in our study displayed an increase in pied crow abundance across South Africa. However, a large proportion of cells also showed a decline. This is the first study to demonstrate a shift in pied crow range and to highlight regions of potential concern where corvid impacts on local biodiversity may increase – namely the Karoo, fynbos, Albany thicket and urban regions. An increase in a predatory species, such as the pied crow, can alter ecological functioning through changes in species interactions, increased predation pressure, and it can potentially shift a highly diverse region towards a biologically homogenous one. The causes of pied crow shift were shown in this study to be linked to temperature and rainfall change, where hotter and wetter regions are being tracked by the crow population, with positive trends in transmission lines. However, the impact of pied crows on vulnerable species such as tortoise (e.g. geometric tortoise *Psammobates geometricus*) have not been quantified, and there is a need for research on direct pied crow impacts on biodiversity. Nevertheless, anecdotal evidence coupled with pied crow increases is strengthening a cause for concern. Consequently, the underlying cause for pied crow expansion and increase in abundance is ultimately anthropogenically-driven ecological change, which potentially could indirectly lead to further loss of biodiversity.

CHAPTER 4

CONCLUSIONS, STUDY LIMITATIONS,FUTURE RESEARCH RECOMMENDATIONS, & IMPLICATIONS

Conclusions

The impacts of predators on target species' populations is of huge interest to conservationists and game managers (Park *et al.* 2008). Corvids in particular have been consistently reported as the dominant nest predator (Baláž *et al.* 2007), listed as the main cause of mortality (Haskell 1995) and referred to as a species' of concern (Luginbuhl *et al.* 2012). However, until now no review has been undertaken to assess overall patterns of corvid impacts, and thus the likely relationships between corvid numbers and target species. Although several reviews have been conducted on the impacts of predators (see Côté & Sutherland 1997; Valkama *et al.* 2005; Holt *et al.* 2008; Smith *et al.* 2010), one was lacking for corvids, and also a genus-specific one for *Corvus*.

This thesis outlined the issue surrounding predation and explores the impacts of *Corvus* crow and ravens on biodiversity. This is particularly topically, because several corvid species are showing positive population growth and range expansion, which could potentially impact species that are not familiar with such an avian predator. This thesis quantifies the changes in abundance and range expansion of an indigenous corvid species – the pied crow *Corvus albus* – and explores potential reasons driving their abundance change.

From Chapter 1 and 2 it is clear that predators can impact target species populations, but that this is not necessarily always the case. Whether a predator has the capacity to impact a species' population depends on the predator-prey interactions, and how the predator responds to changes in the target-species abundance changes. In other words, predation impacts vary depending on whether and how the predator responds numerically or functionally with prey population size. This determines changes in predation pressure, which ultimately defines how prey species' will be impacted. The systematic literature review (Chapter 2) indicates that corvids most frequently have no effect on studied species, although positive effects of their removal were occasionally found, especially when removed alongside other predators. It is therefore difficult to decouple the impacts of corvids from that of other predators.

Also, there are inconsistencies in trends, for example where studies on the same corvid and target species show opposite findings (Erikstad *et al.* 1982; Parker 1984). This demonstrates that several factors come into play when assessing the impact of crows – e.g. habitat, availability of food, composition of other predators etc. This study highlights the need to explore correlative trends and then investigate interesting findings through rigorous experimental studies of crow removals. Especially when lethal control is considered, robust evidence is needed before the impacts of corvids on biodiversity are concluded as negative, because this is not always the case.

Finally, as anecdotal observations had suggested, I confirmed in Chapter 3 that pied crows are increasing in South Africa, and moving rapidly into new areas. My findings suggest that this was not a uniform trend throughout the country, with increases in the west happened at the same time as decreases in the east. Perhaps the most important finding of this study was that pied crows are apparently showing abundance and range changes in response to climate change, specifically with temperature changes. Pied crows are therefore showing positive population trends in regions that are becoming hotter and wetter, and where transmission lines can act as potential nest sites in previously uninhabitable environments. Lastly, pied crows are increasing significantly in urban areas, possibly due to the availability of resources and predator reduction. The impact of pied crows on biodiversity needs to be further explored as this species is increasing in certain regions, and being a generalist predator can potentially have negative consequences on South Africa's biodiversity. No focussed correlative or experimental studies have ever been published on this issue and this knowledge gaps remains to be addressed.

Study limitations

Despite concerted attempts to minimise or correct for bias or data gaps in this study, some limitations still exist. Firstly, there are difficulties in gathering all information regarding the impacts of corvids, especially in the allocated time of this minor dissertation, because certain papers will always 'slip through the cracks' due to incorrect indexing, occurring only in grey literature, or because of misleading or uninformative titles. Nevertheless, a stringent search protocol was conducted and I am confident I included all the main papers regarding corvid predation. With regards to recorded predation events, it is nearly impossible to quantity how much corvids themselves contribute to predation because I would have to collect every predation study ever conducted in order to quantify the proportion of predation events by corvids compared to other predators. For this reason the predation events section is a smaller, sub-section in Chapter 2 and is more applicable to species-specific studies than to a broad review of corvid predation.

Regarding Chapter 3, there are inherent issues regarding the comparability of SABAP1 with SABAP2 due to the spatial and temporal differences between them. Unfortunately, nothing can be done about the fact that the two surveyed periods were conducted differently, even though the decision to change SABAP2 protocol was to obtain more rigorous data. I do feel, however, that these differences are more likely to generate bias with the analysis of rare or declining species, as SABAP1 could potentially overestimate a species range, and therefore detect a greater decline over the two periods. Since this study shows that pied crows are increasing, the limitations to comparing the two SABAP periods need to be accepted but acknowledged (Bonnevie 2011). Also, the analysis regarding spatial autocorrelation could be performed using a more powerful model, however this is very difficult to interpret and I was constrained in time from applying a more complex statistical model. However, this was overcome by using two different models to describe and explore pied crow abundance changes and correct for spatial autocorrelation when possible. Another limitation is the under-sampled regions of the country, but this is a feature of all atlas projects and the SABAP2 project is taking steps to minimise data gaps in under-covered areas.

One of the shortcomings of the SABAP data is that the interior of the country is greatly under-sampled and had to be excluded from this analysis because of the 5 card minimum threshold. This region is vital to measure the increase and colonisation events of pied crows, especially because the cards that were included in this analysis showed the greatest increases and colonisation events in this region (the Nama Karoo).

Future research recommendations

In terms of the systematic review, more studies need to be conducted on crow only removals and species-specific studies on corvids and their impacts, especially in the southern hemisphere. No studies, to my knowledge, have been conducted in South Africa on the impacts of pied crows – or any crow – on local biodiversity. I urgently recommend a pied crow removal study to be conducted to quantify the potential impacts of this increasing predator. One potential site for such a removal experiment is the West Coast National Park (WCNP) which has seen recent pied crow colonisation and subsequent increase over the last 10 years.

Furthermore, this study highlights the importance of inferring large-scale changes in climate and land cover by investigating a common species.

Lastly, several great and useful sources and information exist that are not published and are therefore difficult to access or utilise. Examples of grey literature studies include Simmons & Barnard (2011) and Lambrechts (2012). These are important sources that are difficult to get hold of, so publishing needs to be encouraged to capture the true impact of pied crows in South Africa.

Implications of this study

1. Experimental studies removing corvids only are the most robust to assess the true impact of corvids on prey species of interest
2. Correlative studies are useful in highlighting relationships, but these need to be explored further to distinguish causative from spurious relationships.
3. Removing corvids alone will likely not improve a target species population, however removing corvids in conjunction with other predators might. However, this could cause trophic destabilisation and present ethical dilemmas.
4. Waders are not shown to more vulnerable than other species, however demonstrates that species-specific case studies are needed.
5. Clutch success should always be included in studies quantifying the impacts of corvids (or nest-robbing predators), as this parameter is apparently the most affected by predation.
6. In South Africa, managers in protected areas (particularly the western regions) should begin monitoring programmes to establish whether pied crows are increasing and which species are potentially under threat.

7. Climate change is a potential driver for the range expansion of predatory species, and this needs to be acknowledged when looking at the impacts of climate change on South African biodiversity.
8. This study illustrates an east-west range shift of a generalist predator due to climate change. This has important ecological and conservation implications in understanding climate change driven range shifts.
9. Finally, this study contributes to understanding climate change induced range shifts in the southern hemisphere, an area of research that is under-represented in scientific publications.

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APPENDIX

Appendix A: Experimental Studies

Table A: Summary of experimental predator control studies showing the effect (response) of several breeding and population parameters of avian species to predator removal. Eight studies removed corvids only. Cases where multiple-predator species were removed alongside corvids are described in the footnote. PS = population size.

Predator*	Corvid only	Location	Prey Species	Avian Group	Ground-nesting	Parameter	Response	Source
American crow	yes	USA	ducks	wader	exclude	productivity	none	Clark *et al.* 1995
American crow + Common raven[4]	no	USA	piping plover	wader	yes	productivity	none	Struthers & Ryan 2005
American crow[9, 10]	no	USA	pheasant	galliform	yes	productivity	none	Chessness *et al.* 1968
American crow[9, 10]	no	USA	pheasant	galliform	yes	breeding PS	none	Chessness *et al.* 1968
American crow[9, 10]	no	USA	pheasant	galliform	yes	clutch size	-	Chessness *et al.* 1968
American crow[9, 10]	no	USA	pheasant	galliform	yes	productivity	-	Chessness *et al.* 1968
Carrion crow	yes	UK	black grouse	galliform	yes	productivity	none	Summers *et al.* 2004
Carrion crow	yes	UK	capercaillie	galliform	yes	productivity	none	Summers *et al.* 2004
Carrion crow[2]	yes	UK	blackbird	passerine	no	productivity	none	Stoate & Szczur 2005
Carrion crow[2]	yes	UK	whitethroat	passerine	yes	productivity	none	Stoate & Szczur 2005
Carrion crow[1, 2, 3, 5, 7,13, 14, 16, 17]	no	UK	grey partridge	galliform	yes	post-breeding PS	-	Tapper 1996
Carrion crow[1, 2, 3, 5, 7,13, 14, 16, 17]	no	UK	grey partridge	galliform	yes	breeding PS	-	Tapper 1996

Predator*	Corvid only	Location	Prey Species	Avian Group	Ground-nesting	Parameter	Response	Source
Carrion crow[1, 2, 3, 5, 7,13, 14, 16, 17]	no	UK	grey partridge	galliform	yes	clutch size	-	Tapper 1996
Carrion crow[2, 5, 7, 12, 13]	no	UK	blackbird	passerine	no	productivity	-	White *et al.* 2008
Carrion crow[2, 5, 15, 16]	no	UK	spotted flycatcher	passerine	no	productivity	-	Stoate & Szczur 2006
Carrion crow[2, 5, 7, 12, 13]	no	UK	blackbird	passerine	no	post-breeding PS	none	White *et al.* 2008
Carrion crow[4]	no	UK	curlew	wader	yes	productivity	-	Parr 1993
Carrion crow[4]	no	UK	curlew	wader	yes	breeding PS	none	Parr 1993
Carrion crow[4]	no	UK	golden plover	wader	yes	productivity	none	Parr 1993
Carrion crow[4]	no	UK	golden plover	wader	yes	breeding PS	none	Parr 1993
Carrion crow[4]	no	UK	lapwing	wader	yes	productivity	-	Parr 1993
Carrion crow[4]	no	UK	lapwing	wader	yes	breeding PS	none	Parr 1993
Carrion crow[4]	no	UK	oystercatcher	wader	yes	productivity	none	Parr 1993
Carrion crow[4]	no	UK	oystercatcher	wader	yes	breeding PS	none	Parr 1993
Carrion crow[4]	no	UK	redshank	wader	yes	breeding PS	none	Parr 1993
Carrion crow[4]	no	UK	redshank	wader	yes	productivity	-	Parr 1993
Carrion crow[5]	no	UK	lapwing	wader	yes	productivity	-	Bolton *et al.* 2007
Carrion crow[5]	no	UK	lapwing	wader	yes	productivity	none	Bolton *et al.* 2007
Carrion crow[5]	no	UK	lapwing	wader	yes	post-breeding PS	none	Bolton *et al.* 2007
Carrion crow[5]	no	UK	curlew	wader	yes	productivity	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	curlew	wader	yes	breeding PS	none	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	golden plover	wader	yes	productivity	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	golden plover	wader	yes	breeding PS	none	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	lapwing	wader	yes	productivity	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	lapwing	wader	yes	breeding PS	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	meadow pipit	passerine	yes	productivity	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	meadow pipit	passerine	yes	breeding PS	none	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	red grouse	galliform	yes	productivity	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	red grouse	galliform	yes	breeding PS	-	Fletcher *et al.* 2010
Carrion crow[5]	no	UK	skylark	passerine	yes	breeding PS	none	Fletcher *et al.* 2010

Predator*	Corvid only	Location	Prey Species	Avian Group	Ground-nesting	Parameter	Response	Source
Carrion crow[5]	no	UK	snipe	wader	yes	breeding PS	none	Fletcher *et al.* 2010
Common raven[6]	no	USA	sandhill crane	gruiform	yes	productivity	-	Littlefield 2003
Hooded crow	yes	UK	hen harrier	raptor	yes	lay date	none	Amar & Redpath 2002
Hooded crow	yes	UK	hen harrier	raptor	yes	clutch size	none	Amar & Redpath 2002
Hooded crow	yes	UK	hen harrier	raptor	yes	productivity	none	Amar & Redpath 2002
Hooded crow	yes	Norway	fieldfare	passerine	no	breeding PS		Slagsvold 1980
Hooded crow	yes	Norway	common Eider	wader	yes	productivity	none	Stein *et al.* 2010
Hooded crow + Common raven	yes	Norway	willow ptarmigan	galliform	yes	productivity	-	Erikstad *et al.* 1982
Hooded crow + Common raven[5, 11, 12]	no	Sweden	willow ptarmigan	galliform	yes	productivity	none	Steen & Haugvold 2009
Hooded crow + Common raven[2]	yes	Norway	black grouse	galliform	yes	breeding PS	none	Parker 1984
Hooded crow + Common raven[2]	yes	Norway	black grouse	galliform	yes	productivity	none	Parker 1984
Hooded crow + Common raven[2]	yes	Norway	black grouse	galliform	yes	productivity	none	Parker 1984
Hooded crow + Common raven[2]	yes	Norway	willow ptarmigan	galliform	yes	productivity	none	Parker 1984
Hooded crow[8]	no	UK	lapwing	wader	yes	productivity	none	Bodey *et al.* 2011

*Corvids were often removed in addition to other avian and mammalian predators. Avian: 1=rook, 2=magpie, 3=jackdaw, 4=gull. Mammalian: 5=fox, 6=coyote, 7=stoat, 8=ferret, 9=skunk, 10=raccoon, 11=marten, 12=mink, 13=weasel, 14=feral cat, 15=squirrel, 16=rat, 17=hedgehog.

Appendix B: Correlative Studies

Table B: Correlative studies describing associations between corvid populations and target species' breeding parameters or population sizes. The association between corvid population changes and breeding parameters was noted only if the relationship was statistically significant. The influence of corvids was described as either positive (+), negative (-), or showing no response (none). Several studies examined the influence of multiple-predator species alongside corvids. These have been identified with superscript numbers and described in the footnotes below. Studies that removed corvids are presented in this table if they measured the response of the prey parameter in relation to known corvid population fluctuations. The study by Newson *et al.* 2010 included two separate bird studies and therefore some species are described twice.

Predator species*	Location	Prey Species	Ground nesting	Family Groups	Prey Response	Impact	Source
Common raven	UK	curlew	yes	wader	abundance	none	Amar *et al.* 2010
Common raven	UK	dunlin	yes	wader	abundance	none	Amar *et al.* 2010
Common raven	UK	golden plover	yes	wader	abundance	none	Amar *et al.* 2010
Common raven	UK	lapwing	yes	wader	abundance	none	Amar *et al.* 2010
Common raven	UK	snipe	yes	wader	abundance	none	Amar *et al.* 2010
Carrion crow	UK	curlew	yes	wader	abundance	none	Amar *et al.* 2011
Carrion crow	UK	dunlin	yes	wader	abundance	none	Amar *et al.* 2011
Carrion crow	UK	golden plover	yes	wader	abundance	none	Amar *et al.* 2011
Carrion crow	UK	lapwing	yes	wader	abundance	-	Amar *et al.* 2011
Carrion crow	UK	snipe	yes	wader	abundance	none	Amar *et al.* 2011
Carrion crow[5, 6]	UK	capercaillie	yes	galliform	productivity	-	Baines *et al.* 2004
Carrion crow[6, 7]	UK	curlew	yes	wader	abundance	-	Baines *et al.* 2008
Carrion crow[6, 7]	UK	golden plover	yes	wader	abundance	-	Baines *et al.* 2008
Carrion crow[6, 7]	UK	lapwing	yes	wader	abundance	-	Baines *et al.* 2008
Carrion crow[6, 7]	UK	snipe	yes	wader	abundance	+	Baines *et al.* 2008
Unknown corvids	Slovakia	blackcap	no	passerine	productivity	-	Baláž *et al.* 2007
Carrion crow	Portugal	European rabbit	-	mammal	abundance	none	Beja *et al.* 2009
Carrion crow	Portugal	Iberian hare	-	mammal	abundance	none	Beja *et al.* 2009

Predator species*	Location	Prey Species	Ground nesting	Family Groups	Prey Response	Impact	Source
Carrion crow	Portugal	red-legged partridge	yes	galliform	abundance	none	Beja *et al.* 2009
Common raven	Switzerland	peregrine falcon	no	raptor	productivity	-	Brambilla *et al.* 2004
Common raven	USA	sage-grouse	yes	galliform	predation rate	none	Bui *et al.* 2007
Common raven	USA	sage-grouse	yes	galliform	productivity	-	Coates & Delehanty 2010
Carrion crow[1, 3, 4]	UK	yellowhammer	yes	passerine	chick condition & growth	-	Dunn *et al.* 2010
Carrion crow[1, 3, 5]	UK	yellowhammer	yes	passerine	parental provisioning	+	Dunn *et al.* 2010
Carrion crow[1, 3, 6]	UK	yellowhammer	yes	passerine	productivity	-	Dunn *et al.* 2010
American crow	USA	little blue heron	no	pelicaniform	productivity	-	Frederick *et al.* 1992
American crow	USA	snowy egret	no	ciconiiform	productivity	-	Frederick *et al.* 1992
American crow	USA	tricoloured Heron	no	pelicaniform	productivity	-	Frederick *et al.* 1992
American crow[6]	USA	ducks	-	wader	productivity	-	Johnson *et al.* 1988
Jungle crow	Japan	black-tailed gull	yes	seabird	productivity	-	Kazama 2007
Common raven	USA	great egret	no	ciconiiform	adult survival	-	Kelly *et al.* 2005
Carrion crow	UK	lapwing	yes	wader	predation rate	none	MacDonald & Bolton 2008
American crow[1]	Canada	sharp-tailed grouse	yes	galliform	adult survival	-	Manzer & Hanon 2005
Carrion crow	UK	blackbird	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	blackbird	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	blue tit	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	blue tit	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	bullfinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	bullfinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	chaffinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	chaffinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	chiffchaff	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	chiffchaff	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	coal tit	no	passerine	abundance	none	Newson *et al.* 2010

Predator species*	Location	Prey Species	Ground nesting	Family Groups	Prey Response	Impact	Source
Carrion crow	UK	coal tit	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	dunnock	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	dunnock	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	garden warbler	no	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	garden warbler	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	goldfinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	goldfinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	great tit	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	great tit	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	green woodpecker	no	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	green woodpecker	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	greenfinch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	greenfinch	no	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	house sparrow	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	house sparrow	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	lapwing	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	lapwing	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	linnet	no	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	linnet	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	meadow pipit	yes	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	meadow pipit	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	mistle thrush	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	mistle thrush	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	nuthatch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	nuthatch	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	reed bunting	no	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	reed bunting	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	robin	no	passerine	abundance	+	Newson *et al.* 2010

Predator species*	Location	Prey Species	Ground nesting	Family Groups	Prey Response	Impact	Source
Carrion crow	UK	robin	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	skylark	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	skylark	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	song thrush	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	song thrush	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	spotted flycatcher	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	spotted flycatcher	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	starling	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	starling	no	passerine	abundance	-	Newson *et al.* 2010
Carrion crow	UK	tree sparrow	no	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	tree sparrow	no	passerine	abundance	-	Newson *et al.* 2010
Carrion crow	UK	willow warbler	yes	passerine	abundance	+	Newson *et al.* 2010
Carrion crow	UK	willow warbler	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	wren	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	wren	no	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	yellow wagtail	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	yellow wagtail	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	yellowhammer	yes	passerine	abundance	none	Newson *et al.* 2010
Carrion crow	UK	yellowhammer	yes	passerine	abundance	none	Newson *et al.* 2010
American crow	USA	brown-headed cowbird	-	passerine	productivity	-	Rodewald & Yahner 2001
Common raven	USA	common murres	no	seabird	productivity	-	Schauer & Murphy 1996
Fish crow	USA	white ibis	no	pelicaniform	adult survival	-	Shields & Parnell 1986
Carrion crow[1, 2]	UK	several species[c]	-	passerine	species richness	none	Sims *et al.* 2008
Hooded crow	Norway	fieldfare	no	passerine	species richness	+	Slagsvold 1980
Carrion crow	UK	blackbird	no	passerine	productivity	-	Stoate & Szczur 2001
Carrion crow	UK	chaffinch	no	passerine	productivity	none	Stoate & Szczur 2001
Carrion crow	UK	dunnock	no	passerine	productivity	-	Stoate & Szczur 2001

Predator species*	Location	Prey Species	Ground nesting	Family Groups	Prey Response	Impact	Source
Carrion crow	UK	song thrush	no	passerine	productivity	-	Stoate & Szczur 2001
Carrion crow	UK	whitethroat	yes	passerine	productivity	-	Stoate & Szczur 2001
Carrion crow	UK	yellowhammer	yes	passerine	productivity	none	Stoate & Szczur 2001
Carrion crow[1]	UK	blackbird	no	passerine	productivity	none	Stoate & Szczur 2005
Carrion crow[1]	UK	whitethroat	yes	passerine	productivity	none	Stoate & Szczur 2005
Carrion crow & Hooded crow	UK	horned grebes	yes	wader	productivity	-	Summers *et al.* 2009
Carrion crow	UK	black grouse	yes	galliform	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	curlew	yes	wader	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	golden plover	yes	wader	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	lapwing	yes	wader	abundance	-	Tharme *et al.* 2001
Carrion crow	UK	meadow pipit	yes	passerine	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	red grouse	yes	galliform	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	skylark	yes	passerine	abundance	-	Tharme *et al.* 2001
Carrion crow	UK	snipe	yes	wader	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	wheatear	yes	passerine	abundance	none	Tharme *et al.* 2001
Carrion crow	UK	whinchat	yes	passerine	abundance	none	Tharme *et al.* 2001
Common raven	Poland	27 different birds$^{\phi}$	-	passerine	abundance	+	Tryjanowski 2001

*Corvids were often removed in addition to other avian and mammalian predators. Avian: 1=rook, 2=magpie, 3=jackdaw, 4=gull. Mammalian: 5=fox, 6=coyote, 7=stoat, 8=ferret, 9=skunk, 10=raccoon, 11=marten, 12=mink, 13=weasel, 14=feral cat, 15=squirrel, 16=rat, 17=hedgehog.

$^{\phi}$Eurasian skylark, western yellow wagtail, corn bunting, yellowhammer, common whitethroat, white wagtail, Eurasian linnet, reed bunting, meadow pipit, common chaffinch, common blackbird, marsh warbler, common starling, Eurasian tree sparrow, European goldfinch, common cuckoo, European greenfinch, common quail, whinchat, ortolan bunting, great grey shrike, corn crake, common nightingale, great tit, hoopoe, common chiffchaff, common redstart

Table C: Correlative studies which examined the correlations between of corvid abundance and predation rates (clutch survival) on artificial nests. The relationship with corvids abundance can be either positive (+), negative (-), or show no response (none). Several studies included multiple-predator species alongside corvids. These have been described in the footnotes below. Studies that removed corvids are presented in this table if they measured the response of the prey parameter in relation to known corvid population fluctuations.

Predator species*	Location	Response	Source
Common raven	USA	-	Kristan and Boarman 2003
Common raven	USA	-	Coates *et al.* 2007$^{\Delta}$
Common raven + American crow	USA	-	Marzluff and Neatherlin 2006
Common raven + American crow[1]	USA	none	Luginbuhl *et al.* 2001
Hooded crow	Finland	none	Jokimäki *et al.* 2005
Hooded crow	Italy	none	Jokimäki *et al.* 2005
Hooded crow[1,2]	Sweden	-	Soderstrom *et al.* 1998

*Authors noted corvid effects in combination with other corvid species: 1=magpie, 2=jay

$^{\Delta}$ Study experimentally removed corvids and observed changes in artificial nest survival. Only the control of this experiment was included as this reflected an un-manipulated association between corvid population changes and artificial nest survival.

Appendix C: Combining experimental & correlative studies

Table D: Summary of 46 experimental and correlative studies showing the effect (prey response) of corvids on several breeding and population parameters of species. Numeric subscripts are cases where multiple-predator species were removed or correlated alongside corvids, and those species involved are described in the footnote. PS = population size.

Predator*	Location	Prey Species	Avian Group	Ground-nesting	Prey Parameter	Prey Response	Study type	Source
American crow	USA	ducks	wader	exclude	productivity	none	Exp.	Clark *et al.* 1995
American crow	USA	little blue heron	pelicaniform	no	productivity	-	Corr.	Frederick *et al.* 1992
American crow	USA	snowy egret	ciconiiform	no	productivity	-	Corr.	Frederick *et al.* 1992
American crow	USA	tricoloured Heron	pelicaniform	no	productivity	-	Corr.	Frederick *et al.* 1992
American crow	USA	brown-headed cowbird	passerine	-	productivity	-	Corr.	Rodewald & Yahner 2001
American crow + Common raven[4]	USA	piping plover	wader	yes	productivity	none	Exp.	Struthers & Ryan 2005
American crow[1]	Canada	sharp-tailed grouse	galliform	yes	adult survival	-	Corr.	Manzer & Hanon 2005
American crow[6]	USA	ducks	wader	-	productivity	-	Corr.	Johnson *et al.* 1988
American crow[9, 10]	USA	pheasant	galliform	yes	productivity	none	Exp.	Chessness *et al.* 1968
American crow[9, 10]	USA	pheasant	galliform	yes	breeding PS	none	Exp.	Chessness *et al.* 1968
American crow[9, 10]	USA	pheasant	galliform	yes	clutch size	-	Exp.	Chessness *et al.* 1968
American crow[9, 10]	USA	pheasant	galliform	yes	productivity	-	Exp.	Chessness *et al.* 1968
Carrion crow	UK	black grouse	galliform	yes	productivity	none	Exp.	Summers *et al.* 2004
Carrion crow	UK	capercaillie	galliform	yes	productivity	none	Exp.	Summers *et al.* 2004
Carrion crow	UK	curlew	wader	yes	abundance	none	Corr.	Amar *et al.* 2011
Carrion crow	UK	dunlin	wader	yes	abundance	none	Corr.	Amar *et al.* 2011
Carrion crow	UK	golden plover	wader	yes	abundance	none	Corr.	Amar *et al.* 2011
Carrion crow	UK	lapwing	wader	yes	abundance	-	Corr.	Amar *et al.* 2011
Carrion crow	UK	snipe	wader	yes	abundance	none	Corr.	Amar *et al.* 2011
Carrion crow	Portugal	European rabbit	mammal	-	abundance	none	Corr.	Beja *et al.* 2009
Carrion crow	Portugal	Iberian hare	mammal	-	abundance	none	Corr.	Beja *et al.* 2009
Carrion crow	Portugal	red-legged partridge	galliform	yes	abundance	none	Corr.	Beja *et al.* 2009
Carrion crow	UK	lapwing	wader	yes	predation rate	none	Corr.	MacDonald & Bolton 2008

Predator*	Location	Prey Species	Avian Group	Ground-nesting	Prey Parameter	Prey Response	Study type	Source
Carrion crow	UK	blackbird	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	blackbird	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	blue tit	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	blue tit	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	bullfinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	bullfinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	chaffinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	chaffinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	chiffchaff	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	chiffchaff	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	coal tit	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	coal tit	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	dunnock	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	dunnock	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	garden warbler	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	garden warbler	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	goldfinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	goldfinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	great tit	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	great tit	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	green woodpecker	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	green woodpecker	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	greenfinch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	greenfinch	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	house sparrow	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	house sparrow	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	lapwing	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	lapwing	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	linnet	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	linnet	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	meadow pipit	passerine	yes	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	meadow pipit	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	mistle thrush	passerine	no	abundance	none	Corr.	Newson *et al.* 2010

Predator*	**Location**	**Prey Species**	**Avian Group**	**Ground-nesting**	**Prey Parameter**	**Prey Response**	**Study type**	**Source**
Carrion crow	UK	mistle thrush	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	nuthatch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	nuthatch	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	reed bunting	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	reed bunting	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	robin	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	robin	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	skylark	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	skylark	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	song thrush	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	song thrush	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	spotted flycatcher	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	spotted flycatcher	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	starling	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	starling	passerine	no	abundance	-	Corr.	Newson *et al.* 2010
Carrion crow	UK	tree sparrow	passerine	no	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	tree sparrow	passerine	no	abundance	-	Corr.	Newson *et al.* 2010
Carrion crow	UK	willow warbler	passerine	yes	abundance	+	Corr.	Newson *et al.* 2010
Carrion crow	UK	willow warbler	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	wren	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	wren	passerine	no	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	yellow wagtail	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	yellow wagtail	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	yellowhammer	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	yellowhammer	passerine	yes	abundance	none	Corr.	Newson *et al.* 2010
Carrion crow	UK	blackbird	passerine	no	productivity	-	Corr.	Stoate & Szczur 2001
Carrion crow	UK	chaffinch	passerine	no	productivity	none	Corr.	Stoate & Szczur 2001
Carrion crow	UK	dunnock	passerine	no	productivity	-	Corr.	Stoate & Szczur 2001
Carrion crow	UK	song thrush	passerine	no	productivity	-	Corr.	Stoate & Szczur 2001
Carrion crow	UK	whitethroat	passerine	yes	productivity	-	Corr.	Stoate & Szczur 2001
Carrion crow	UK	yellowhammer	passerine	yes	productivity	none	Corr.	Stoate & Szczur 2001
Carrion crow	UK	black grouse	galliform	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow	UK	curlew	wader	yes	abundance	none	Corr.	Tharme *et al.* 2001

Predator*	Location	Prey Species	Avian Group	Ground-nesting	Prey Parameter	Prey Response	Study type	Source
Carrion crow	UK	golden plover	wader	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow	UK	lapwing	wader	yes	abundance	-	Corr.	Tharme *et al.* 2001
Carrion crow	UK	meadow pipit	passerine	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow	UK	red grouse	galliform	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow	UK	skylark	passerine	yes	abundance	-	Corr.	Tharme *et al.* 2001
Carrion crow	UK	snipe	wader	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow	UK	wheatear	passerine	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow	UK	whinchat	passerine	yes	abundance	none	Corr.	Tharme *et al.* 2001
Carrion crow & Hooded crow	UK	horned grebes	wader	yes	productivity	-	Corr.	Summers *et al.* 2009
Carrion crow[1]	UK	blackbird	passerine	no	productivity	none	Corr.	Stoate & Szczur 2005
Carrion crow[1]	UK	whitethroat	passerine	yes	productivity	none	Corr.	Stoate & Szczur 2005
Carrion crow[1, 2]	UK	several species[c]	passerine	-	species richness	none	Corr.	Sims *et al.* 2008
Carrion crow[1, 2, 3, 5, 7,13, 14, 16, 17]	UK	grey partridge	galliform	yes	post-breeding PS	-	Exp.	Tapper 1996
Carrion crow[1, 2, 3, 5, 7,13, 14, 16, 17]	UK	grey partridge	galliform	yes	breeding PS	-	Exp.	Tapper 1996
Carrion crow[1, 2, 3, 5, 7,13, 14, 16, 17]	UK	grey partridge	galliform	yes	clutch size	-	Exp.	Tapper 1996
Carrion crow[1, 3, 4]	UK	yellowhammer	passerine	yes	chick condition & growth	-	Corr.	Dunn *et al.* 2010
Carrion crow[1, 3, 5]	UK	yellowhammer	passerine	yes	parental provisioning	+	Corr.	Dunn *et al.* 2010
Carrion crow[1, 3, 6]	UK	yellowhammer	passerine	yes	productivity	-	Corr.	Dunn *et al.* 2010
Carrion crow[2]	UK	blackbird	passerine	no	productivity	none	Exp.	Stoate & Szczur 2005
Carrion crow[2]	UK	whitethroat	passerine	yes	productivity	none	Exp.	Stoate & Szczur 2005
Carrion crow[2, 5, 15, 16]	UK	spotted flycatcher	passerine	no	productivity	-	Exp.	Stoate & Szczur 2006
Carrion crow[2, 5, 7, 12, 13]	UK	blackbird	passerine	no	productivity	-	Exp.	White *et al.* 2008
Carrion crow[2, 5, 7, 12, 13]	UK	blackbird	passerine	no	post-breeding PS	none	Exp.	White *et al.* 2008
Carrion crow[4]	UK	curlew	wader	yes	productivity	-	Exp.	Parr 1993
Carrion crow[4]	UK	curlew	wader	yes	breeding PS	none	Exp.	Parr 1993

Predator*	**Location**	**Prey Species**	**Avian Group**	**Ground-nesting**	**Prey Parameter**	**Prey Response**	**Study type**	**Source**
Carrion crow[4]	UK	golden plover	wader	yes	productivity	none	Exp.	Parr 1993
Carrion crow[4]	UK	golden plover	wader	yes	breeding PS	none	Exp.	Parr 1993
Carrion crow[4]	UK	lapwing	wader	yes	productivity	-	Exp.	Parr 1993
Carrion crow[4]	UK	lapwing	wader	yes	breeding PS	none	Exp.	Parr 1993
Carrion crow[4]	UK	oystercatcher	wader	yes	productivity	none	Exp.	Parr 1993
Carrion crow[4]	UK	oystercatcher	wader	yes	breeding PS	none	Exp.	Parr 1993
Carrion crow[4]	UK	redshank	wader	yes	breeding PS	none	Exp.	Parr 1993
Carrion crow[4]	UK	redshank	wader	yes	productivity	-	Exp.	Parr 1993
Carrion crow[5]	UK	lapwing	wader	yes	productivity	-	Exp.	Bolton *et al.* 2007
Carrion crow[5]	UK	lapwing	wader	yes	productivity	none	Exp.	Bolton *et al.* 2007
Carrion crow[5]	UK	lapwing	wader	yes	post-breeding PS	none	Exp.	Bolton *et al.* 2007
Carrion crow[5]	UK	curlew	wader	yes	productivity	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	curlew	wader	yes	breeding PS	none	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	golden plover	wader	yes	productivity	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	golden plover	wader	yes	breeding PS	none	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	lapwing	wader	yes	productivity	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	lapwing	wader	yes	breeding PS	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	meadow pipit	passerine	yes	productivity	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	meadow pipit	passerine	yes	breeding PS	none	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	red grouse	galliform	yes	productivity	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	red grouse	galliform	yes	breeding PS	-	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	skylark	passerine	yes	breeding PS	none	Exp.	Fletcher *et al.* 2010
Carrion crow[5]	UK	snipe	wader	yes	breeding PS	none	Exp.	Fletcher *et al.* 2010
Carrion crow[5, 6]	UK	capercaillie	galliform	yes	productivity	-	Corr.	Baines *et al.* 2004
Carrion crow[6, 7]	UK	curlew	wader	yes	abundance	-	Corr.	Baines *et al.* 2008
Carrion crow[6, 7]	UK	golden plover	wader	yes	abundance	-	Corr.	Baines *et al.* 2008
Carrion crow[6, 7]	UK	lapwing	wader	yes	abundance	-	Corr.	Baines *et al.* 2008
Carrion crow[6, 7]	UK	snipe	wader	yes	abundance	+	Corr.	Baines *et al.* 2008

Predator*	**Location**	**Prey Species**	**Avian Group**	**Ground-nesting**	**Prey Parameter**	**Prey Response**	**Study type**	**Source**
Common raven	UK	curlew	wader	yes	abundance	none	Corr.	Amar *et al.* 2010
Common raven	UK	dunlin	wader	yes	abundance	none	Corr.	Amar *et al.* 2010
Common raven	UK	golden plover	wader	yes	abundance	none	Corr.	Amar *et al.* 2010
Common raven	UK	lapwing	wader	yes	abundance	none	Corr.	Amar *et al.* 2010
Common raven	UK	snipe	wader	yes	abundance	none	Corr.	Amar *et al.* 2010
Common raven	Switzerland	peregrine falcon	raptor	no	productivity	-	Corr.	Brambilla *et al.* 2004
Common raven	USA	sage-grouse	galliform	yes	predation rate	none	Corr.	Bui *et al.* 2007
Common raven	USA	sage-grouse	galliform	yes	productivity	-	Corr.	Coates & Delehanty 2010
Common raven	USA	great egret	ciconiiform	no	adult survival	-	Corr.	Kelly *et al.* 2005
Common raven	USA	common murres	seabird	no	productivity	-	Corr.	Schauer & Murphy 1996
Common raven	Poland	27 different birds$^{\phi}$	passerine	-	abundance	+	Corr.	Tryjanowski 2001
Common raven[6]	USA	sandhill crane	gruiform	yes	productivity	-	Exp.	Littlefield 2003
Fish crow	USA	white ibis	pelicaniform	no	adult survival	-	Corr.	Shields & Parnell 1986
Hooded crow	UK	hen harrier	raptor	yes	lay date	none	Exp.	Amar & Redpath 2002
Hooded crow	UK	hen harrier	raptor	yes	clutch size	none	Exp.	Amar & Redpath 2002
Hooded crow	UK	hen harrier	raptor	yes	productivity	none	Exp.	Amar & Redpath 2002
Hooded crow	Norway	fieldfare	passerine	no	breeding PS	-	Exp.	Slagsvold 1980
Hooded crow	Norway	common Eider	wader	yes	productivity	none	Exp.	Stein *et al.* 2010
Hooded crow	Norway	fieldfare	passerine	no	species richness	+	Corr.	Slagsvold 1980
Hooded crow + common raven	Norway	willow ptarmigan	galliform	yes	productivity	-	Exp.	Erikstad *et al.* 1982
Hooded crow + Common raven[2]	Norway	black grouse	galliform	yes	breeding PS	none	Exp.	Parker 1984
Hooded crow + Common raven[2]	Norway	black grouse	galliform	yes	productivity	none	Exp.	Parker 1984
Hooded crow + Common raven[2]	Norway	black grouse	galliform	yes	productivity	none	Exp.	Parker 1984
Hooded crow + Common raven[2]	Norway	willow ptarmigan	galliform	yes	productivity	none	Exp.	Parker 1984
Hooded crow + Common raven[5, 11, 12]	Sweden	willow ptarmigan	galliform	yes	productivity	none	Exp.	Steen & Haugvold 2009
Hooded crow[8]	UK	lapwing	wader	yes	productivity	none	Exp.	Bodey *et al.* 2011

Predator*	Location	Prey Species	Avian Group	Ground-nesting	Prey Parameter	Prey Response	Study type	Source
Jungle crow	Japan	black-tailed gull	seabird	yes	productivity	-	Corr.	Kazama 2007
Unknown corvids	Slovakia	blackcap	passerine	no	productivity	-	Corr.	Baláž *et al.* 2007

*Corvids were often removed in addition to other avian and mammalian predators. Avian: 1=rook, 2=magpie, 3=jackdaw, 4=gull. Mammalian: 5=fox, 6=coyote, 7=stoat, 8=ferret, 9=skunk, 10=raccoon, 11=marten, 12=mink, 13=weasel, 14=feral cat, 15=squirrel, 16=rat, 17=hedgehog.

$^{\phi}$Eurasian skylark, western yellow wagtail, corn bunting, yellowhammer, common whitethroat, white wagtail, Eurasian linnet, reed bunting, meadow pipit, common chaffinch, common blackbird, marsh warbler, common starling, Eurasian tree sparrow, European goldfinch, common cuckoo, European greenfinch, common quail, whinchat, ortolan bunting, great grey shrike, corn crake, common nightingale, great tit, hoopoe, common chiffchaff, common redstart

Table E: Summary of 46 experimental and correlative studies sorted by family group showing the effect (response) of the presence of corvids on several breeding and population parameters of species. Numeric subscripts are cases where multiple-predator species were removed or correlated alongside corvids, and those species involved are described in the footnote. PS = population size

Avian Group	Prey Species	Ground-nesting	Predator*	Location	Prey Parameter	Prey Response	Study type	Source
Ciconiiform	snowy egret	no	**American crow**	USA	productivity	-	Corr.	Frederick *et al.* 1992
	great egret	no	**Common raven**	USA	adult survival	-	Corr.	Kelly *et al.* 2005
Galliform	sharp-tailed grouse	yes	**American crow**[1]	Canada	adult survival	-	Corr.	Manzer & Hanon 2005
	pheasant	yes	**American crow**[9, 10]	USA	productivity	none	Exp.	Chessness *et al.* 1968
	pheasant	yes	**American crow**[9, 10]	USA	breeding PS	none	Exp.	Chessness *et al.* 1968
	pheasant	yes	**American crow**[9, 10]	USA	clutch size	-	Exp.	Chessness *et al.* 1968
	pheasant	yes	**American crow**[9, 10]	USA	productivity	-	Exp.	Chessness *et al.* 1968
	black grouse	yes	**Carrion crow**	UK	productivity	none	Exp.	Summers *et al.* 2004
	capercaillie	yes	**Carrion crow**	UK	productivity	none	Exp.	Summers *et al.* 2004
	red-legged partridge	yes	**Carrion crow**	Portugal	abundance	none	Corr.	Beja *et al.* 2009
	black grouse	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	red grouse	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	grey partridge	yes	**Carrion crow**[1, 2, 3, 5, 7,13, 14, 16, 17]	UK	post-breeding PS	-	Exp.	Tapper 1996
	grey partridge	yes	**Carrion crow**[1, 2, 3, 5, 7,13, 14, 16, 17]	UK	breeding PS	-	Exp.	Tapper 1996
	grey partridge	yes	**Carrion crow**[1, 2, 3, 5, 7,13, 14, 16, 17]	UK	clutch size	-	Exp.	Tapper 1996
	red grouse	yes	**Carrion crow**[5]	UK	productivity	-	Exp.	Fletcher *et al.* 2010
	red grouse	yes	**Carrion crow**[5]	UK	breeding PS	-	Exp.	Fletcher *et al.* 2010
	capercaillie	yes	**Carrion crow**[5, 6]	UK	productivity	-	Corr.	Baines *et al.* 2004
	sage-grouse	yes	**Common raven**	USA	predation rate	none	Corr.	Bui *et al.* 2007
	sage-grouse	yes	**Common raven**	USA	productivity	-	Corr.	Coates & Delehanty 2010
	willow ptarmigan	yes	**Hooded crow + common raven**	Norway	productivity	-	Exp.	Erikstad *et al.* 1982

Avian Group	Prey Species	Ground-nesting	Predator*	Location	Prey Parameter	Prey Response	Study type	Source
Galliform	black grouse	yes	**Hooded crow + Common raven**[2]	Norway	breeding PS	none	Exp.	Parker 1984
	black grouse	yes	**Hooded crow + Common raven**[2]	Norway	productivity	none	Exp.	Parker 1984
	black grouse	yes	**Hooded crow + Common raven**[2]	Norway	productivity	none	Exp.	Parker 1984
	willow ptarmigan	yes	**Hooded crow + Common raven**[2]	Norway	productivity	none	Exp.	Parker 1984
	willow ptarmigan	yes	**Hooded crow + Common raven**[5, 11, 12]	Sweden	productivity	none	Exp.	Steen & Haugvold 2009
	sandhill crane	yes	**Common raven**[6]	USA	productivity	-	Exp.	Littlefield 2003
Mammal	European rabbit	-	**Carrion Crow**	Portugal	abundance	none	Corr.	Beja *et al.* 2009
	Iberian hare	-	**Carrion Crow**	Portugal	abundance	none	Corr.	Beja *et al.* 2009
Passerine	brown-headed cowbird	-	**American crow**	USA	productivity	-	Corr.	Rodewald & Yahner 2001
	blackbird	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	blackbird	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	blue tit	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	blue tit	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	bullfinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	bullfinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	chaffinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	chaffinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	chiffchaff	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	chiffchaff	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	coal tit	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	coal tit	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	dunnock	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	dunnock	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010

Avian Group	Prey Species	Ground-nesting	Predator*	Location	Prey Parameter	Prey Response	Study type	Source
Passerine	garden warbler	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	garden warbler	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	goldfinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	goldfinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	great tit	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	great tit	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	green woodpecker	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	green woodpecker	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	greenfinch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	greenfinch	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	house sparrow	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	house sparrow	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	lapwing	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	lapwing	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	linnet	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	linnet	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	meadow pipit	yes	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	meadow pipit	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	mistle thrush	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	mistle thrush	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	nuthatch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	nuthatch	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	reed bunting	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	reed bunting	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	robin	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	robin	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	skylark	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	skylark	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010

Avian Group	**Prey Species**	**Ground-nesting**	**Predator***	**Location**	**Prey Parameter**	**Prey Response**	**Study type**	**Source**
Passerine	song thrush	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	song thrush	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	spotted flycatcher	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	spotted flycatcher	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	starling	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	starling	no	**Carrion crow**	UK	abundance	-	Corr.	Newson *et al.* 2010
	tree sparrow	no	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	tree sparrow	no	**Carrion crow**	UK	abundance	-	Corr.	Newson *et al.* 2010
	willow warbler	yes	**Carrion crow**	UK	abundance	+	Corr.	Newson *et al.* 2010
	willow warbler	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	wren	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	wren	no	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	yellow wagtail	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	yellow wagtail	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	yellowhammer	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	yellowhammer	yes	**Carrion crow**	UK	abundance	none	Corr.	Newson *et al.* 2010
	blackbird	no	**Carrion crow**	UK	productivity	-	Corr.	Stoate & Szczur 2001
	chaffinch	no	**Carrion crow**	UK	productivity	none	Corr.	Stoate & Szczur 2001
	dunnock	no	**Carrion crow**	UK	productivity	-	Corr.	Stoate & Szczur 2001
	song thrush	no	**Carrion crow**	UK	productivity	-	Corr.	Stoate & Szczur 2001
	whitethroat	yes	**Carrion crow**	UK	productivity	-	Corr.	Stoate & Szczur 2001
	yellowhammer	yes	**Carrion crow**	UK	productivity	none	Corr.	Stoate & Szczur 2001
	meadow pipit	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	skylark	yes	**Carrion crow**	UK	abundance	-	Corr.	Tharme *et al.* 2001
	wheatear	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	whinchat	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	blackbird	no	**Carrion crow**[1]	UK	productivity	none	Corr.	Stoate & Szczur 2005
	whitethroat	yes	**Carrion crow**[1]	UK	productivity	none	Corr.	Stoate & Szczur 2005

Avian Group	Prey Species	Ground-nesting	Predator*	Location	Prey Parameter	Prey Response	Study type	Source
Passerine	several species[c]	-	**Carrion crow**[1, 2]	UK	species richness	none	Corr.	Sims *et al.* 2008
	yellowhammer	yes	**Carrion crow**[1, 3, 4]	UK	chick condition & growth	-	Corr.	Dunn *et al.* 2010
	yellowhammer	yes	**Carrion crow**[1, 3, 5]	UK	parental provisioning	+	Corr.	Dunn *et al.* 2010
	yellowhammer	yes	**Carrion crow**[1, 3, 6]	UK	productivity	-	Corr.	Dunn *et al.* 2010
	blackbird	no	**Carrion crow**[2]	UK	productivity	none	Exp.	Stoate & Szczur 2005
	whitethroat	yes	**Carrion crow**[2]	UK	productivity	none	Exp.	Stoate & Szczur 2005
	spotted flycatcher	no	**Carrion crow**[2, 5, 15, 16]	UK	productivity	-	Exp.	Stoate & Szczur 2006
	blackbird	no	**Carrion crow**[2, 5, 7, 12, 13]	UK	productivity	-	Exp.	White *et al.* 2008
	blackbird	no	**Carrion crow**[2, 5, 7, 12, 13]	UK	post-breeding PS	none	Exp.	White *et al.* 2008
	meadow pipit	yes	**Carrion crow**[5]	UK	productivity	-	Exp.	Fletcher *et al.* 2010
	meadow pipit	yes	**Carrion crow**[5]	UK	breeding PS	none	Exp.	Fletcher *et al.* 2010
	skylark	yes	**Carrion crow**[5]	UK	breeding PS	none	Exp.	Fletcher *et al.* 2010
	27 different birds[Φ]	-	**Common raven**	Poland	abundance	+	Corr.	Tryjanowski 2001
	fieldfare	no	**Hooded crow**	Norway	breeding PS	-	Exp.	Slagsvold 1980
	fieldfare	no	**Hooded crow**	Norway	species richness	+	Corr.	Slagsvold 1980
	blackcap	no	**Unknown corvids**	Slovakia	productivity	-	Corr.	Baláž *et al.* 2007
Pelicaniform	little blue heron	no	**American crow**	USA	productivity	-	Corr.	Frederick *et al.* 1992
	tricoloured Heron	no	**American crow**	USA	productivity	-	Corr.	Frederick *et al.* 1992
	white ibis	no	**Fish crow**	USA	adult survival	-	Corr.	Shields & Parnell 1986
Raptor	peregrine falcon	no	**Common raven**	Switzerland	productivity	-	Corr.	Brambilla *et al.* 2004
	hen harrier	yes	**Hooded crow**	UK	lay date	none	Exp.	Amar & Redpath 2002
	hen harrier	yes	**Hooded crow**	UK	clutch size	none	Exp.	Amar & Redpath 2002
	hen harrier	yes	**Hooded crow**	UK	productivity	none	Exp.	Amar & Redpath 2002
Seabird	common murres	no	**Common raven**	USA	productivity	-	Corr.	Schauer & Murphy 1996
	black-tailed gull	yes	**Jungle crow**	Japan	productivity	-	Corr.	Kazama 2007

Avian Group	Prey Species	Ground-nesting	Predator*	Location	Prey Parameter	Prey Response	Study type	Source
Wader	ducks	exclude	**American crow**	USA	productivity	none	Exp.	Clark *et al.* 1995
	piping plover	yes	**American crow + Common raven**^{4}	USA	productivity	none	Exp.	Struthers & Ryan 2005
	ducks	-	**American crow**^{6}	USA	productivity	-	Corr.	Johnson *et al.* 1988
	curlew	yes	**Carrion crow**	UK	abundance	none	Corr.	Amar *et al.* 2011
	dunlin	yes	**Carrion crow**	UK	abundance	none	Corr.	Amar *et al.* 2011
	golden plover	yes	**Carrion crow**	UK	abundance	none	Corr.	Amar *et al.* 2011
	lapwing	yes	**Carrion crow**	UK	abundance	-	Corr.	Amar *et al.* 2011
	snipe	yes	**Carrion crow**	UK	abundance	none	Corr.	Amar *et al.* 2011
	lapwing	yes	**Carrion crow**	UK	predation rate	none	Corr.	MacDonald & Bolton 2008
	curlew	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	golden plover	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	lapwing	yes	**Carrion crow**	UK	abundance	-	Corr.	Tharme *et al.* 2001
	snipe	yes	**Carrion crow**	UK	abundance	none	Corr.	Tharme *et al.* 2001
	horned grebes	yes	**Carrion crow & Hooded crow**	UK	productivity	-	Corr.	Summers *et al.* 2009
	curlew	yes	**Carrion crow**^{4}	UK	productivity	-	Exp.	Parr 1993
	curlew	yes	**Carrion crow**^{4}	UK	breeding PS	none	Exp.	Parr 1993
	golden plover	yes	**Carrion crow**^{4}	UK	productivity	none	Exp.	Parr 1993
	golden plover	yes	**Carrion crow**^{4}	UK	breeding PS	none	Exp.	Parr 1993
	lapwing	yes	**Carrion crow**^{4}	UK	productivity	-	Exp.	Parr 1993
	lapwing	yes	**Carrion crow**^{4}	UK	breeding PS	none	Exp.	Parr 1993
	oystercatcher	yes	**Carrion crow**^{4}	UK	productivity	none	Exp.	Parr 1993
	oystercatcher	yes	**Carrion crow**^{4}	UK	breeding PS	none	Exp.	Parr 1993
	redshank	yes	**Carrion crow**^{4}	UK	breeding PS	none	Exp.	Parr 1993
	redshank	yes	**Carrion crow**^{4}	UK	productivity	-	Exp.	Parr 1993
	lapwing	yes	**Carrion crow**^{5}	UK	productivity	-	Exp.	Bolton *et al.* 2007
	lapwing	yes	**Carrion crow**^{5}	UK	productivity	none	Exp.	Bolton *et al.* 2007

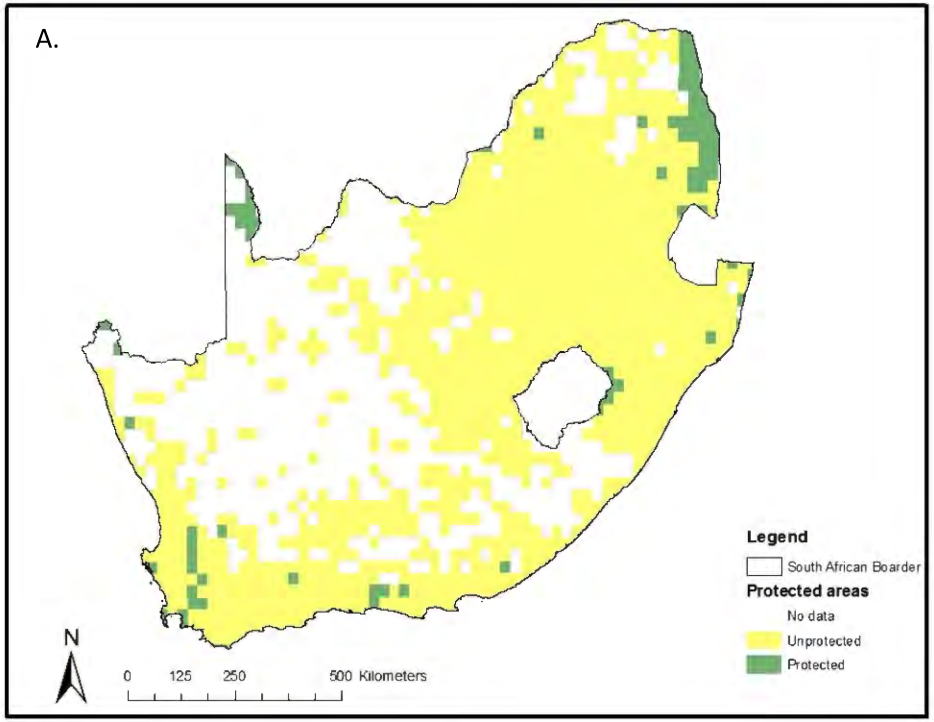
Avian Group	Prey Species	Ground-nesting	Predator*	Location	Prey Parameter	Prey Response	Study type	Source
Wader	lapwing	yes	**Carrion crow**^{5}	UK	post-breeding PS	none	Exp.	Bolton *et al.* 2007
	curlew	yes	**Carrion crow**^{5}	UK	productivity	-	Exp.	Fletcher *et al.* 2010
	curlew	yes	**Carrion crow**^{5}	UK	breeding PS	none	Exp.	Fletcher *et al.* 2010
	golden plover	yes	**Carrion crow**^{5}	UK	productivity	-	Exp.	Fletcher *et al.* 2010
	golden plover	yes	**Carrion crow**^{5}	UK	breeding PS	none	Exp.	Fletcher *et al.* 2010
	lapwing	yes	**Carrion crow**^{5}	UK	productivity	-	Exp.	Fletcher *et al.* 2010
	lapwing	yes	**Carrion crow**^{5}	UK	breeding PS	-	Exp.	Fletcher *et al.* 2010
	snipe	yes	**Carrion crow**^{5}	UK	breeding PS	none	Exp.	Fletcher *et al.* 2010
	curlew	yes	**Carrion crow**$^{6, 7}$	UK	abundance	-	Corr.	Baines *et al.* 2008
	golden plover	yes	**Carrion crow**$^{6, 7}$	UK	abundance	-	Corr.	Baines *et al.* 2008
	lapwing	yes	**Carrion crow**$^{6, 7}$	UK	abundance	-	Corr.	Baines *et al.* 2008
	snipe	yes	**Carrion crow**$^{6, 7}$	UK	abundance	+	Corr.	Baines *et al.* 2008
	curlew	yes	**Common raven**	UK	abundance	none	Corr.	Amar *et al.* 2010
	dunlin	yes	**Common raven**	UK	abundance	none	Corr.	Amar *et al.* 2010
	golden plover	yes	**Common raven**	UK	abundance	none	Corr.	Amar *et al.* 2010
	lapwing	yes	**Common raven**	UK	abundance	none	Corr.	Amar *et al.* 2010
	snipe	yes	**Common raven**	UK	abundance	none	Corr.	Amar *et al.* 2010
	common Eider	yes	**Hooded crow**	Norway	productivity	none	Exp.	Stein *et al.* 2010
	lapwing	yes	**Hooded crow**^{8}	UK	productivity	none	Exp.	Bodey *et al.* 2011

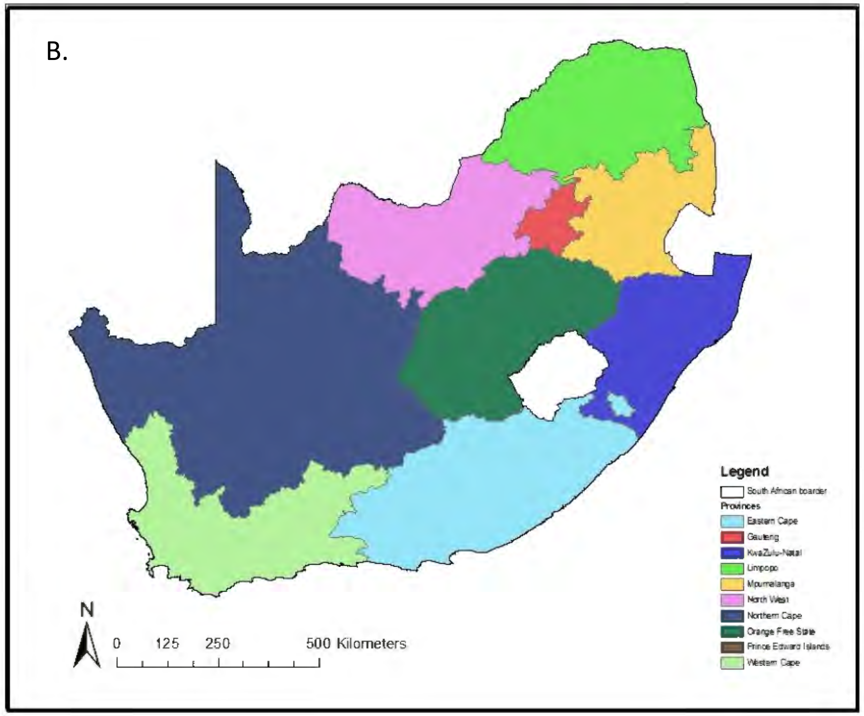
*Corvids were often removed in addition to other avian and mammalian predators. Avian: 1=rook, 2=magpie, 3=jackdaw, 4=gull. Mammalian: 5=fox, 6=coyote, 7=stoat, 8=ferret, 9=skunk, 10=raccoon, 11=marten, 12=mink, 13=weasel, 14=feral cat, 15=squirrel, 16=rat, 17=hedgehog.

$^{\phi}$Eurasian skylark, western yellow wagtail, corn bunting, yellowhammer, common whitethroat, white wagtail, Eurasian linnet, reed bunting, meadow pipit, common chaffinch, common blackbird, marsh warbler, common starling, Eurasian tree sparrow, European goldfinch, common cuckoo, European greenfinch, common quail, whinchat, ortolan bunting, great grey shrike, corn crake, common nightingale, great tit, hoopoe, common chiffchaff, common redstart

Appendix D: Environmental covariate maps used for Chapter 3

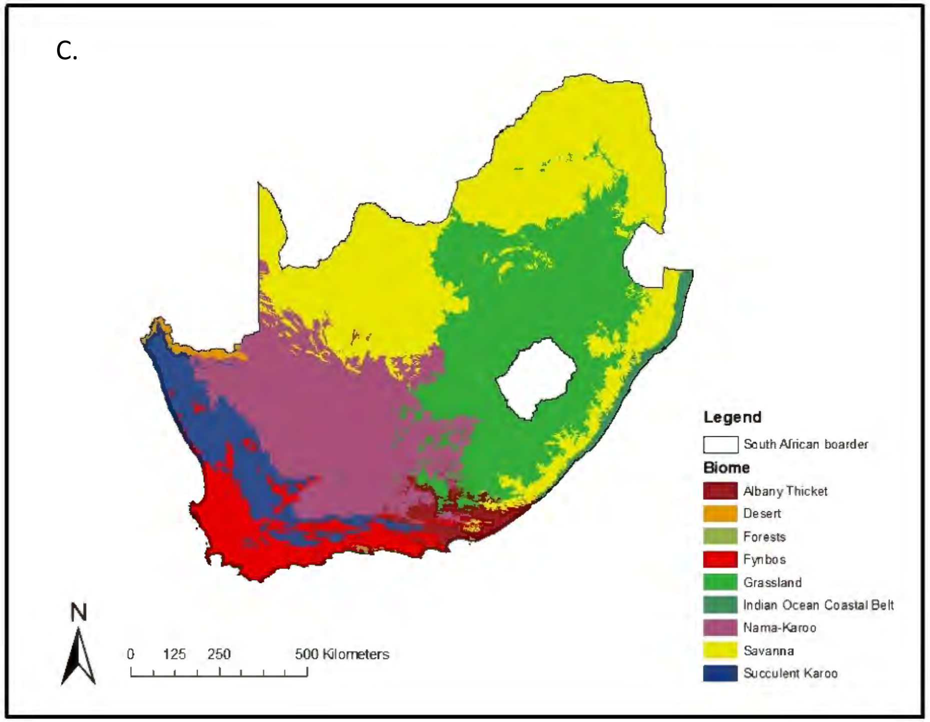
Maps showing protected areas, provinces, biomes, land cover types and transmission lines used in the analyses to explore causes of change in pied crow (*Corvus albus*) abundance throughout South Africa.

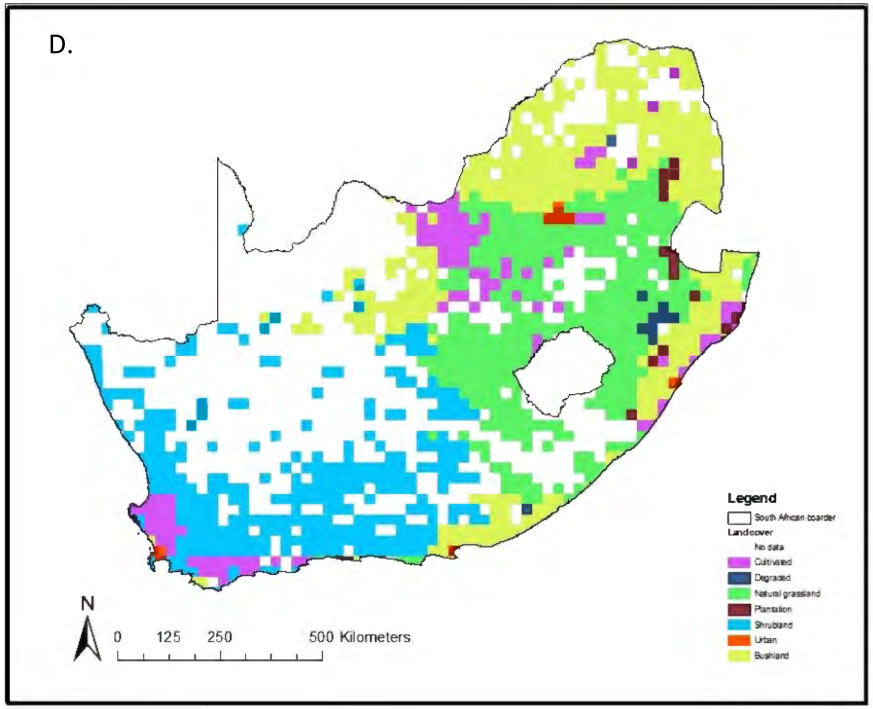




[A] Map showing the QDGC cells that were classified as protected in this study. Cells were regarded as protected if >50% of their land area fell within informal or formal protected areas. Data was derived from National Protected Area Expansion Strategy 2002 (updated in June 2006) (BGIS 2011); World Database of Protected Areas (www.protectedplanet.org); and the National Biodiversity Assessment (BGIS 2011).

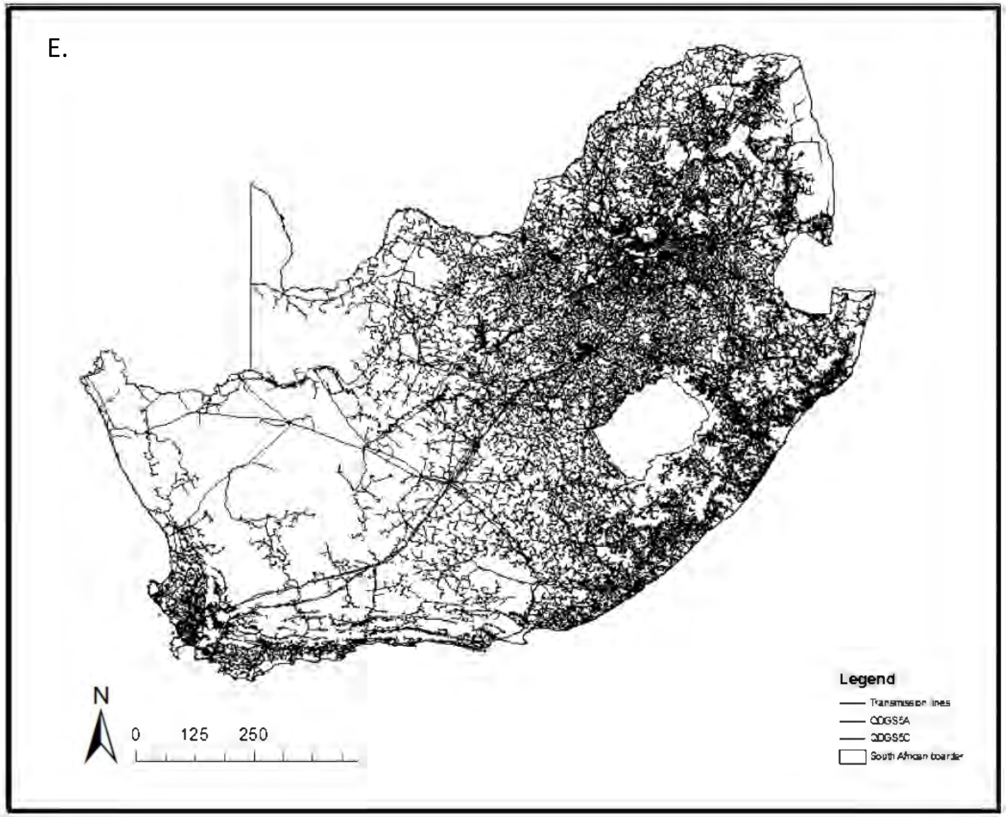
[B] Map of the nine provinces in South Africa.





[C] Map showing the distribution of the main biomes in South Africa. Data was derived from Mucina and Rutherford (2006).

[D] Map showing the QDGC cells that were classified as different land cover categories in this study. Cells were classified into categories in terms of the dominant land cover type per land area. Data was derived from the National Agricultural Research Council, version 1.1.



[E] Map of transmission line distributions across South Africa. Data was derived from Eskom (2011), South Africa's electricity supplier.