Investigating ecological impacts of the non-native population of rose-ringed parakeets (*Psittacula krameri*) in the UK

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Declaration of Originality

This thesis is result of my own work. Any contribution to this work by others is appropriately acknowledged.

Hannah Peck, December 2013

Copyright Declaration

Abstract

The rose-ringed parakeet has been present in the South East of England since at least the 1970s. However, there is little understanding about the impact that this exotic, gregarious bird has on native wildlife and therefore whether anything should or can be done to restrict potential impacts. The aim of this thesis is to provide an updated census of South East England's parakeet population size and growth, and investigate any evidence of ecological impacts to help inform policy makers making decisions on mitigation strategies for the rose-ringed parakeet. This has been achieved through using roost counts to regularly survey the population over three years and by carrying out two garden feeding experiments to look at effects of parakeet presence on bird feeding behaviour and on competition for food. I show that the rose-ringed parakeet population is well established in the UK, with over 30,000 individuals, has undergone rapid growth since 1996 but that the core London population appears to have reached capacity. I also show evidence of competition for food between parakeets and native birds, causing negative impacts on native bird foraging behaviour and resulting in a reduction in garden bird species accessing food. The overall findings of this research are that parakeets have the potential to reach high numbers in urban areas and that they do compete for food with native birds, but as yet there is no evidence for population level effects on native species. This adds to the knowledge of ecological impacts of the rose-ringed parakeet and provides further insight into the behavioural impacts that non-native species can have on native wildlife. I discuss the implications of these findings for future management and policy.

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Chapter 1

Introduction and review of the potential ecological impacts on native wildlife of non-native populations of rose-ringed parakeet

Introduction

The rose-ringed parakeet (*Psittacula krameri* Scopoli, 1769) is an increasingly common non-native species across Europe (Strubbe & Matthysen 2009a) and in the UK has established in Greater London and South East England. The UK population has been surveyed in the past (Pithon & Dytham 1999a; Butler 2003), but little is known about the current population size and trends. There have been concerns about the ecological impacts of the parakeet population on native species (GB Non-native Species Secretariat 2005) however very little research has investigated this both in Europe and the UK (Newson et al. 2011; Strubbe et al. 2010). In particular behavioural impacts of invasive vertebrates have been found to be important (for example Kiesecker et al. 2001; Dame et al. 2006) but there is little known about behavioural impacts of parakeets. Without detailed species specific knowledge of invasive species informed policy decisions are difficult to make. Consequently a greater understanding of the current UK parakeet population status and its potential ecological impacts on native species is needed to help inform policy and management strategies. In this review chapter I explore the current knowledge of the non-native population of rose-ringed parakeet in Europe. I explore how the parakeet could potentially impact native species in light of work that has investigated impacts caused by other non-native species. I then discuss how researchers have attempted to investigate impacts of the parakeet population and what gaps in knowledge of parakeet impacts still need addressing.

Invasive species threat

Invasive species are those that have been introduced and successfully established and spread beyond the site of introduction (Kolar & Lodge 2001; Duncan et al. 2003) and as a result "threaten ecosystems, habitats or species with economic or environmental harm" (McNeely 2001). There is clear evidence that non-native invasive species can have devastating impacts on native fauna (Human & Gordon 1996; Townsend 1996; Lowe et al. 2000; Bertolino & Genovesi 2003; Wiles et al. 2003; Gurnell et al. 2004) with the spread of invasive species stated as being the biggest threat to biodiversity after habitat loss (Wilcove et al. 1998).

Despite the clear threat of some non-native species, the value of non-native species research is a continuous topic of debate. While most scientists propose that more needs to be done to investigate the impacts of invasive species and their management (Waage 2001; Speziale & Lambertucci 2010; Lerdau & Wickham 2011), some argue that too much effort is expended in eradicating invasive species and that efforts should be expened depending on the environmental impacts of a species rather than where it originates (Davis et al. 2011; Thompson & Davis 2011). It is in fact known that the majority of established non-native species do not become 'invasive' and detrimental to biodiversity (Mack et al. 2000; Manchester, Sarah & Bullock 2009), but those that do can have devastating impacts (Mooney 2000; Pimentel et al. 2001; Vilà et al. 2010).

Despite the incentive provided by these impacts, we currently lack the ability to predict the invasive potential of non-native species, ortheir ecological impacts. The majority of work on impacts carried out on species which affect the economy, including 'provisioning services' such as crop production (Vilà et al. 2010). In order for any ecological impacts to be mitigated they need to be identified and quantified. Research on invasive species has historically taken place after the population density is too great to attempt eradication (Kolar & Lodge 2001; Puth & Post 2005). Increasingly focus has turned to ascertaining the characteristics of a species that predispose it to become invasive and so allow taxon specific trends to be documented, to help quantify the invasive potential of other species (Kolar & Lodge 2001).

Of invasive vertebrates, birds have been particularly well studied, with excellent recording of species introductions around the world (Duncan et al. 2003), with little evidence that invasive birds are having strong negative impacts through competition or predation (Blackburn et al. 2009). However, there is a need for greater research on the influence of avian invasions on native biodiversity (Duncan et al. 2003). A recent review of the literature in Europe found that there is a limited number of studies on the impacts of invasive birds and of these most are based on anecdotal evidence rather than well-planned research (Strubbe et al. 2011).

Blackburn et al (2009) reviewed evidence for ecological impacts of non-native bird species based on species interaction categories of competition, predation, mutualism (mutualistic interactions which alter the environment) and disease transmission (Blackburn et al. 2009). These are summarised in Table 1.1 with the addition of two extra categories: acoustic niche competition and habitat alteration.

Table 1.1. Summary and examples of the types of ecological impacts caused by invasive avian species. Reviewed by and updated from (denoted by *) Blackburn et al (2009).

Impact	Study	Details	Strength of impact
Competition: causing adjustment of foraging behaviour	(Kawakami & Higuchi 2003)	The Bonin white-eye (*Apalopteron familiare*) in the presence of the exotic white-eye (*Zosterops japonicas*)	Low due to differences in habitat preference and no negative effect detected
Competition: causing reduced consumption of a shared food source	(Garrick 1981)	The New Zealand pipit (*Anthus novaeseelandiae*) and the exotic European skylark (*Alauda arvensis*)	Low due to differences in food groups consumed
Competition: reduced access to nest resources/sites	(Harper et al. 2005)	Exotic common myna (*Acridotheres tristis*) predating nests.	High
	(Wiebe 2003)	European starling (*Sturnus vulgaris*) evicting primary cavity excavators in the USA	High, but little evidence yet for population declines
***Competition:** Acoustic niche competition and noise disturbance	Theoretical: No examples as yet in avian species but it has occurred between exotic and native anuran species' vocalisations (Both & Grant 2012)	Exotic bird species may produce vocalisations which use similar frequencies to native species and therefore mask the native song. Or vocalisations may be so loud that vocal communication or predator avoidance is disturbed in other species.	No evidence in birds
Competition: Apparent competition via increased predation by a	Theoretical: No studies as yet	Exotic species may be able to establish in the presence of exotic natural predator species providing extra food for the predator but being able to better avoid predation than the native	No evidence

Impact	Study	Details	Strength of impact
shared natural enemy		birds, so that the native species declines.	
Predation	(Harrisson 1971)	Exotic Chimango caracara (*Milvago chimango*) on Easter Island, preyed on young of native nesting birds	High
	*(Clergeau & Yésou 2006)	*Exotic sacred ibis (*Threskiornis aethiopicus*) in France have been reported to prey on eggs and young of wader species.	Unknown
Mutualisms: pollination and dispersal of exotic plants	(Simberloff & Holle 1999)	Exotic red-whiskered bulbul (*Pycnonotus jocosus*), disperses seeds of exotic plant species resulting in competition with native plants	Unknown
Disease transmission	(Riper III et al. 2002)	Exotic birds including the Japanese white eye on Hawaii are thought to be a vectors of avian malaria , resulting in a decline in the endemic Hawaiian honey creeper	High – decline and possible extinction
***Habitat alteration:** Foraging or nesting habits resulting in death of plants/trees	Theoretical: no studies as yet in birds but seen in invasive brushtail possum (*Trichosurus vulpecula*) in New Zealand through selective browsing causing elimination of certain food plants (Clout 2002)	Damage to plant species, resulting in change in species composition and reduction of resources for native species	As yet no evidence in birds

Invasive species policy

Non-native vertebrates also provoke a high degree of public interest due to their visibility and emotiveness (Orueta & Ramos 2001), such as in the: grey squirrel (*Sciurus carolinensis*) in Italy where animal rights groups took legal action to prevent eradication (Bertolino 2003), the European hedgehog (*Erinaceus europaeus*) on the Hebridean islands, where public raised objections to eradication (Bremner & Park 2007), and most recently, the monk parakeet (*Myiopsitta monachus*), which was the subject of a public petition against its culling in North London (Brock & Richardson 2011). This offers a further challenge for policy makers and researchers as public attitude and media influence play a strong role in the possibilities of mitigation strategies (Bremner & Park 2007; García-Llorente et al. 2008)

To mitigate the increasing threat of invasive species spread in Europe, the EU strategy on invasive species is part of the six key objectives of the EU adopted in May 2011 (EuropeanParliament 2012). The EU 2020 Biodiversity Strategy aims to ensure measures are put in place to prevent establishment of invasive alien species, to reduce spread of established invasive alien species and to increase the knowledge base of invasive alien species, in order to halt biodiversity loss by 2020. This strategy accompanies the already existing European Initiative, the Delivering Alien Species Inventories for Europe (DAISIE) project, which provides a “one-stop-shop” for information on biological invasions in Europe (DAISIE 2012). In addition, the European Commission developed a proposal which was released in September 2013 aiming to establish a comprehensive framework for action to prevent and mitigate adverse impacts of invasive alien species on biodiversity and ecosystem services in Europe (European Commission 2013). This proposal sets out to tackle the problem that few invasive alien species are addressed by EU legislation and therefore guidelines on the regulation of most invasive alien species do not exist, creating lack of coordination and differences in efforts between European member states in tackling invasive alien species.

In the Great Britain, the invasive non-native species framework strategy was set up in 2008, which provides a means by which to assess and mitigate against invasive species (DEFRA 2008). This includes the GB non-native species risk analysis mechanism which ensures risk assessments are carried out on an individual species level before management strategies are implemented. However, the lack of direct research into individual species impacts is likely to make it difficult to implement invasive species policy and mitigation strategies, such as these risk assessments. It is therefore clear that more research into invasive species' ecological impacts is required.

Study-species: the rose-ringed parakeet

This thesis aims to address one part of this research need by directly exploring the potential ecological impacts of an invasive bird species that is commonly found in urban areas across Europe: the rose-ringed parakeet also referred to as ring-necked parakeet (hereafter often simply 'parakeets'). The rose-ringed parakeet, has recently spread across the UK and Europe with new populations arising rapidly (Pithon & Dytham 2002; Butler 2003; Strubbe & Matthysen 2009a). It is native to sub-Saharan Africa and Asia, including Afghanistan, west Pakistan, Nepal, the Indian subcontinent and Myanmar (Shwartz A & Shirley S 2007; CABI International 2012) (see Fig.1.1). The most recent literature dictates that there are 4 subspecies: two African subspecies, *P. k. krameri* and *P. k. parvirostris*; and two Asian subspecies *P. k. borealis* and *P. k. manilleansis* (Juniper & Parr 2003) (see Fig. 1.1 for distribution). It breeds in tree cavities, although it has also adapted to use cavities in buildings and its diet consists of a wide variety of plant materials (Ali & Ripley 2002). It is a long lived species, reported to have survived up to 34 years old in captivity

(Brouwer et al. 2000), although life span in the wild is likely to be much lower. It only starts to breed at 2-3 years old (Butler 2003). In its native range it is an agricultural pest, raiding a variety of crops including several fruits, seeds and grain (Iqbal et al. 2000; Khan et al. 2011; Patel 2011; Ahmad et al. 2012) and is found in cultivated and urban areas (Khan et al. 2004).

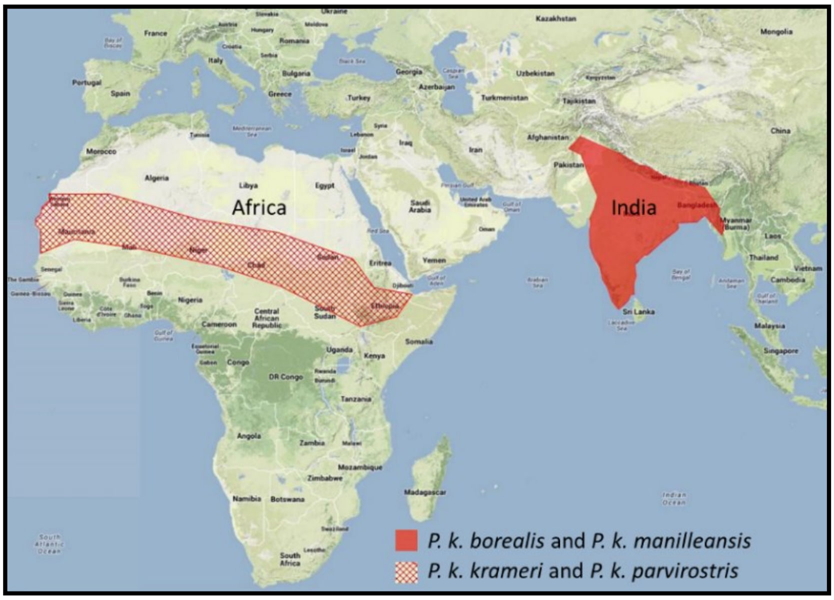

Figure 1.1. Native global range of the four sub-species of rose-ringed parakeet (adapted from Groombridge et al 2004)

<u>Non-native distribution and establishment</u>

The rose-ringed parakeet is established in Europe as a non-native species and can been found in many urban cities across the western and southern countries of Europe (Strubbe & Matthysen 2009a) (see Fig. 1.2 and Table 1.2). It has been a popular pet in Europe for centuries, reported to have been kept by the Romans (Strubbe 2009), is established as a non-native species in at least 32 countries worldwide (CABI International 2012) and is now found in every continent except Antarctica (Butler 2003). The popularity of this colourful and charismatic species as a pet is a crucial factor in explaining its the wide distribution (Fletcher & Askew 2007), as through numerous introduction events due to release or escapes from captivity, propagule pressure is likely to have been high in locations around the world resulting in its wide establishment. The long life span of the species in captivity and its loud vocalisations (Arora et al. 2012) may have resulted in the deliberate release of the species in to the wild from captivity on numerous occasions (Engebretson 2006).

The wide natural distribution of the species (Fig. 1.1) illustrates its ability to inhabit a broad range of environmental conditions from the dry desert of sub-Saharan Africa to the cool lower mountain regions of the Himalayas. However analyses of data on introductions of parrot species globally found that range size (km^2) and latitudinal range (°) do not have a significant effect on establishment success and that propagule pressure, broader diets and sedentary behaviour are greater predictors (Blackburn et al. 2004; Cassey et al. 2004). A climate matching study of introduction and establishment locations of rose-ringed parakeets in Europe found establishment to be negatively associated with the number of frost days, with success only in areas with fewer than 50 frost days (Strubbe & Matthysen 2009a). This shows that despite their broad native range establishment is restricted by cooler climates. The same study found that even after controlling for the location of introduction events, human dominated areas were a key factor to their successful establishment. In addition a study using ecological niche modelling of an established population in northern Belgium found that the parakeets were particularly associated with landscape with old forest patches and parks near to urban areas (Strubbe & Matthysen 2008). This suggests that the adaptability of the rose-ringed parakeet to human dominated landscapes could be a contributing factor to its successful establishment in so many regions across the globe.

Table 1.2. Estimated population sizes of rose-ringed parakeet in European countries reported between 2002 and 2008 (collated by Strubbe & Matthysen 2007)

Country	**Year**	**Approximate population size**	**Source**
UK*	2002	5439	(Butler 2003, 2005)
Belgium	2006	8500	(Weiserbs & Jacob 2007)
The Netherlands	2004	5400	(Van Diek 2004)
Germany	2003	5700	(Braun 2004)
Paris, France	2008	1100	(Clergeau et al. 2009)

* Extrapolated based on growth rate estimates by Butler (2005) to be approximately 10,000 in 2004

Figure 1.2. European distribution of established populations of Rose-ringed parakeet (adapted from locations collated in Strubbe & Matthysen 2009a)

Breeding performance in Europe

Knowledge of rose-ringed parakeet populations' breeding performance in Europe is needed to understand the mechanisms behind variation in establishment success and to predict future trends. Monitoring of wild rose-ringed parakeet populations' breeding performance has occurred in England from 1997-1998 (Pithon & Dytham 1999b) and from 2001-2003 (Butler et al. 2013), and in Israel from 2005-2006 (Shwartz et al. 2009), as well as a captive population bred in an outdoor aviary in north-east England between 2006-2007 (Lambert et al. 2009). For both the England and Israel populations, the earliest date of 1st eggs laid was in February, showing the species starts to breed early in the year. Average fledgling success per nest was 2.25 (±s.e. 0.2, 52 nests) in Israel (Shwartz et al. 2009) and 1.40 ±0.3 (108 nests) in south-east England (Butler et al. 2013). These studies indicate that the breeding success of the introduced populations are less than those in the native range (India), where 19 populations monitored had an average of 2.59 ± 0.24 (n=50) fledglings per nest (Shwartz et al. 2009), and so suggests although there has been establishment success, the introduced populations have so far been hindered by differences in the environment compared to the native range. The climate matching study of European introduction discussed earlier also shows this is likely to be the case (Strubbe & Matthysen 2009a). Further long–term monitoring is required to establish how breeding success changes with environmental variation such as winter temperature and with size and density of establishing populations.

Foraging preferences in the non-native range

The broad diet of the rose-ringed parakeet is likely to be a contributing factor in the establishment success of the species over such a large range, as an ability to adapt foraging behaviour benefits establishment success (Sol et al. 2012a). Feeding ecology of established populations of rose-ringed parakeet has been observed across a range of urban areas in both South East England and Paris.

These studies found that the species eats a very wide variety of both native and exotic plants growing in parks, gardens, woodland and orchards, totalling over thirty different plant species and feeds on multiple parts of the plants, including buds, seeds, fruit, leaves and bark (Feare 1996; Pithon 1998; Butler 2005; Fletcher & Askew 2007; Clergeau & Vergnes 2011). The observations of parakeet feeding ecology in the Paris suburbs used more than 300 feeding events and over 150 hours of four radio tracked individual parakeets, and found that as well as the species foraging on a wide variety of native and exotic plants, it spends approximately half its time feeding at bird feeders which consisted mostly of seeds and fat balls (Clergeau & Vergnes 2011). A survey of records of parakeets feeding from more than 40 gardens in south east England between 1996 and 1998 found peanuts from bird feeders to be the most commonly reported food consumed (Pithon 1998). This shows the importance of supplemental bird food in the diet of introduced parakeet populations and indicates the adaptability of the species to urban living.

In its native range the rose-ringed parakeet is known as the worst avian agricultural pest, due to it damaging a variety of crops (Khan et al. 2011). However there are surprisingly few reports of damage to agriculture from parakeets in Europe, with a handful of cases reported on fruit crops in South England (agricultural damage reviewed in (Fletcher & Askew 2007; FERA 2009)). Cases are likely to have gone unreported and it is possible that parakeets could utilise crops more as food sources in the future (FERA 2009).

<u>The role of predation in establishment</u>

As well as breeding success and foraging adaptability, predation can play a role in the likelihood of establishment. Release from natural predators can provide a means by which a non-native species' establishment can rapidly occur, as the predators in its new distribution have not co-evolved with the non-native species and therefore may not be adapted to predate the new species (Brown & Chivers 2005). However it can also be the case that a non-native species lacks suitable predator-avoidance strategies and so provides an easy prey for native predators (Carlsson et al. 2009). There are very few accounts in the literature of predation of parakeets in introduced populations and so the influence of predation on population establishment and growth is not yet known. Predation of eggs by grey squirrels (*Sciurus carolinensis*) was reported occurring at four nests out of 108 monitored in SouthEast England between 2001and2003 (Butler et al. 2013). Forty monitored nests in parks in the Rhine Valley, Germany between 2006 and 2008 found no incidents of nest predation (Braun & Wink 2013). A study comparing breeding success between nests in the native (India, n=128) and non-native range (Israel n=39 and UK n=89,) found that although nest predation was the main factor for reduced fecundity in the native range, with 0.23 probability of predation, it had no significant effect on the monitored nests in the UK (0.08 probability) and Israel (0.02). However, breeding success was still higher in the native than in the non-native range (Shwartz et al. 2009).

Species that could potentially predate on parakeets in the UK, either on eggs, nestlings or individual birds, include sparrow hawk (*Accipiter nisus*) (see observation of parakeet predation Fig. 1.3) , hobby (*Falco subbuteo*) (although a very small bird of prey, the hobby has been seen attempting to catch parakeets in flight at a roost in Surrey, England; H.L.Peck personal observations), peregrine falcon (*Falco peregrinus*), goshawk (*Accipiter gentilis*), gull species such as the great black backed gull (*Larus marinus*), corvid species, particularly crows (*Corvus corone*), magpies (*Pica pica*) and jays (*Garrulus glandarius*), grey squirrels, weasels (*Mustela nivalis*) and stoats (*Mustela erminea*) and the domestic cat (Gibbons et al. 2007). Further monitoring of nests would be needed to see if with increased establishment and density of parakeets, predation by native species occurs more frequently. It could be that native predators adapt to the new source of prey as interactions become more frequent (Carlsson et al. 2009).

Figure 1.3. Sparrow hawk (*Accipiter nisus*) predating a rose-ringed parakeet in Surrey, England. December 2011. Photo Credit: Mark Stanley

Impact of disease on establishment success

In addition to predation, infectious disease can affect non-native species' establishment success. On the one hand the non-native species may have no immunity to disease found in the introduced location and so disease may reduce or even prevent establishment. This has been found with decline in population size of the house finch (*Carpodacus mexicanus*) in the introduced population in east of the United States (Hochachka & Dhondt 2000). On the other hand the non-native species can bring a pathogen that has not occurred in the new location and therefore provides a threat to native species which will not have evolved immunity (Kundu et al. 2012). There are records of psittacine beak and feather disease (PBFD) in the invasive population of rose-ringed parakeet on the island of Mauritius and there is evidence of viral transmission to the endemic and endangered echo parakeet (*Psittacula echo*) (Kundu et al. 2012) and recent evidence shows occurence of PBFD in the South East England population. As this disease is thought only to affect psittacine species it should not pose a threat to native birds in Europe as there are no native psittacine species, but it is prevalent in captive psittacines in the pet trade in Europe (Julian et al. 2013). It is therefore possible that the disease could spread to wild parakeet populations in Europe. It is not yet known what role, disease transmission between parakeets plays in the population dynamics of introduced populations.

<u>Rose-ringed parakeet current policy and mitigation in the UK</u>

The rose-ringed parakeet was acknowledged as a category C species (established exotic) by the British Ornithologists Union in 1983 (Butler 2003) and the species was protected under the Wildlife and Protection Act 1981 so individual licences needed to be obtained in order to control parakeet numbers. But as of 1st January 2010 Natural England policy change became effective and parakeets were added to the general licence for the conservation of wild birds and flora and fauna and for the protection of crops (Natural England 2009). This means parakeets may be killed by landowners or occupiers under general licence if they are causing damage to crops or posing a risk to wild birds. Under the general licence an individual application does not need to be obtained to control the parakeets but action must meet the terms and conditions stipulated under the general licence (Natural England 2013a, 2013b)

To my knowledge there has been no recorded coordinated control of the Rose-ringed parakeets in the UK and only small numbers have been killed under licence (Fletcher & Askew

2007). There have been anecdotal reports by members of the public of pollarding of trees by local councils to move parakeet roosts elsewhere but it is unclear whether these were parakeet management or routine tree maintenance. Investigation is needed to record the occurrence of any management strategies and outcomes.

Through modelling of the population growth rate, it has been estimated that in order to prevent further increases in the population, there would need to be a removal of 30% of the population annually (Butler 2003). This research is, however, now ten years out of date so may not apply to the current population. With a lack of knowledge of ecological impact, there is little to inform policy and mitigation strategies for the established populations in the UK.

Studies on ecological impacts of the invasive parakeet to date

It is clear there is potential for parakeets to be interacting and sharing space with a wide variety of native flora and fauna, given its widespread occurrence, use of a variety of habitats including foraging areas such as gardens, parks and woodland and also the use of areas of large trees for breeding. Taking into account published literature on the impacts of other avian invasive species (summarised in Table 1.1) and the information on the natural history of the rose-ringed parakeet, here I summarise potential ecological impacts of introduced parakeet populations in Europe, discussing any evidence of impacts from the literature and highlighting where research is still needed.

Competition for nest sites between parakeets and native species

To my knowledge, the only research carried out to specifically investigate competitive impacts of rose-ringed parakeet on native fauna is nest site competition. These studies have been carried out in Belgium (Strubbe & Matthysen 2007, 2009b; Strubbe 2009; Strubbe et al. 2010), the UK (Newson et al. 2011) and Germany (Czajka et al. 2011) and on nest cavity excavation interactions and competition in Israel (Orchan et al. 2012). Here I summarise the findings.

The 2007 Belgian study hypothesised that the Eurasian nuthatch (*Sitta europaea*) and the European starling (*Sturnus vulgaris*) were the species most likely to suffer from competition with parakeets because they largely depend on woodpecker-made cavities, as these have anentrance size preferred by parakeets (Strubbe & Matthysen 2007). The study found a negative association between the parakeets and nuthatch abundance but no relationship with the other cavity nesting species including starlings. They also found that the two species prefer different vegetation types, with nuthatch preferring beech, (*Fagus sylvatica*) and parakeets preferring ash, (*Fraximus excelsior*), although both did use a variety of the same tree species as well.

The negative correlation found between nuthatch and parakeet abundance in Strubbe & Matthysen's (2007) study was attributed to competition for nest sites with the parakeets. This was found by comparing breeding success over two breeding seasons, where for one season cavity availability was reduced by half (Strubbe & Matthysen 2009b). This study found that with reduced cavity availability there was a significant decline of breeding pairs of nuthatches but not of parakeets. Nuthatch decline was largely attributed to nest take-overs by parakeets and there was no occurrence of nest takeover of previous parakeet nests by nuthatches. Therefore parakeets were competing for cavities with nuthatch and dominating the cavity occupancy. It was also suggested that the ability of the parakeets to occupy nest holes previously used by nuthatches is because the parakeets start breeding much earlier than nuthatches and so choose nest sites before the nuthatches.

A later study investigating the abundance and predicted abundance of the two species in Belgium, across a variety of habitats using species distribution modelling, found when taking into consideration the difference in preferred habitat use of the two species, the competition strength was only moderate, with at the most one-third of the population of nuthatches at risk from parakeet nest site competition (Strubbe et al. 2010).

A separate study carried out in the Upper Rhine Valley in Germany where a rose-ringed parakeet population has been established for at least 15 years, investigated nest site use by parakeets and European starling (Czajka et al. 2011). The study found that the two species had niche separation in both use of tree species and tree diameter for nest sites, and therefore there was low competition between the two species. They also observed starlings taking over two nests occupied by parakeets and one case of the reverse, showing that starlings are capable of evicting parakeets (Czajka et al. 2011). This study was limited by being only in four study sites all of which were old landscaped parks and so may not be representative of all breeding habitats used by parakeets in region, but does indicate that as also found with the 2007 Belgian study (Strubbe and Matthysen 2007) there is little or no adverse effect of competition for cavities between parakeets and starlings.

It has been speculated that in the UK the species also most at risk from nest-site competition are other cavity nesting birds including: kestrel (*Falco tinnunculus*); stock dove (*Columba oenas*); green woodpecker (*Picus viridis*); jackdaw (*Corvus monedula*); European starling; greater spotted woodpecker (*Dendrocopus major)*; nuthatch; great tit (*Parus major*); tree sparrow (*Passer montanus*); little owl (*Athene noctua*); and tawny owl (*Strix aluco*) (Butler 2003; Feare 1996; Fletcher & Askew 2007; Strubbe & Matthysen 2009). However it has been noted that jackdaw and stock dove prefer wider natural cavities than parakeets (Strubbe & Matthysen 2007) and starlings' aggressive behaviour enables them to evict birds from cavities, including parakeets (Strubbe & Matthysen 2007; Czajka et al. 2011). Woodpeckers are usually primary cavity nesters and breed later than the parakeets therefore are unlikely to be evicted from their nests by parakeets (Strubbe & Matthysen 2007).

It has been reported that the majority of nest cavities used by parakeets in the UK are originally excavated by green woodpecker (Butler 2003), although a more detailed census of parakeet nest sites would be needed to be certain of this. Competition between green woodpeckers and parakeets for nesting sites is currently thought to be negligible, particularly as green woodpeckers re-use only 20% of their nest cavities (Fletcher & Askew 2007).

A 2011 study by the British Trust for Ornithology (BTO) and the Food and Environment Research Agency (FERA), used British Breeding Bird Survey (BBS) data to look at the population level impact of the rose-ringed parakeet on eight native cavity-nesting birds in England (Newson et al. 2011). They used BBS data from between 1994 and 2008 from 180 sites where parakeets have been recorded as present and the abundance of the eight cavity nesting bird species within these sites, including the green woodpecker, great spotted woodpecker, great tit, blue tit, jackdaw, stock dove and European starling. They accountedfor human habitation in their analysis by including landcover type. As well as investigating the potential for parakeets to compete for nesting sites they also viewed the potential for all the species to compete with each other for cavities. They demonstrated that parakeet occupancy is positively associated with human habitation but that there was no association between parakeets and any of the other cavity nesting species and therefore no direct evidence for any impact of rose-ringed parakeets on native hole-nesting birds in the UK (Newson et al. 2011).

An observational study carried out in a parakeet frequented park in Israel in 2005 and 2006 also found no stong evidence for negative impact of competition of parakeets with native cavity nesting birds in an urban park (this included four species, the Syrian woodpecker (*Dendrocopos syriacus*), Scops owl (*Otus scops*), great tit and house sparrow However they did find that the parakeets' widening of cavity entrances provided a benefit for another invasive species, the common myna (*Acridotheres tristis*), therefore showing the potential for establishment of one invasive species to benefit the establishment of another (Orchan et al. 2012).

In conclusion, the findings from nest site competition studies show that there is no strong evidence that parakeets are causing significant negative impacts. They suggest although parakeets do have the potential to compete with native cavity nesting species, niche separation in prefered cavity habitats between parakeets and potential competing species means that the competition is not strong. It seems likely that if tree cavities were to become more limited then competition could affect native species more significantly and therefore warrants continued monitoring.

Disease transmission between parakeets and native species

The only investigation into transmission of disease between an introduced population of rose-ringed parakeets and native species is on the transmission of beak and feather disease virus (BFDV) from the introduced populations of rose-ringed parakeet on the island of Mauritius to the endangered native population of echo parakeets (*Psittacula echo*). This has been studied as it is thought to have contributed to decline of the echo parakeets (Kundu et al. 2012). As there are no native parrots in the UK and BFDV is a Pscittacine-specific disease, it is unlikely to cause any negative impacts to native species. However, captive Pscittacine species could be affected, particularly birds in outside aviaries. The use of communal roosts where thousands of individuals come together each night (Pithon & Dytham 1999a) provides the potential for disease to spread rapidly through the population. In addition, parakeets' use of garden bird feeders means that if they were infected with a pathogen that could spread to native birds and vice versa it seems plausible that this could happen fairly easily (Robb et al. 2008). It is clear however that little is known about the potential for disease transmission from parakeets to other species in the introduced locations. It is therefore important that research is conducted into potential disease transmission between non-native populations of parakeets and other species.

Acoustic niche competition for call communication and noise disturbance

Rose-ringed parakeets are highly vocal (Arora et al. 2012) and the formation of night time roosts with thousands of birds results in periods of very loud vocalizations in the evening and at dawn when the birds are entering and leaving the roost (H.L. Peck, personal observations). There has been no research into whether this affects other wildlife. However there is clear evidence that noise pollution can have negative effects of on bird communication (Francis et al. 2009; Nemeth et al. 2013; Arroyo-Solís et al. 2013). For example, increases in noise level have been found to alter spatial and singing behaviour in the Eurasian robin (*Erithacus rubecula*) (McLaughlin & Kunc 2013). So it is possible that other species which use auditory cues for signalling, foraging or predation avoidance may be affected by the loud vocalisations of parakeets at roosts, and potentially daytime vocalisations from foraging flocks of parakeets.

Habitat alteration: plant damage

Parakeet foraging behaviour can be very wasteful, with feeding habits involving much of plant material being dropped to floor rather than eaten (see Fig. 1.4) (FERA 2009). This has been shown with destruction of crops in their native range (as reviewed in Feare 1996). There is an account of parakeets stripping bark from young stems in Australian trees resulting in some trees dying (Fletcher & Askew 2007), and reports of parakeets defoliating roost trees in Belgium and Germany (Strubbe 2009). Parakeets often forage in flocks (Kotagama 1981) and observations of parakeets foraging on trees in Paris found the parakeets kept returning to the same tree until the resource was depleted (Clergeau & Vergnes 2011). Therefore if large numbers of parakeets were to feed on the same plants, particularly if this occurred year after year, it seems plausible that damage could result in plants being unable to recover. This would result in the depletion and complete removal of a resource for other species in the future, and so potentially lead to changes in the habitat's plant species composition. Experimental study would be needed to test the effect of vegetation damage to plants in the long-term. However given that parakeet distribution is generally in urban areas (Strubbe & Matthysen 2007), any impacts are likely to be to managed vegetation such as in gardens and parks and so less likely to occur to native wild habitats.

Figure 1.4. Plant material (rowan berrie and leaves (*Sorbus domesticus*) crab apple (*Malus hupehensis*) and eating apple (*Malus pumila*) dropped to the floor by foraging parakeets in a garden in Richmond, S.W. London. (Photo credit H.L.Peck)

Feeding competition

The parakeet's highly varied diet (Feare 1996), its ability to eat non-native plants and human-provided food sources (Koutsosms et al. 2001; Clergeau & Vergnes 2011) and the fact that individuals have been found to spend half their feeding time at artificial bird feeders (Clergeau & Vergnes 2011), means that it has potential to compete with a wide variety of native bird species particularly in urban gardens and at garden bird feeders. Also its relatively large size compared to many other garden bird species which use feeders in the UK (rose-ringed parakeet 400 mm length, mass 120g (Snow et al. 1998)), is generally thought to give it an advantage in interspecific interactions (Alatalo & Moreno 1987; Schro et al. 2009; Robinson et al. 2013 but see Poling & Hayslette 2006). To date there has been no investigation into competition between parakeets and other species for food. Foraging competition between parakeets and native birds therefore has potential for significant impacts on native urban birds and warrants investigation.

Conclusion

From the published research on ecological impacts of invasive populations of rose-ringed parakeets on native species to date, it is clear that apart from nest site competition between cavity nesting birds, there are huge gaps in the knowledge of ecological impacts of the parakeets. These include impacts through mechanisms such as disease transmisison, acoustic effects, habitat alteration and foraging competition. Without further research, providing balanced and scientifically sound evidence into the ecological impacts of the rose-ringed parakeet in the UK, informed policy and mitigation strageties cannot be made. It is therefore important that knowledge of the status of the UK's population of rose-ringed parakeets is brought up to date through a population census and that further research is carried out on the potential ecological impacts of the population on native wildlife. In this thesis I address these needs by providing a current census and analysis of the population ecology of the UK's main population of parakeets in south-east England. I then focus on one potential ecological impact that parakeets may be having on native species, namely foraging competition. I focus on this because given the high occurance of parakeets at supplemental feeders in gardens, the broad diet of the species, the likelihood of high interspecific interactions and the potential for a variety of species to be affected, foraging competition provides an ideal system in which to investigate potential ecological impacts of rose-ringed parakeets on native species.

Thesis Aims

The aim of this thesis is to provide balanced scientific evidence of the UK's rose-ringed parakeet population status and ecological impacts (see summary diagram Fig. 1.1). There are 3 main objectives:

1. To quantify the size and distribution of the population.
2. To measure ecological impacts of the population on UK native biodiversity, using feeding competition with native garden birds as an indicator of wider impacts.
3. To assess the need for management of the parakeet population to reduce impacts on native wildlife

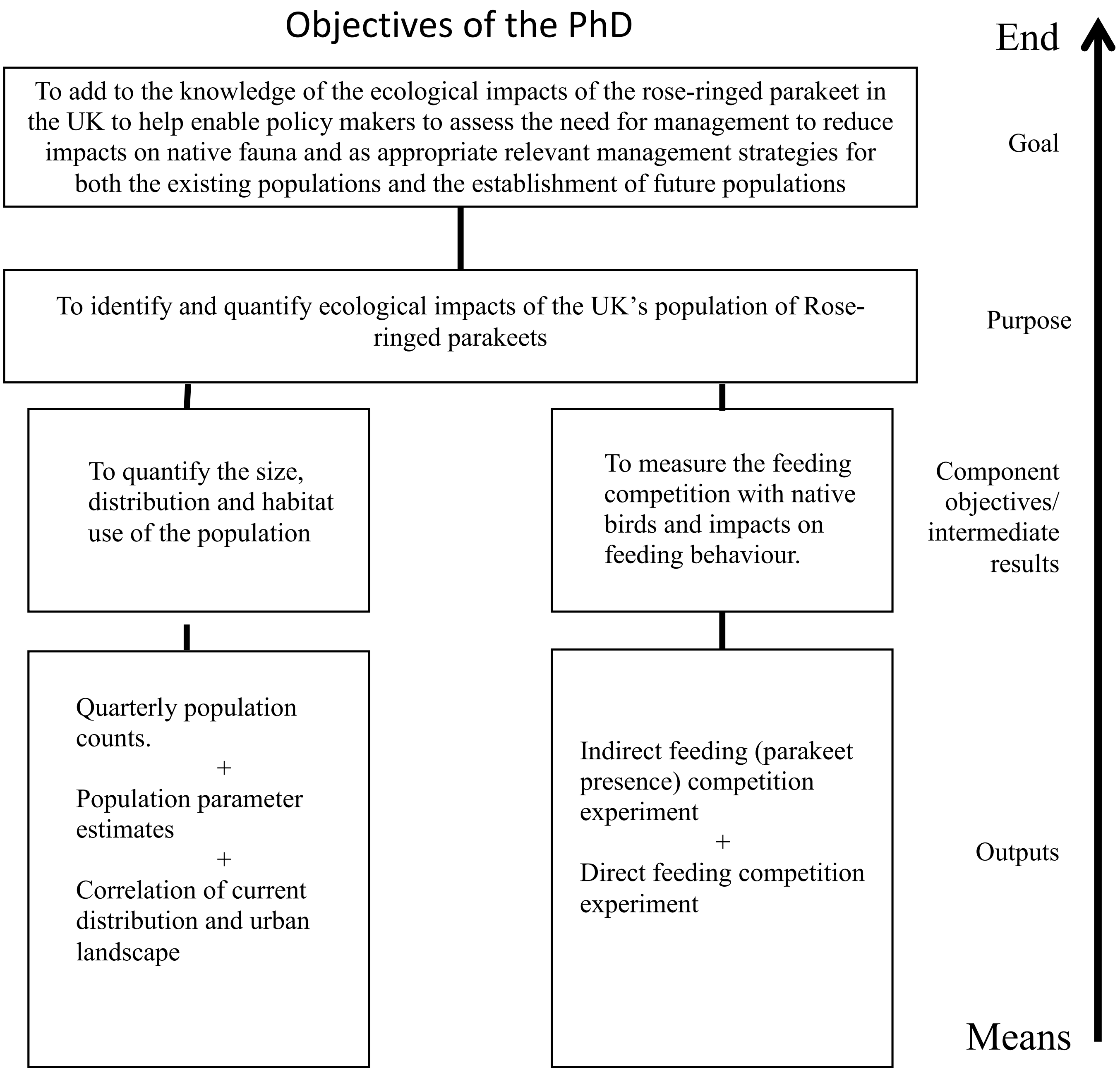

Figure 1.1: Summary of PhD objectives from outputs to end goal

Thesis Structure

In order to meet the objectives of this study I present my research findings in the form of six main chapters, three of which are data chapters (chapters 3, 4 and 5) and are written as research papers. In addition there is a general methods chapter (chapter 2), and a final discussion chapter (chapter 6) summarising the findings of the data chapters and their significance. In light of the findings, I also make suggestions for future research and a discussion on management recommendations of the parakeet population. These chapters are structured as follows:

Chapter 2 introduces the study system, including details on the study species and the study site. It then provides an overview of the general methods behind the whole study including details of general data collection methods used in the following data chapters.

Chapter 3 surveys the current population size in South East England using quarterly roost counts over three years and compares these results to previous surveys of the same population. The seasonal changes in roost counts within years are used to extrapolate population parameter estimates to explore reasons for the status of the current population. Reasons for the current population status are further explored by comparing the population distribution and land use.

Chapter 4 investigates the impacts of the presence of parakeets at a food source on the foraging behaviour of native birds. It does this using an experiment in gardens across Greater London and demonstrates that the presence of parakeets significantly affects foraging behaviour among native bird species, reducing the rate of feeding and increasing vigilance.

Chapter 5 investigates further the impact of parakeets on foraging behaviour of native birds by testing whether, in addition to the effects found in chapter 4, ifwild parakeets are competing directly for food with garden birds. It does this using a yearlong experiment restricting access of parakeets to supplemental food sources in urban gardens in London and tests how food consumption by native bird species changes with parakeet restriction.

Chapter 6 discusses the over arching implications of the findings of the previous chapters for our understanding of the parakeet population in south east England, and particularly the impacts on native species. It also considers how this improved understanding might have implications for policy and mitigation of invasive parakeets.

Chapter 2

Study System and General Methods

Study System

Study species

The study species of this thesis is the rose-ringed parakeet (*Psittacula krameri*) (Scopoli) 1769. It is a small parrot, of the Psittacidae family and order Psittaciformes, native to South East Asia and Sub-Saharan Africa (Juniper & Parr 2003). The species has bright green feathers, a dark red beak and distinctive long green and yellow tail feathers, which make it easy to identify in flight as well as a loud squawking call. It has an approximate length of 400mm, 173.37mm ±5.2wing length, tail length: 207.0mm ±28.9 (Butler & Gosler 2004) and males weigh: 142.2g ±9.0, females: 140.4±12.1g (Butler 2003). The species is sexually dimorphic, with the males being slightly larger and developing a full collar of rose-coloured feathers ,with a black bib along the underside of the collar and up to the lower beak, at the age approximately 3 years while females remain collarless and are indistinguishable from juveniles (Juniper & Parr 2003) (see Fig2.1).

Figure 2.1. a) Adult male and b) female or juvenile rose-ringed parakeet (Photo credit: H.Peck)

Study sites

This study focuses on the introduced population of rose-ringed parakeets in South East England (see Fig. 2.2 distribution). Small populations have established in other urban areas in the UK such as Manchester and Birmingham (see Fig.2.2), but at the start of this study in January 2010 reports from the media, Birdtrack (BirdTrack 2013) and sightings from members of the public that contacted me, all suggested that the populations elsewhere were too small (<100 birds) to warrant including in the population counts.

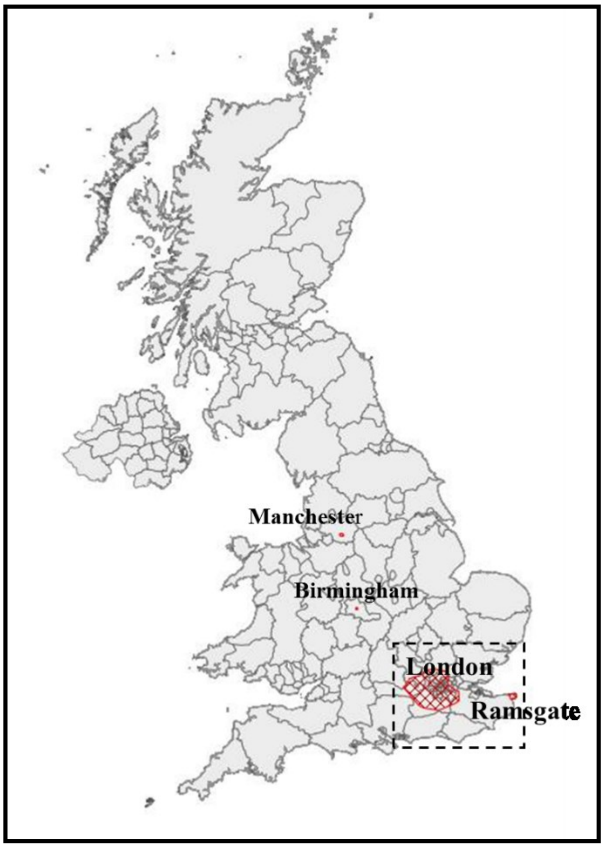

Figure 2.2 Map of Britain showing main areas of rose-ringed parakeet establishment in red and the area of study within the dashed square.

The parakeets in South East England are found in green spaces in urban areas, with most parakeets in Greater London and Ramsgate, Kent. They inhabit areas with trees in urban areas such as parks, gardens, but also in trees around infrastructure such as along railway lines and road ways. They are particularly associated with gardens with bird feeders and park land in urban areas with large trees suitable for breeding sites, particularly with species of ash (*Fraxinus sp.*) and oak (*Quercus sp.*) (Butler et al. 2013) .

Specific study sites used for research in this thesis were private gardens and roost sites. The method of location of the roost sites and recruitment of gardens are described in the general methods section.

Description of roost sites

Parakeet roosts are groups of trees which parakeets gather together at dusk and stay for the duration of the night, leaving at dawn. They vary in size, number and species of trees used and can be located in various landscape types (see Fig. 2.3). Of the twelve roosts monitored for this study, locations were in recreational fields and parks (n=6), common land (n=2), a disused gravel pit and site of nature conservation (n=1), trees lining railways (n=2), and trees lining a motorway (n=1), (see appendix Table S2.2 and Chapter 3 Fig. 3.3 for map of roost locations). All roost sites were characterised by being stands of trees in areas of open space (ie. at least one side of the roost trees had clear flight access for at least 100m). The species of trees used were predominantly poplar (*Populus* sp.), with five of the twelve sites being formed solely of stands of poplar trees, but other genera noted to have been used were willow (*Salix* sp.), sycamore (*Acer* sp.), birch (*Betula* sp.), cherry (*Prunus* sp.) and oak (*Quercus* sp.)

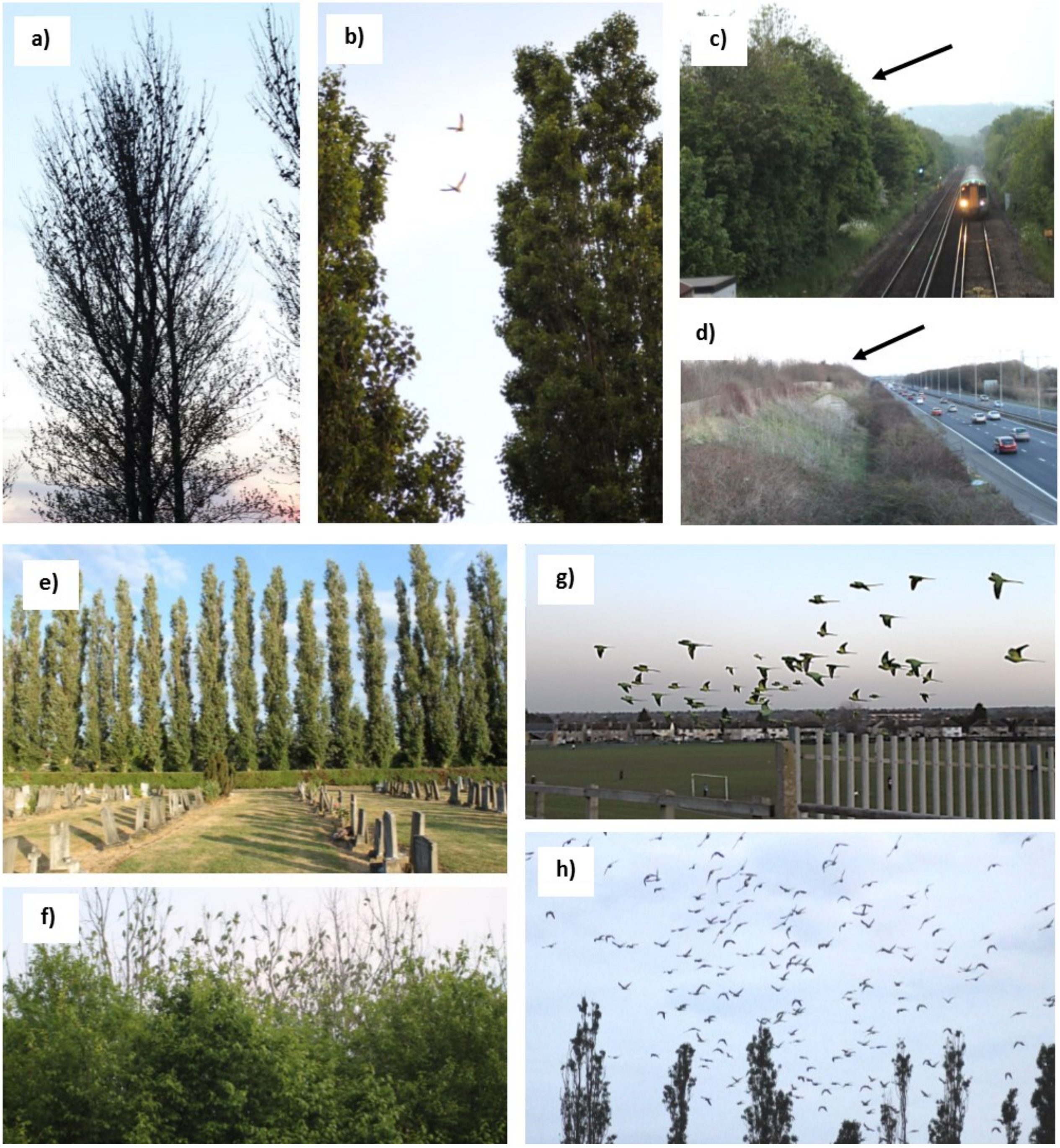

Figure 2.3. Variation in roost site characteristics: a) a roost tree in winter with parakeets visible on the branches, b) roost trees in summer with leaves obscuring parakeets on the branches, c) roost site next to a railway line and d) next to a motorway, arrows mark the position of the roost trees, e) a roost consisting of a stand of poplar trees (*Populus* sp.), f) a roost consisting of mixed species of trees, g) a small flock of parakeets flying in just above ground level to the roost, h) a large flock of parakeets flying in to the roost from above the roost height.

Description of garden sites used for the feeding experiments

All garden sites were private gardens of volunteers or the gardens of Imperial College's Silwood Park. All gardens were located within Greater London or the Home Counties. All gardens had previously had bird feeders in the garden providing seed, nuts and or fat balls to garden birds (see maps of garden locations in Chapter 4 Fig.4.1 and Chapter 5 Fig. 5.1)

General Methods

Here I describe details of general methods used throughout the thesis research, the specific details of which are in each of the chapters.

Public outreach and volunteer recruitment

The research throughout this thesis was dependent on the use of citizen science as a means to monitor the location of roosts sites, to collect behavioural data in the field, to crowd–source study sites, to maintain bird feeders used in the feeding experiments and generally to monitor the population distribution and parakeet activity.

In order to encourage members of the public to contact me with information and to recruit volunteers, public outreach was used. This was done through various methods (detailed below) but the main means was through creating a project identity specifically for this research in order to recruit volunteers and as an interface with the public. Project Parakeet was therefore set up and run online using www.projectparakeet.co.uk (see Fig. 2.4) and @projectparakeet on twitter and a facebook group (all no longer online).

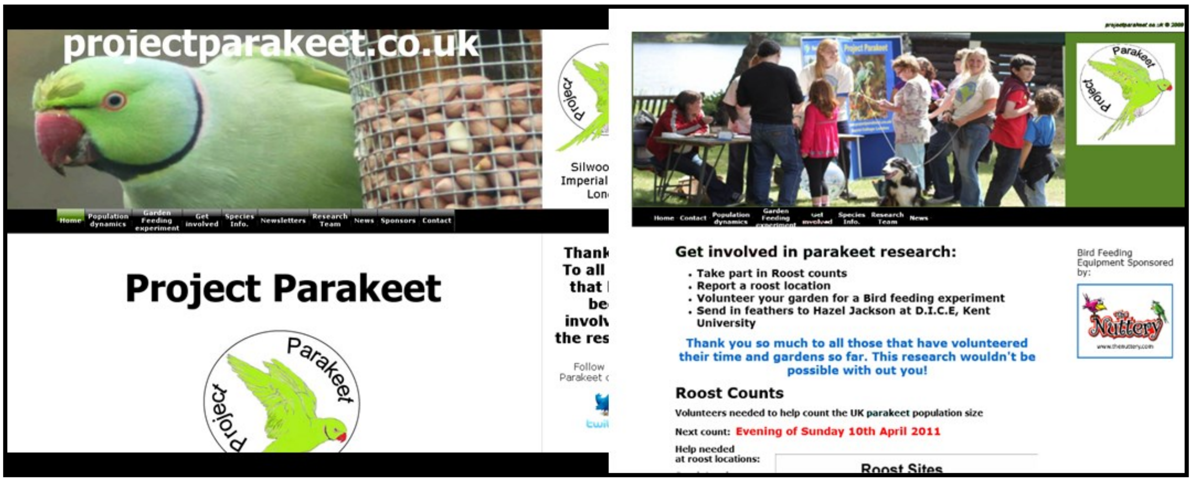

Figure 2.4 Screen shots from the Project Parakeet website (now offline)

In addition to outreach through 'Project Parakeet', the media were used to advertise the research to widen publicity and encourage people to contact with information. This included radio, newspapers, television (BBC's Country file), an online video (see Levey 2011) and through talks given both at birds clubs, community clubs and conferences. Meetings were also held with organisations to increase awareness of the research to interested stakeholders (The Royal Parks, The Crown Estate, BTO, RSPB, FERA). In addition a project stall with posters and information on the research was run at family open days (Osterley Park, National Trust; the Royal Military Academy, Sandhurst Family open day; Richmond Park open day).

In order to help motivate continued participation in the research, the volunteers were kept up-to-date with the research through a 6 monthly newsletter sent to all volunteers and through updates on the website and Facebook page, and by occasional emails.

Roost monitoring and counts

To monitor the population size of the parakeets in South East England over three years (January 2010 to October 2012), roost sites needed to be located and monitored, and the parakeets counted at each roost site simultaneously every three months.

Locating and monitoring roosts

In order to locate the roost sites, literature and grey material from previous surveys of the location of historical roosts were collated and records of more recent roost locations were acquired through a combination of advertising via local media campaigns, social media sites, the research website and contact with local bird clubs and landowners.

All roost locations required verification in person through a visit to the site to check that the site was an actual roost and not a pre-roost (where the birds gather before going on to the final roost location where they spend the night) or simply a daytime foraging site. This resulted in visits to thirty three sites, revealing twelve actual roosts and the rest pre-roosts or foraging sites. A site visit was also required to gain knowledge of the site characteristics for describing the exact location of the roost trees to the volunteers and to check that the site was suitable for volunteers to count at (ie. that there was public access).

Where only a vague area of a roost's location was reported, the roost site was searched for by examining satellite imagery and landscape use using Google maps (www.googlemaps.com) to check for areas of green space that could be used as a roost site. These areas were then visited and either driven or cycled round at early evening in order to find the direction of flight of parakeet flocks in the area, the flocks were then followed where possible to identify the final roost site. When roosts sites were checked at times of the day when the roost was not occupied (ie. any time during the day other than dawn and dusk), sightings of droppings and feathers under trees were used to confirm the exact trees used as roosts (see Fig. 2.5).

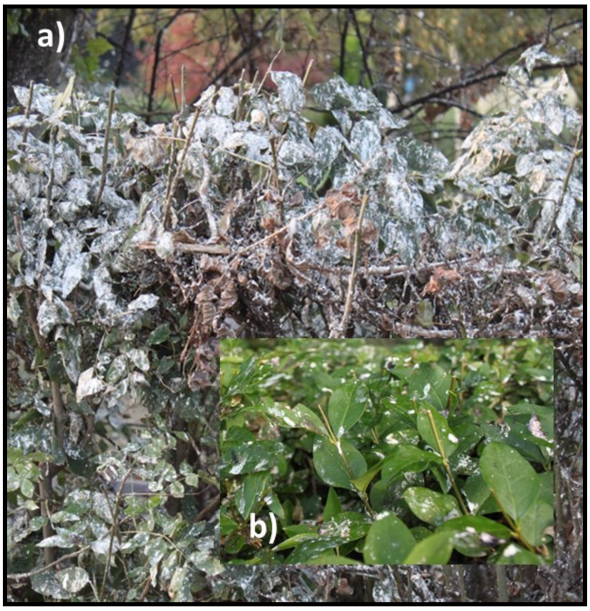

Figure 2.5 a) Extreme build-up of parakeet droppings under a large roost (>8000 birds), b) typical dropping coverage on foliage under a roost (Photo credit: H. Peck)

Once roosts were located, permission from landowners for access to the roosts on private land were requested and arrangements made for access. For example, the roost at Hither Green Cemetery was closed to the public after dark and so access had to be arranged with the Lewisham Council for every roost count in order for the cemetery gates to be unlocked.

Where possible, roosts were monitored a week or so before each simultaneous count every three months to check that roosts had not moved position. This was because some roosts moved to different trees in the area. For example of the twelve roost sites, nine moved location at some point over the three years or abandoned the site altogether. Any change in the directions of incoming parakeet flocks were also checked in order to locate the most advantageous position from which to view the incoming birds in order to count them.

Recruitment of volunteers for the simultaneous counts

Volunteers were recruited to count by continuous advertising for the need for volunteers via the general recruitment methods described above. In addition group emails were sent out to previous volunteers a month before each roost count to provide details of the date and time of the count. This also provided feedback on the numbers of volunteers available to be able to ensure enough people were allocated to each roost site in order to get good coverage of the site. For example the largest sites required at least eight volunteers, while the smallest could be counted with two.

Roost count volunteers were emailed a detailed description of the roost site, a map with details of the position of the roost trees, the likely direction of flight of the incoming parakeet flocks, information on public transport and access to the site, a detailed methods sheet, and a data collection sheet. At least one experienced volunteer (ie. someone that had counted at the roost before) was assigned to each roost. A mobile number was also provided for volunteers to contact me with any questions or problems during the count.

Details on counting the parakeets

Once at a roost site, volunteers coordinated with each other so that all flight directions of incoming parakeet flocks would be viewed by at least one volunteer. This meant volunteers were spread out around the roost trees, at least 20m away from the trees to be able to get a clear view of the sky. Where enough volunteers were available they counted the flocks of incoming birds in pairs, although this was done without comparing counts to avoid bias in count estimates. This was to allow comparison of count estimates at a later date to get an idea of the variance in count estimates but also to provide the opportunity to average counts to reduce error in estimates.

Birds were counted individually for flock sizes under 10 and then counted in multiples of increasing numbers depending on the size of the incoming flocks, for example, some flocks could be fewer than 50 birds and so counted in blocks of 10, while others could be as many as 500 and so required counting in blocks of at least 50 birds (see Fig. 2.3 g and h for example of different flock sizes).

An attempt was also made to count the parakeets in the trees once they had stopped flying in to the roost. This was only possible in roosts where all trees were visible (i.e. three of the roosts were clumped so trees at the centre of the roost could not be viewed, for example see Fig. 2.3 f). As the parakeets do not usually settle in the trees until the light has started to fade, tree counts were only possible on nights where the light was still bright enough to be able to distinguish individual birds in the trees. During the July and October counts, the leaves on most of the roost sites trees made it too difficult to view the parakeets so that tree counts were not possible (see Fig. 2.3 a and b).

Volunteers either emailed or sent copies of their count sheets in the days after the simultaneous count. An email reporting the roost totals was then sent to all volunteers to let them know the results and to thank them for participating.

<u>Behavioural data collection for garden bird feeding behaviour experiment (chapter 4)</u>

Captive parakeet and great-spotted woodpecker pair husbandry

For the behavioural feeding experiment (Chapter 4), a captive pair (male and female) of parakeets and of great spotted woodpeckers (*Dendrocopos major*) were required to measure the behaviour of garden birds in their presence.

The pairs of birds were caught using mist nets by a BTO licenced ringer and kept under a Natural England (NE) licence (number 20101145). The woodpecker pair were caught at Silwood Park, Ascot during a routine ringing survey and the parakeets were caught in a garden in Richmond, London by using an apple to entice them near the mist net.

The birds were kept as pairs in two aviaries at Silwood Park. These were wooden framed aviaries with wire mesh walls. The aviaries were large enough that the birds could fly around (4m long, 2m wide, 2m high). They were half covered to provide shelter from the wind and rain and each bird was provided with a wooden nest box with sawdust to sleep in and hide. Enrichment was provided by placing perches in the form of branches strung across the inside of the aviaries. These were moved around and replaced regularly and food was placed in different parts of the aviary to require the birds to find it to provide. Fresh food and water were provided daily and bird vitamin supplements were added to the water once a week. The birds were weighed every 3 days to check for any changes in weight and examined in the hand to check for body condition.

As rose-ringed parakeets are a popular pet in the UK access to information on keeping them in captivity was abundant so advice on husbandry was easily acquired. However, no information could be found on keeping great-spotted woodpeckers in captivity, or in fact on keeping any woodpecker species. Therefore the aviary was kept as natural as possible to conditions in the wild, which involved providing rotten logs with bark still attached and branches of trees. The woodpeckers were fed with both live and freeze dried mealworm (*Tenebrio molitor*) and greater waxmoth larvae (*Galleria mellonella)* and these were placed where possible in to holes in the logs and branches. The woodpeckers were found to frequently peck at the logs, resulting in them being reduced to wood chips and so logs were replaced regularly. Peanuts were also provided in a hanging log feeder. Other foods were also provided including live and dead crickets and raw eggs but appeared to not be eaten. The woodpeckers were able to chip pieces out of the wooden frame of the aviary so the aviary was reinforced with wire mesh on the inside of the wooden frame. The parakeets were provided with a variety of bird seeds, peanuts, fruit (particularly apples), vegetables, cuttlebone and branches with blossom when available.

The birds were transported separately to and from garden experiment sites in carry cages, these were provided with perches, water bowls and food and covered with a waterproof sheet to shield from light and weather and to minimise stress. As required by the NE licence, after all experiments were completed, the woodpeckers were given a two week soft-release at Silwood Park with open access to the aviary for food, water and shelter and the parakeets were re-homed in captivity.

Experimental set up in gardens

Gardens were recruited via the methods detailed earlier. All locations of sites were therefore constrained by the location of the garden owned by those that volunteered (see Chapter 4 Fig.4.1 for garden locations). This meant that gardens were turned if they weretoo close to each other to avoid measuring behaviour of the same birds in different gardens.

The recruitment of volunteers was also restricted by the need to find parakeet free sites within 70km of London. This proved difficult due to the distribution of parakeets across most of Greater London, therefore leaving few areas that were still parakeet free. This meant that extra effort had to be made to recruit parakeet free gardens. This was done by targeting publicity in areas that were known to be still free of parakeets.

Volunteer requirements were kept to a minimum, with them simply providing access to their garden, once to install the feeders in the garden and then two weeks later to carry out the experiment. They were also asked to keep the feeders topped up during the two week interim with black sunflower seed and peanuts provided by the project. Henrietta Pringle or myself carried out the feeder instalment and carried out the experiment in each of the gardens.

The bird feeders used in the experiment were two squirrel proof metal caged feeders, one designed for peanuts and the other for bird seed. Squirrel proof feeders were required due to the disruption that would be caused by a squirrel visiting the feeder during the experiment (see the bird feeders Fig. 2.6). The feeders were donated by the Nuttery (www.nuttery.com) for use in the research.

The experiment was set up during the day at a time convenient for the garden owner but also when there was enough hours of light available to fit in the three hours of experimental treatments required. Weather conditions were checked before carrying out the experiment to avoid conditions that would affect the feeding behaviour (ie. very strong winds and heavy rain were avoided). Feeders were placed in a position that was visible from the house or shed so that the equipment could be monitored at all times during the experiment without disturbing the garden birds (see Fig. 2.6).

Figure 2.6. Garden bird feeding experiment set up. Bird feeders with peanut and sunflower seed, a shepherds' hook feeder pole, cage with captive woodpecker on tripod stand. A video camera was placed on a tripod 2m from the feeders to record the birds feeding.

Recruitment of volunteers for extraction of behavioural data from the video files

The video camera data collected from the experiments resulted in approximately 120 hours of video footage needing to be watched to extract the feeding behaviour data of the garden birds. Depending on the number of birds visiting the feeder, each 20 minute video took from 1 hour to 7days to process.Therefore, volunteers were recruited to help extract the data from approximately a quarter (n= 77) of the videos. This was done by emailing biology students and graduates at academic institutions to recruit volunteers wanting research experience. Detailed instructions on the methods needed and a sample data sheet with example data, were sent by email to each volunteer and where needed methods were talked through by myself on the phone. Video analysis software AVS video editor 6.3 (www.avs4you.com) was downloaded by the volunteers to ensure exactly the same methods were used. All volunteer data was checked for errors by myself by going through 5 minute sample sections of videos and by scanning through all the data. Video files were downloaded by volunteers using Imperial College's online file sharing software.

The parakeet feeding restriction experiment (Chapter 5)

Recruitment and training of garden volunteers

The recruitment of gardens for use as sites was carried out in the same way as described in the previous experiment and in Chapter 4, however some previous volunteers also volunteered for this experiment. In addition a refund of £70 towards bird seed costs was offered to reduce costs for the volunteer (see Chapter 5, Fig. 5.1 for map of garden site locations). Six months in to the experiment , volunteers were also sent a 'halfway there' report of the results gained from the first six months of the experiment (see Appendix S1.1) to encourage continued participation in the rest of the experiment.

For this experiment the volunteers carried out 20 minute weekly observations of the bird feeder for an entire year (December 2011 to December 2012). Volunteers were provided with a file binder with information on the research, instructions on measuring the seed refills of the bird feeder, the observation methods, a sample observation sheet (see Fig 2.7) and a year's worth of observation sheets to record the data. The methods were also run through in person with each volunteer by myself ,and the volunteers' bird species identification skills were checked by talking through the birds they were likely to see and providing a link to an online bird identification site (http://www.rspb.org.uk/wildlife/birdidentifier/).

Example form

Weekly 20 min Observations

Observer: *Joe Bloggs*
Date: *29/09/2011* **Time:** *4pm*

Weather: *overcast, light drizzle, very windy*

Food top up since previous week (circle): 0, 1/4, 1/2, Refills 1, 2, 3, 4, 5, (for the grey feeder please only fill half way and count that as a full Refill).

Observations over the past week
Days seen parakeets (circle): 0 / 1-2 / 3-5 / 6-7 **Max number at once:** *5*
Parakeet and plants: *6 parakeets seen eating beech nuts from the tree at the end of garden. Handful of beech nuts scattered on floor*
Parakeets and other wildlife: *Jackdaws mobbed a parakeet in a tree*
Other observations: *Next door's cat preventing birds feeding half the week. Jackdaws raided the feeder and ate all the seeds.*

Species	Max Number at one time	Total number of visits made by the species
Blue tit	6	15
Great tit	5	13
Nuthatch	2	4
Goldfinch	1	1
Robin	1	1
Greater Spotted Woodpecker	1	1
Parakeets	2	2
Jackdaw	1	1

Figure 2.7. An observation sheet with an example 20min weekly observation

The volunteer data were collected through an online questionnaire using Questionpro (www.questionpro.com). For those volunteers without internet access or unwilling to use the online form, the data sheets were sent direct to me in the post.

Experimental set up and equipment

The experiment involved using two types of bird feeders each separately for 6 months: a parakeet accessible feeder and a parakeet restrictive feeder. Therefore gardens were visited twice, once to install the first feeder type and to explain the protocol for weekly bird feeding observations to be carried out by the volunteers, and again. But also six months later to install the second feeder type. This provided the opportunity also to provide personal feedback to the volunteers and encourage continuation of the weekly observations.

The same squirrel proof bird seed feeder provided by the Nuttery was used in the experiment as the parakeet 'accessible' feeder (see Fig. 2.8a). The second bird feeder, the parakeet 'restrictive' feeder, was sourced from ebay (www.ebay.co.uk, the only details specified were: Made in China, Product code HW2089, Imported by Eurotrade (Wholesale) M8 8QJ, see Fig 2.8b). What was left of the stock was bought for the experiment and it appears to be no longer manufactured. The 'accessible' feeder was adjusted to make the number of access points for the birds to the food exactly the same as the 'restrictive' feeder, by removing the access to the second set of access points to the food in the centre of the feeder by taping them shut, therefore both feeders only had two access point at the bottom of the feeder. These feeders differed in the width of the wire mesh gaps and the distance of the wire mesh to the feeder dispenser at the centre of the mesh cage (the 'accessible' feeder dimensions 20.3 x 20.3 x 34.3cm, size of mesh squares 5.2cm x 2.8 cm, distance from mesh cage to food 6 cm, the 'restrictive' feeder dimensions 21.2 x 21.2 x 23.2 cm, size of mesh squares 2.6cm x 3.55cm, distance from mesh cage to food 6.5cm , see Fig. 2.8). Small garden birds could still access the food in the restrictive feeder but the larger size of the parakeet meant it was extremely difficult to reach the food. However, a few individual parakeets did manage to access the feeder by squeezing their heads through the mesh, resulting in

22 out of 583 observations having a parakeet access the food from the restrictive feeder in a total of 6 out of 33 gardens. This resulted in the feeders being 'restrictive' rather than completely parakeet proof. By reducing the gaps in the mesh any further, other bird species would have also been restricted from accessing the food. Both feeder types were reported to have been accessed by squirrels and parakeets on a few occasions by lifting the lid off the feeder. This resulted in the addition of wire ties being applied to the lids to secure them down.

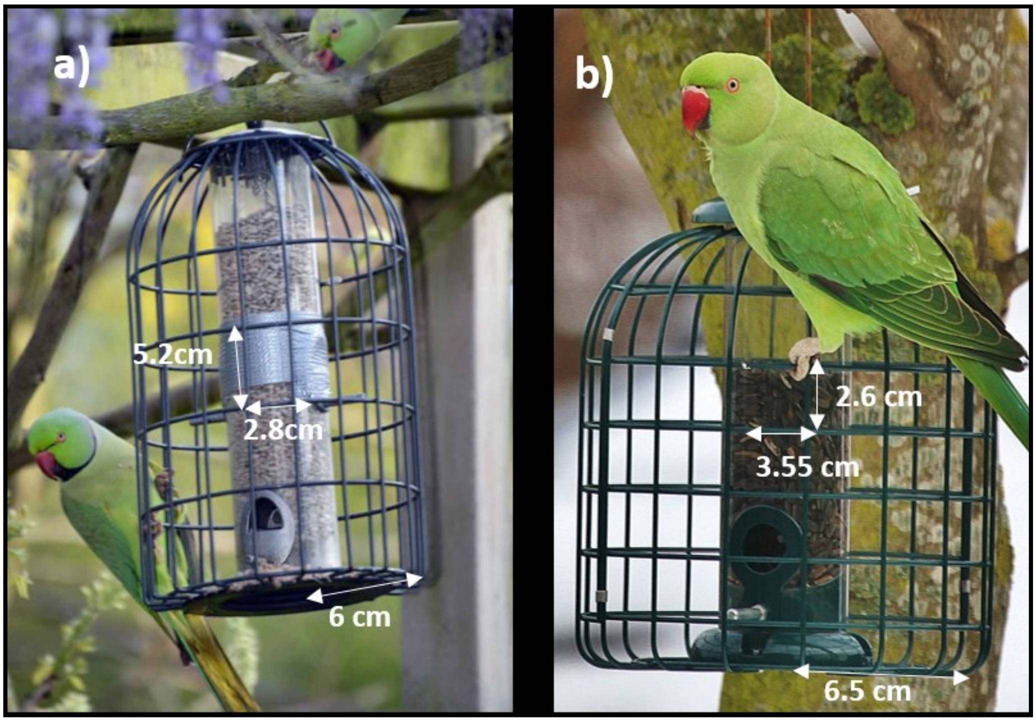

Figure 2.8. a) Parakeet 'accessible' feeder (Photo credit: Martin Purkis) and b) parakeet 'restrictive' feeder (Photo credit: Richard Kinzler)

Chapter 3

Population ecology of the rose-ringed parakeet in South East England

Abstract

The rose-ringed parakeet (*Psittacula krameri*) has been established in South East England since at least the 1970s and has been increasingly establishing in urban areas across Europe. As an introduced species and an agricultural pest in its native range, it has the potential to have ecological and economic impacts and therefore up-to-date information is needed on the population size, population growth and potential distribution to inform any mitigation strategies. However, the last full population count was conducted in 2002, when the population was estimated to be around 5500 birds and growing rapidly. Using simultaneous roost counts we measured the population size in South East England at quarterly periods over three years from 2010 to 2012. We used the seasonal changes in population size at the roosts to extrapolate population parameters to investigate possible reasons for lack of change in the population size over the three years. We then used presence-absence distribution data and general land use information to investigate if the land use of the areas where parakeets are currently present can explain the current population status. We show that the population has grown by an average of 26% per year since 1996 and the population now comprises over 30,000 individuals and appears to be currently stable in the surveyed area. Population parameter estimates show that the number of breeding individuals has remained stable and non-breeding individuals increased, a trait often associated with populations that are reaching capacity. We show that although the distribution has continued to increase outside of Greater London, the spread has

slowed down and that the spread may be slowed by restriction to the urban landscape. The implications of these findings are that the increasing establishment of non-native parakeet populations elsewhere in the UK and Europe may have the potential for similar rapid population growth but that this may be restricted to urban areas.

Introduction

Invasive species can have devastating impacts on native wildlife (Human and Gordon 1996; Townsend 1996; Lowe et al. 2000; Bertolino and Genovesi 2003; Wiles et al. 2003; Gurnell et al. 2004) and cause economic damage (Pimentel et al. 2001; Vilà et al. 2010). Although the majority of non-native species introductions do not end up causing detrimental impacts (Mack et al. 2000; Manchester, Sarah and Bullock 2009) once the populations have established enough for impacts to be detected it can be extremely difficult and costly to mitigate them (Kolar and Lodge 2001; Puth and Post 2005). In order to determine the most effective mitigation strategies and to predict the likelihood of future impacts to prevent further damage, detailed knowledge of the distribution, population size, population demographics, population growth rate and environmental factors in establishment success is required (Gurevitch et al. 2011). Therefore the monitoring of non-native species introductions is essential to provide knowledge for putting mitigation into action as soon as possible and for reducing potential impacts of establishing populations elsewhere in the future (Mack et al. 2000).

The rose-ringed parakeet (*Psittacula krameri*) has been present as an exotic species in South East England since at least the 1970s (Lever 2005). It is as an agricultural pest in its native range (Dhindsa and Saini 1994) and so has the potential to cause economic impacts, while its broad diet (Clergeau and Vergnes 2011) and use of tree cavities for breeding (Newson et al. 2011) means it has potential to compete with native species for resources. Despite this, before this study, estimates of the population size of the species in South East England were nearly a decade out of date and there was little understanding of the population demography and how the population size and distribution might change in the future (FERA 2009). Without greater understanding of the population status it is not possible to put in to context any impacts that the species may be having and therefore to what extent mitigation strategies might be needed. Here I will review the history of establishment of the parakeet population in South East England and how the parakeet population size, growth and habitat preference has previously been studied. I will summarise the missing knowledge of the population and then discuss how I aimed to address this.

The first successful breeding of rose-ringed parakeet in the wild in Britain was reported in 1971 in Surrey (Lever 2005). Parakeets are reported as breeding as long ago as 1855 in Norfolk but the population did not persist (Butler 2003). The source of both of these first breeding populations in the wild is unknown but they are likely to have been pets that had escaped or been released. Introduced populations of Rose-ringed parakeet are also found across Europe, where at least 65 separate populations have established, with higher establishment of populations at the end of the 20th century, indicating that the European population is increasing (Strubbe and Matthysen 2009).

The rose-ringed parakeet has been a very popular pet in the UK, with an estimated minimum of 802 reared per year in captivity and at least 20,105 held in captivity between 1990-2004 (Fletcher and Askew 2007). Analysis of CITES import data show 24,480 rose-ringed parakeets were imported between 1975 and 2005; the highest numbers coming from Senegal, India and Pakistan (CITES Secretariat 2013). It is also a long-lived species, with a report of it living up to 34 years in captivity (Brouwer et al. 2000), which could be a driver for the release of captive birds in to the wild. It has been proposed that this popularity as a pet, resulting in frequent escapes, is very likely to be the source of new populations occurring in separate parts of the country, and occasional additions to established populations elsewhere (Fletcher and Askew 2007).

For the period 1995 to 2011 the observed population growth rate of the rose-ringed parakeet in England as shown by the Breeding Bird Survey (BBS) is the highest observed in current UK bird populations with a 1058% increase. (95% confidence interval: 395-4191%) (Risely et al. 2013). Although BBS data could be used to produce estimates of population size, the confidence intervals around these would be large. The direct estimation of population size is likely to give a more accurate answer and hence be important in developing parakeet management and mitigation strategies.

Parakeets are highly visible, being brightly coloured and big enough to see clearly (length of 40cm).They are also highly vocal, frequently calling loudly while flying and perching, and have distinct long tail feathers making them easy to identify from other birds species in the UK in flight. This means they are very easy to detect and distinguish from native species. The parakeets roost communally in trees at night gathering together at dusk and finally settling together in specific trees (Pithon and Dytham 1999). This behaviour provides a means to directly estimate the minimum population size through counts at all roosts, performed simultaneously to control for any day to day movement of birds between roosts (Pithon and Dytham 1999).

To my knowledge, there appears to be no record of the use of simultaneous roost counts for estimating population sizes of species other than the rose-ringed parakeet, except for the

Rodrigues fruit bat (*Pteropus rodricensis*) on Rodrigues Island, a small island in the Indian Ocean (Powell and Wehnelt 2003). Other parrot species population sizes have been counted using roost counts, for example green rumped parrotlets (*Forpus passerine*) in Venezuela (Casagrande and Beissinger 1997) and Red-tailed Amazons (*Amazona brasiliensis*) in East Brazil (Cougill and Marsden 2004), but these have not been simultaneous. This lack of use of simultaneous roost counts is likely be because of the logistical difficulties in covering large areas, detecting all roosts and in needing enough people available to count at each roost location at the same time (Casagrande and Beissinger 1997).

The first simultaneous count of the UK parakeet population was carried out in September 1996 and was repeated monthly until September 1998. Of these counts, only three were full counts, with all the others having one or more roosts missing. These full simultaneous counts took place in October 1996, August 1997 and September 1998 and totalled 1508, 1880 and 2060 respectively (Pithon and Dytham 2002). Given that only three full simultaneous roost counts over three years Pithon et al (2002) concluded that apart from determining the current population trends, there was limited use for the data to examine the population dynamics (Pithon 1998). The population has not been counted simultaneously since 1998 although partial counts were carried out between 1998 and 2002 (Butler 2003) with the highest partial count being around 5500 birds, (for details of all past counts see Appendix Table S2.1).

Survival rates in the wild would be needed to make any projections on future population change. Without sufficient mark-recapture data, mortality rates of parakeets are unknown. Butler (2003) attempted to overcome this lack of survival data by using survivability data from literature of similar parakeet species, Monk parakeet, (*Myiopsitta monachus*) and Puerto Rican parrot, (*Amazona vittata*). Population projections were then modelled for the time period 1997 to 2001 and the model with the species survivability which projected the closest fit to the population in 2001 used (Butler 2003). Using these mortality estimates, the count estimates and fledgling success estimated from regular monitoring of 108 nests, a population viability analysis was run which predicted a growth rate of 30% per year between 1997 and 2001 (Butler 2003).

As well as providing a means to monitor the changes in annual population size, monitoring of seasonal changes can allow some population parameters to be investigated, including aspects of demography, breeding success, mortality and roost movement (Keijl 2001; Butler 2003; Strubbe 2009). There is radio tracking evidence that during the breeding season, breeding females stay on their nest at night whilst males return to the roost (Butler 2003; Strubbe and Matthysen 2011). In support of this, past studies also found that there was a drop in parakeet numbers at roosts in the Spring, followed by the largest parakeet numbers being recorded in the summer months (Pithon and Dytham 1999; Butler 2003). This is consistent with breeding females being absent during the spring but returning to the roosts with the new fledglings in the summer (Butler 2003). This provides a potential means to estimate the number of breeding pairs in the population by monitoring the decrease in numbers at the roosts during the breeding season (Keijl 2001; Butler 2003; Strubbe 2009). Therefore, by using full simultaneous counts to give seasonal changes in the population size and the identification of the number of females missing from roosts during the breeding season, in combination with estimates of mortality, a simple analysis should allow quantification of the number of breeding individuals in the population, as well as juvenile recruitment, to be calculated.

A 2009 investigation into the distribution of the Greater London parakeet population found it to be mainly distributed in urban and sub-urban areas, but that there appeared to be no distinct barrier in the landscape that has prevented parakeet spread (FERA 2009). It was concluded that more detailed knowledge of parakeet habitat requirements is needed to make more detailed predictions of the potential spread of the population. Studies comparing distribution and landuse of rose-ringed parakeet populations in Europe have found that parakeets appear to prefer habitats neighbouring urban areas near green space such as parks and forests with trees of unequal age, but avoid agricultural areas and areas of coniferous forest (Strubbe and Matthysen 2007; Strubbe and Matthysen 2008; Strubbe and Matthysen 2009). This has been hypothesised to be because the parakeets utilise food sources in urban areas such as garden bird feeders and exotic plants in parks and gardens (Strubbe and Matthysen 2009; Clergeau and Vergnes 2011), while needing to be near areas of old trees with cavities for breeding sites (Strubbe and Matthysen 2009; Strubbe and Matthysen 2011). This poses the question of whether patterns in distribution of the Greater London population are related to land use. This would be crucial in helping to predict how the distribution of the parakeet popualtion might change in the future.

Until this study, there had been no complete census of the parakeet population in South East England since 2001, so the current population size was unknown. The best estimate of 30,000 was based on the predicted growth rate of 30% per year between 1997 and 2001 (Butler 2003; Tayleur 2010). The BTO/JNCC/RSPB's British Breeding Bird Survey and county recorders have provided some means of monitoring population trends and distribution through recorded presence and count reports (Risely et al. 2013), and Bird Track records provide an up-to-date record of parakeet sightings across the UK. In addition there is potential to exploit quarterly simultaneous roost counts as a method to estimate population parameters without the need for time intensive field work such as daily monitoring of multiple nests in order to measure fledgling success.

In this study I address both the need for an up-to-date survey providing a direct estimate of parakeet population size and an estimation of population parameters. I then combine the up dated population estimate with previous estimates of size and distribution to explore longer-term trends in population size and distribution, and investigate how these trends might be explained by land use patterns.

Methods

Data collection

Simultaneous counts were conducted of the South East England population (Greater London and Ramsgate in Kent) across three annual cycles from 2010 to 2012, allowing us to calculate the minimum current population size and estimate an average growth rate from 1996 and 2010 and between 2010 and 2012. Historical counts between 1996 and 2006 were collated from the literature (Pithon and Dytham 2002; Butler 2003) and county recorders (see Appendix Table S2.1).

Roosts were located using information from previous surveys to locate historical roosts and a combination of advertising via local media campaigns, social media sites, the research website and contact with local bird clubs and landowners (see Appendix, Table S2.2 for details of past and present roost locations and Chapter 2 for methods). This yielded thirty-three potential roost sites. Initial surveys at these locations identified twelve of these as roost sites, with the rest being pre-roosts. A roost was defined as a site where the parakeets remained in the trees after dark. Pre-roosts were those where the parakeets collected but then left before dark. All roost sites were monitored between survey dates as the use of some sites by parakeets was ephemeral during the year. Similarly, contact with local clubs was maintained and reports of roost locations from members of the public were checked during the survey period to identify any new roosts.

Counts were conducted simultaneously at all roosts at three-monthly intervals from January 2010 to October 2012 using a network of volunteers (see Fig 3.3 and Appendix Table S2.2 for locations of roosts). The same methodology used in previous roost surveys (Pithon and Dytham 1999),was followed, allowing a comparison of the roost count estimates to be made. Volunteers arrived at roost locations at least 40 minutes before sunset to ensure they were able to record first arrival of the roosting parakeets and to locate the best vantage points. Incoming birds were recorded from all directions, this was done by allocating vantage points around the roost site so that that all birds incoming from all directions were clearly visible. Boundary divisions were allocated for each vantage point to ensure volunteers did not overlap counts. Where sufficient volunteers were available they recorded in pairs or more, standing within a few metres of each other, and recording birds flying within the same defined boundaries of location and direction of flight. This was done without reference to each other so as to avoid counting bias. The time and direction of flight of each incoming flock was recorded to allow later comparison of observations to check for any large variation in numbers recorded between paired observers. If incoming flocks became too large to count individual birds, counting was done in multiples of 5s, 10s, 50s and 100s. Once the parakeets had settled in the trees, where light was permitting, the parakeets were then counted a second time by each volunteer. As all roost trees were deciduous, this second method was possible in the winter months after roost trees had shed their leaves.

Two roosts were identified subsequent to the start of the survey in January 2010; Hersham in February 2010 and Mitcham in November 2010. Bird club counts were available for Mitcham in January and April 2010. Counts for Hersham in January 2010 and Mitcham in July and October 2010 were estimated by extrapolating the average proportional difference in count size to the previous or following count from 2011 and 2012 (see Appendix Table S2.3).

Observer error

Observer error can be quantified by ensuring that counts are taken by paired or multiple observers (Freckleton et al. 2006). Having more than one observer counting the same individuals can increase the robustness of population estimates, and reduces the likelihood of missing individuals (Utzurrum et al. 2003). A study of observer heterogeneity in detecting forest birds found that averaging counts from pairs of observers compensated for much of the variability introduced into estimates of population sizes owing to observer heterogeneity (Cunningham et al. 1999). Using mean counts taken by more than two observers can help reduce observer error further (Cunningham et al. 1999).

Therefore where possible, roost counts were calculated by averaging counts taken by multiple observers (two or more) per roost. The data were scanned for direction of flight and flock size of the birds to check for double counting.

Observer error was tested for using counts from January 2010 to October 2012, where two independent observers counted the same birds as they flew into a roost. Where independent counts were taken by more than two observers, two counts were chosen at random. A linear model was fitted and this revealed a strong one-to-one relationship between independent observers' counts at each roost (slope= 0.94, S.E.= 0.036, t-value= 26.23, $p< 0.001$, d.f.=37, R^2 =0.95, see Fig.3.1) and indicates consistency in counts across observers, with a mean percentage difference between paired observers of 12.89% (standard deviation ± 9.49%). The two roost count methods (flying count and tree count) were also compared by fitting a linear model and were also found to have a strong one-to-one relationship (slope= 0.94, S.E.=0.040, t-value= 23.30, $p < 0.001$, d.f.=23, R^2 =0.96, see Fig.3.1). In both cases model errors were checked for normal and constant variance. Throughout the analyses we therefore used mean observer counts where available, and as the flying count was possible year round, we used this for analysing the number of individuals unless there were occasions where the view of incoming birds from certain directions was obstructed, in which case a tree count was substituted (n=2).

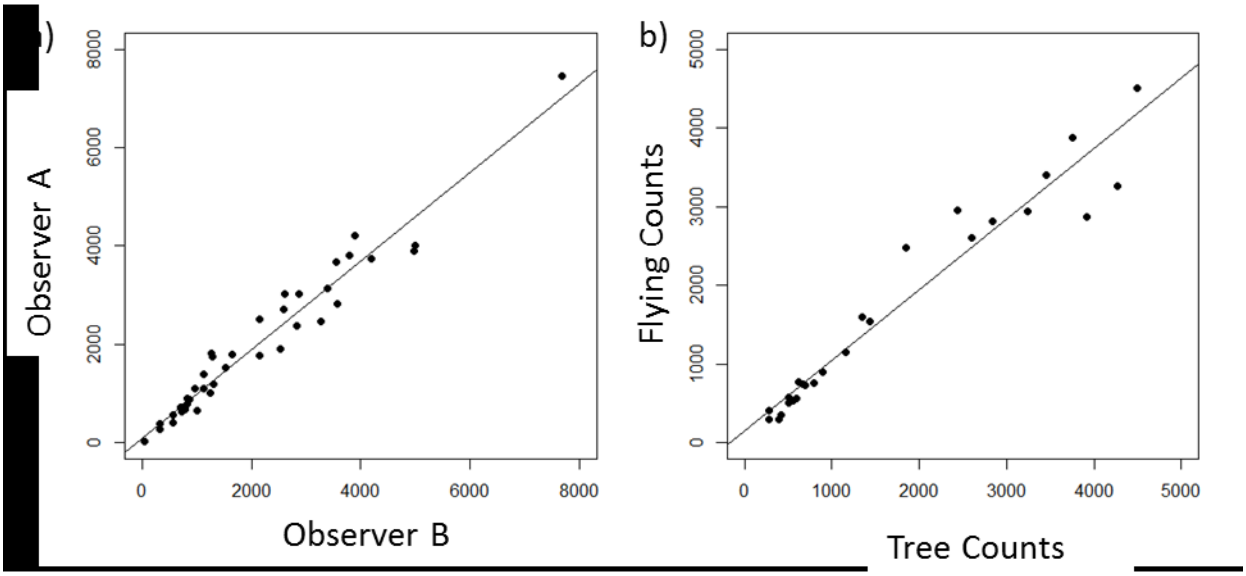

Figure 3.1 Number of rose-ringed parakeets estimated by **a)** observer A and observer B in each roost January 2010 – October 2012, and **b)** using the flying method and the tree method January, April, October 2010-2012 (July counts are omitted due to leaves obscuring the birds for the tree count). The lines represent the one-to-one relationship estimated by fitting linear models.

Previous work by Butler (2003) modelling the population dynamics of the same parakeet population in South East England between 1997 and 2001 separated the Greater London and Ramsgate populations for analysis as they are isolated geographically from each other, and do not necessarily have the same demographic structure, with an apparent difference in the age of onset of breeding, and differences in rate of population growth (Butler 2003).

Between 2008 and 2011, parakeets have been increasingly observed in the areas separating the two populations (Kent Ornithological Society 2013). It is therefore possible that there has been some mixing of birds between the two populations, but I did not find any roosts located between the Ramsgate and Greater London roosts and the distance to the nearest known roost is 97km from Ramsgate (see Fig. 3.4). Therefore for the purpose of this study, the Ramsgate roosts have been analysed separately from the Greater London population.

Analysis

Population growth rate

Counts were summed for each roost to provide a total population size every three months. This provided quarterly population size estimates across the three years January 2010 to October 2012. I estimated the annual population growth over the 14 years between 1996 and 2010 using the highest total count available in 1996 as the starting population size and in 2010 as the final population size.

Annual demographic measurements

Parakeet population processes of breeding and juvenile recruitment into the population occur at discrete times of year. This allowed me to exploit variation in total counts between each quarter to estimate demographic parameters, (see Fig. 3.2). During April breeding females do not return to the roost, allowing me to estimate the number of breeding pairs as the difference between January and April counts. By July breeding females plus new juveniles return to the roost, allowing me to estimate the number of juveniles recruited into the population, and so population fecundity. Between each quarter it is also important to account for adult, yearling and juvenile mortality. Fig. 3.2 below shows how the quarterly counts vary and Fig 3.3 shows how this variation is used to model the population parameters.

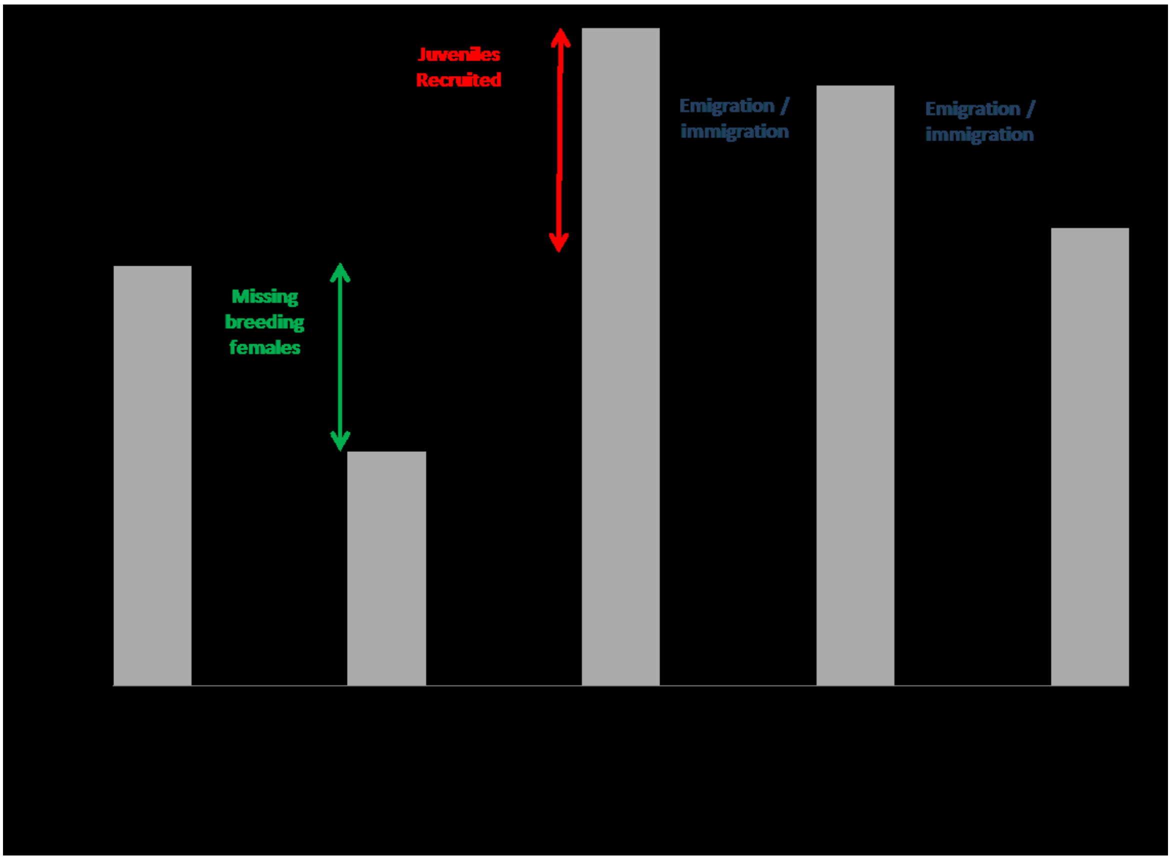

Figure 3.2. Bar plot of the expected pattern in differences in total count size for all roosts at yearly quarters from January to January. The causes for the differences between quarterly population counts and the parameters which can be calculated from these differences are illustrated. Fecundity is calculated from the number of missing females in April (assumed to have stayed at the nest) and the number of juveniles recruited in to the population in July. Colours refer to those used to illustrate the parameters and time steps for the calculations in Fig. 3.3.

In order to calculate demographic parameters from the variation in population size over the year, mortality values for the population at each quarter were required (see Figs 3.2 and 3.3). As there are no estimates of survival available for any wild rose-ringed parakeet population I estimated the annual mortality using values from wild Monk parakeets, *Myiopsitta monachus,* in Argentina based on 19% for adults (2 years old and over) and yearlings (between 1 and 2 years) and 39% for juveniles (under 1 year old) (Spreyer and Bucher 1998). These values have previously been used for population analysis of the rose-ringed parakeet in S.E.

England (Butler 2003) and for the non-native populations of Monk parakeet in the United States (Pruett-Jones et al. 2007) which like rose-ringed parakeets, have also established breeding populations in several non-native countries including temperate countries in Europe (Strubbe and Matthysen 2009) and has a similar life history, reaching sexual maturity at two to three years. These annual mortality values were converted to quarterly rates yielding values of 0.116 for juveniles and 0.0513 for yearlings and adults. It was not possible to calculate the exact proportion of adult (>2years) to yearling (1-2 years) and juvenile (<1year) birds within the population in January 2010 and April 2010 due to there being no counts prior to this. Therefore I calculated the stable age structure (dominant eigenvector) from a Leslie Matrix of the London parakeet population (Butler 2003) (see Appendix Fig. S2.1) and used this as the estimated starting age structure in my model. This gave a proportion of 39% juveniles, 20% yearlings and 41% adults (Fig. 3.3).

The variation in total counts for all Greater London roosts, but excluding Slough, for each quarter from January 2010 to October 2012 were used to model the population parameters at each quarter. This model is described in Fig.3.3.

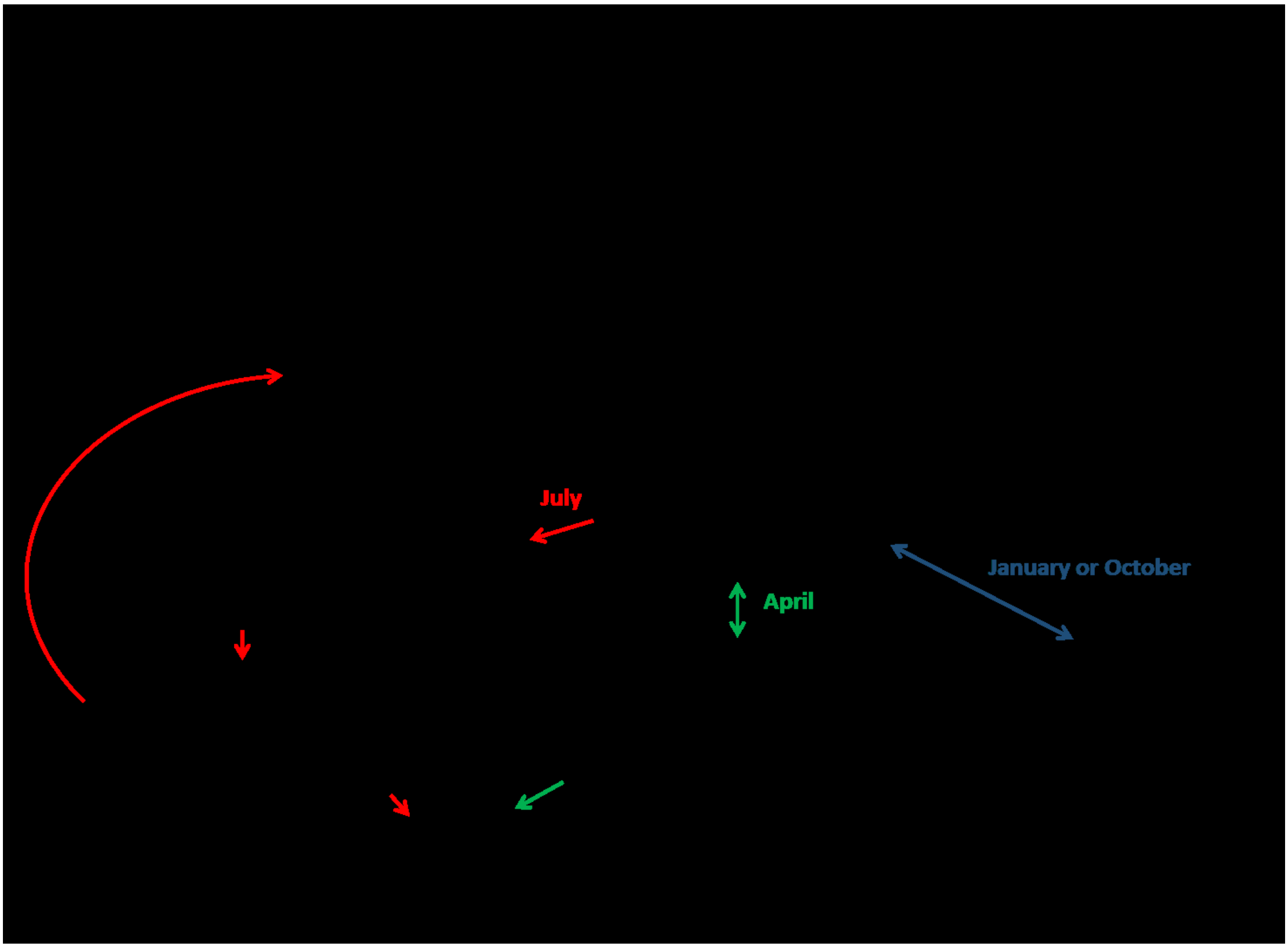

Figure 3.3. A flow chart describing the step-by-step calculations the model used to estimate yearly population parameters from quarterly roost counts. These parameters (in bold) are the number of breeding females, the number of juveniles recruited in to the population that year, the fecundity of breeding females, the estimated total mortality and the estimated number of birds missing from the population given the mortality estimates. Coloured arrows refer to steps only taken in certain quarters (blue = January and October, green = April, red= July), and match the quarterly time steps in Fig. 3.2 at which the different parameters were calculated. The '*Expected* population' is the estimated population size given the previous quarters' count and the mortality estimates. The 'Total Observed population' is the total number of birds counted at all the roosts during a quarterly count. To start the calculations, the first step is to enter the proportions of each age class, adults, yearling and juveniles (the stable age structure), these then do not need to be entered again.

Distribution, rate of spread and density comparison with population size

In order to compare the population size from this study and from the previous two census studies from 1996 to 1998 (Pithon and Dytham 1999) and 2000 to 2001 (Butler 2003) with the distribution of the parakeets over this period, I used BTO/JNCC/RSPB Breeding Bird Survey (BBS) recorded presence and absence (non-detection) data for random 1km survey squares for South East England, from 1996 to 2011, (for details of BBS methods see Risely et al. 2013).The parakeet distribution in Ramsgate, Kent is small and localised and is only covered by one BBS location so it is not possible to analyse the change in distribution for the Ramsgate population.

The distribution of parakeets per year from 1996 to 2011 was mapped using minimal complex polygons for each year with Quantum GIS 1.8.0-Lisboa software (Anon 2013). These were created using the latitude and longitude of the outermost BBS squares where parakeets were recorded as present.

The annual area of distribution was taken as the area of the annual distribution polygons in km^2. The rate of spread was calculated from the difference in area of distribution between years. The density of parakeets within the distribution area per year was calculated by dividing the total roost count population size in July by the area km^2 of the distribution polygon. As BBS data is captured during the months of April to June, the distribution is only reflecting the distribution during those months and may change at other parts of the year (Marchant et al. 2010) and therefore the distribution polygons must be taken as a minimum distribution.

In order to explore and compare trends over time (1996-2012) in a) the highest annual roost count totals, b) the distribution area, c) the rate of spread and d) the population density, these were fitted as response variables in generalised linear models (GLMs) with year as the explanatory variable. I also tested for effects of density dependence in these trends by fitting models including a quadratic year term and comparing these quadratic models to the linear models (this method has been used previously (Oliver, Brereton, and Roy 2012)). In addition I also fitted null models to assess overall model fit. Quasi-Poisson error structures were used for the models. Residual deviance was used to compare the linear models to the quadratic term models, with the model with lower residual deviance being considered the better fit for the data. The quadratic curves were also plotted to see how the curve fit the data.

Land use predictors of parakeet presence

A generalised linear mixed effects model was fitted to predict parakeet presence or absence using broad land use characteristics. This model used data on parakeet presence or absence (1 or 0) at BBS survey squares in the South East UK for 2011 (Marchant et al. 2010) as its response variable. These surveys were matched to generalised land use statistics for each local authority area in the South East UK from 2005 Office of National Statistics generalised land use database (Office for National Statistics 2005). This GIS data set divides south-eastern UK into geographic divisions each containing an average of 1500 residents based on the 2001 UK census data (Office for National Statistics 2005), and describes the proportion of the total area of each of these divisions that fall into the following three categories of land use: green space (defined as parks, other open space and agricultural land but excluding domestic gardens), domestic gardens and area of domestic buildings. This provided a sample size of 876 BBS surveys with corresponding land use data.

. The land use predictors of parakeet presence were analysed using generalised linear models in R (R Core Development Team 2009), using the lme4 package (Bates, Maechler, and Bolker 2012). Models were fitted using a binomial error structure and a logit link function. To account for spread of the parakeet distribution from the area of early establishment, distance from the 1996 centre of distribution was included as an explanatory variable in the model. This distance (km) was calculated from the central BBS point of 1996 distribution to all BBS 2011 data points. To control for spatial autocorrelation, the 10km National Ordnance Survey grid square within which each parakeet presence or absence BBS point lay, was added as a random effect, this method has been used previously (Oliver, Brereton, and Roy 2012) . The minimum adequate models were reached by entering all fixed effects and two-way interactions and dropping them sequentially until only those that explained significant variation remained. At each stage the reduced model was tested against the previous model to check that a significant amount of variation had not been lost using a Chi-squared statistic in an ANOVA comparing AIC scores for each model. Collinearity of fixed effects were checked and any collinear results greater than +/-0.5 were removed from the model.

Results

Total population size and growth 1996 to 2010

I identified ten roost sites in South East England, with 100 to 15,000 individuals per site (Fig. 3.4), giving a total population estimate of 31,685 in July 2010 (Greater London 30,624 and Ramsgate 1,061). This estimate must be taken as a minimum given the small possibility that small, less detectable roosts might not have been included in the survey (Table S2.4 of all roost counts). This compares with a previous estimate of 1,508 (Greater London 1243, Ramsgate 265) individuals for 1996 (Pithon and Dytham 1999) (see Fig. 3.5). For the Greater London population this corresponds to a doubling time of 3.03 years and an average population growth rate of 26% per annum over the 14 years between 1996 and 2010 and for Ramsgate a doubling time of 5.44 years, with a 14% growth rate between 1998 and 2010. The Greater London growth rate is higher than that observed for any of the UK's most common 125 bird species over the same period (Fig. 3.6) (Newson et al. 2005).

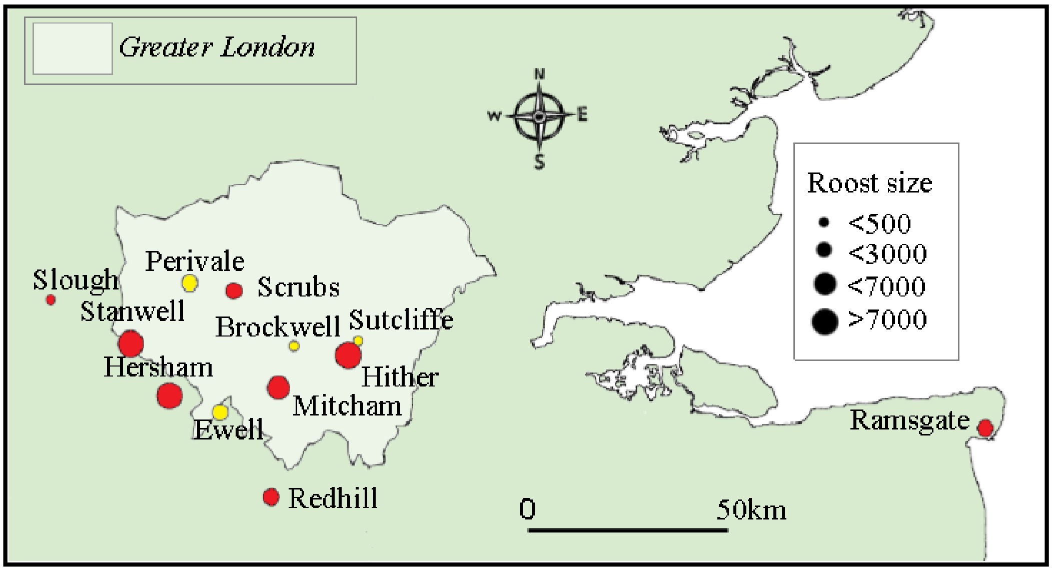

Figure 3.4. Roost distribution of rose-ringed parakeet in South East UK and approximate roost sizes during 2010-2012, red circles represent roosts which still current as of October 2012, yellow were abandoned before October 2012.

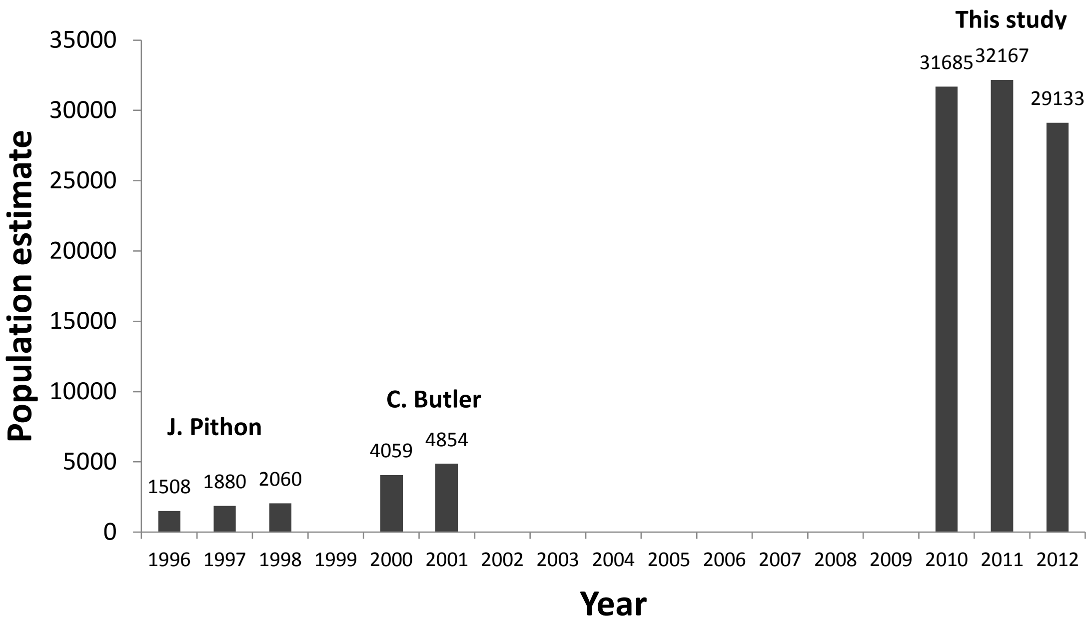

Figure 3.5. Highest annual count totals of rose-ringed parakeets at all known UK roosts 1996-2012.

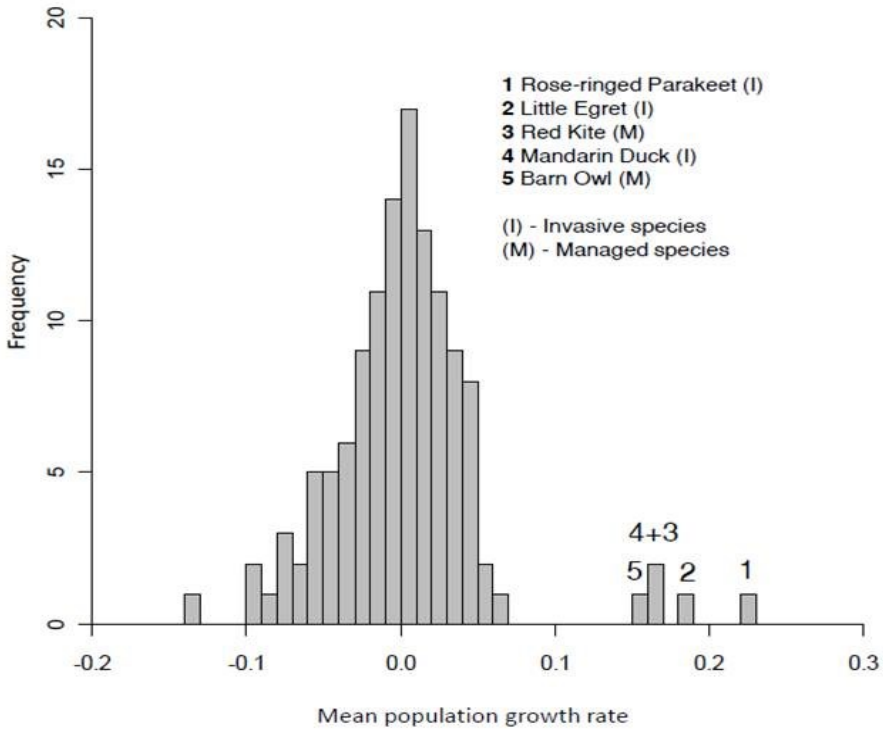

Figure 3.6. Geometric mean annual population growth rates for the 125 commonest UK bird species, BTO/RSPB/JNCC Breeding Bird Survey 1996-2009 (Newson et al. 2005). The five species with the highest growth rates are identified.

Population size and change 2010 to 2012

In the Greater London population, in contrast to the longer term trend, counts undertaken between July 2010 (30624) and 2011 (30604) had 0.1% change in the population using those roosts and between 2011 and 2012 (27761) there was a 9.3% decline. For Ramsgate there was a 32% increase between July 2010 (1061) and 2011 (1563) and a 5% decline between 2011 and 2012 (1487).

Despite little change in the overall population size, six of the twelve roosts used over the three years were either temporarily or permanently abandoned (see Fig. 3.7 and Table S2.4). It was also noted that when Stanwell and Ewell were abandoned in July 2010, the Hersham roost, which is the nearest large roost, almost doubled in size compared to Hersham's subsequent July counts in 2011 and 2012 with an increase of approximately 7000 and 6000, respectively (see Fig. 3.7. and Table S2.4).

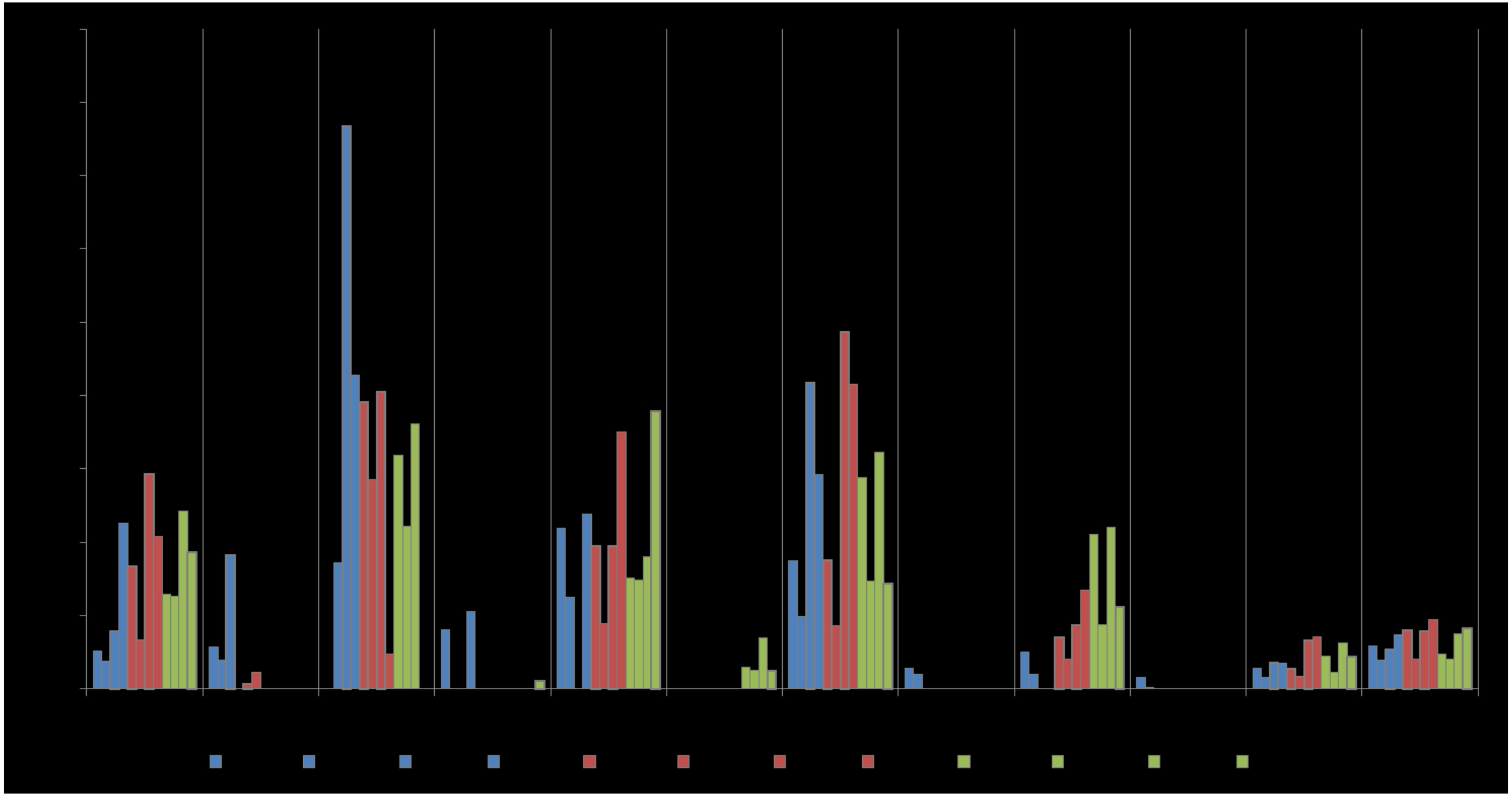

Figure 3.7. Quarterly roost counts of rose-ringed parakeets per roost January 2010 to October 2012, * indicate missed counts, blank spaces indicate roosts that were checked but which were not used by the parakeets. Blue bars are 2010, red bars are 2011 counts and green are 2012.

Within-year variation in total roost counts 2010 to 2012

For the Greater London population, a distinct pattern was found for all three years in total quarterly roost count variation with a decline in April and a large increase in July, followed by a small decrease in October (see Fig. 3.8), (mean % difference ± standard deviation, January-April decrease of 41% ±4.20, April-July increase of 58% ±9.77, July to October decrease of 22.5% ± 13.59 and October to January decrease of 43% ±14.40).

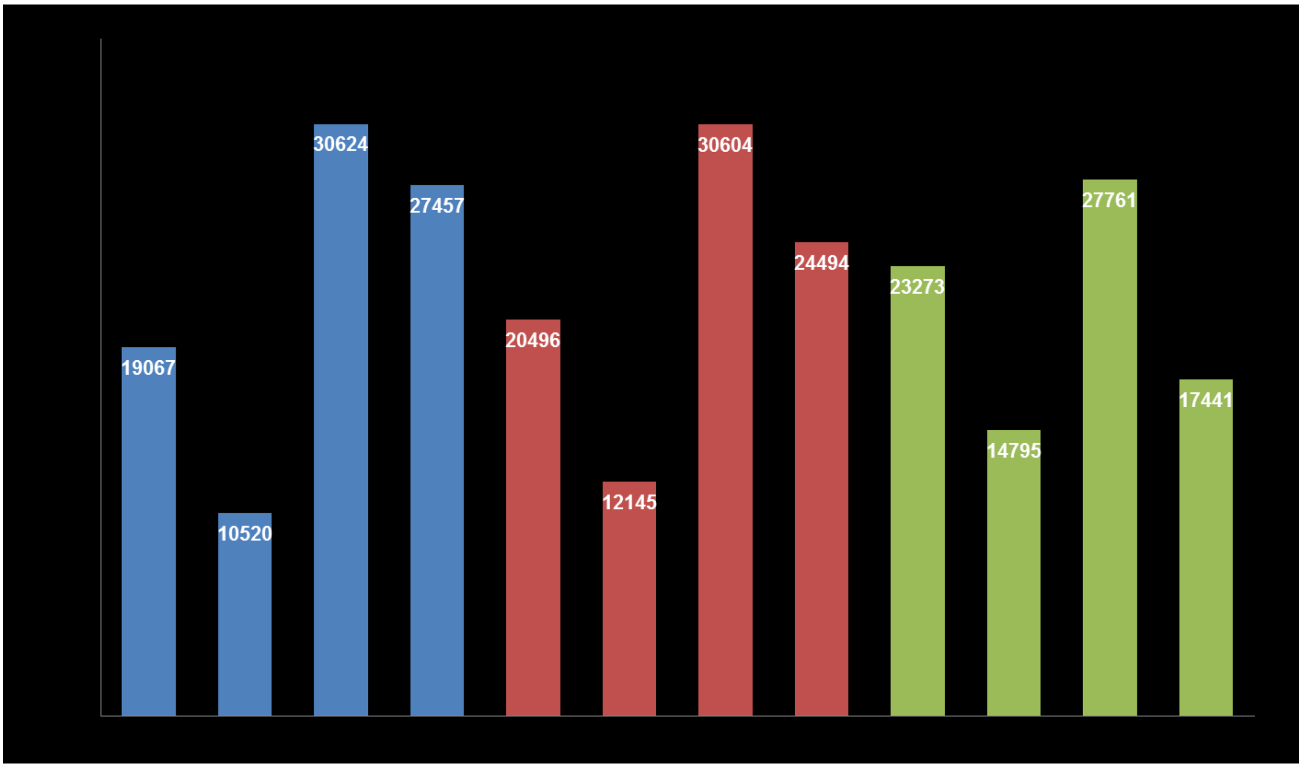

Figure 3.8. Quarterly roost count totals January 2010 to October 2012 (excluding Ramsgate and Slough), blue 2010, red 2011 and green 2012. Annotations explain change in roost size since previous count, **-M** refers to mortality occurring and **±m** possible migration to or from the roost. 'Unknown # missing' in October 2012 refers to the Hersham roost which was disturbed around the count period resulting in the majority of birds using that roost being displaced to an unknown location. This displacement could have been to an existing roost so may have in fact been included or to elsewhere so it is not known how many, if any were missed from the count

The Ramsgate population variation had a similar pattern in change in quarterly count totals except that the October counts were greater than the July counts and January 2011 was higher than October 2010 (Appendix Fig. S2.2), (mean % difference ± standard deviation, January-April decrease of 33% ±18.43, April-July increase of 41% ±11.37, July to October increase of 18.4% ± 8.98, October to January 2011 increase of 8% and October to January 2012 a decrease of 50%). The high counts in all Octobers and January 2011 meant there was inconsistency in the pattern of quarterly roost counts between the three years compared to the quarterly pattern observed in the Greater London counts. This indicated that there was either a difference in timing of recruitment of juveniles to the population or that part of the population was roosting elsewhere in small numbers for part of the year. Ramsgate data were therefore excluded from all further analyses.

Population parameter estimates for 2010 to 2012

The population parameter estimates are summarised in Table 3.1 (for a full set of results see appendix Table S2.5). The estimated breeding numbers were not significantly different across the three years (mean 7057 s.e. ±19.95), while estimated mean fecundity (breeding success per breeding pair) ranged from 1-2 fledglings over the 3 years and the estimated number of non-breeding birds increased, with a 32% increase (1648 birds) from 2010 to 2011 and a 35% increase (2696 birds) from 2011 to 2012. Discrepancy between the expected population size due to predicted mortality and the actual observations also increased over the three years, with just an extra 3% of the observed population in October expected in 2010 (889 birds), an extra 17% expected in 2011(4066 birds) and an extra 50% expected in 2012 (8725 birds).

Table 3.1: Estimated population parameters for the Greater London population (excluding Ramsgate and Slough) from 2010 to 2012.

Year	July total observed count	Annual mortality	Number of breeding pairs	Number of non-breeding birds	Fecundity	Discrepancy in October between observed and expected total counts
2010	30624	4494*	7088	3432	1.94	889
2011	30604	6000	7065	5080	1.71	4066
2012	27761	5488	7020	7776	0.97	8725

NB * annual mortality in 2010 is missing the mortality for the 1st quarter of the year as it was not possible to calculate mortality without a previous count from 2009.

Greater London population size and distribution 1996 to 2011

The quadratic models explained the change in the population size, area of parakeet distribution and rate of spread of the Greater London population between 1996 and 2012 better than the linear models (residual deviance lower, see Table 3.2). The population size and distribution area quadratic models predicted an increase over this period but also a slowing of an increase in the last few years (see Fig. 3.9). The area of distribution increased by an average of 20% per year over 14 years from approximately 569km^2 in 1996 to 7212 km^2 in 2010, with a doubling time of 3.03 years and then reduced slightly to 6988km^2 in 2011 (Fig S2.3 and Table S2.6). The rate of spread peaked in 2003 to 1350 km^2 per year but fluctuated strongly throughout the fourteen year period (see Fig. 3.9 and Table S2.6). For the parakeet population density analysis, the difference in the linear and quadratic models was considered negligible. The estimates of density show an increase over time from 2.2 parakeets per km^2 in 1996 to 4.4 in 2011 (see Table S2.6 for density per year). In all cases the null models' deviance was higher than the linear and quadratic models (see Table 3.2).

Table 3.2: GLM model results for population measures per year (1996 to 2012) without and with the quadratic term

Population measure	Model -/+ quadratic term	Explanatory variable	coefficient	Std. error	t-value	p-value	Residual deviance	n
Population size (roost count totals)	null						112695	8
	-	year	0.191	0.019	10.15	<0.001	3948	
	+	year	60.01	10.13	4.47	0.007	732	
		$year^2$	-0.015	0.003	-4.46	0.007		
Distribution km^2	null						23286	16
	-	year	0.123	0.014	8.69	<0.001	3649	
	+	year	49.12	8.630	5.69	<0.001	1005	
		$year^2$	-0.122	0.002	-5.68	<0.001		
Density within distribution	null						4.15	7
	-	year	0.062	0.021	3.02	0.029	1.56	
	+	year	-33.21	31.89	-1.041	0.356	1.23	
		$year^2$	0.008	0.008	1.043	0.356		
Rate of spread per year km^2	null						8552	14
	-	year	-0.046	0.058	-0.778	0.450	8249	
	+	year	90.410	70.294	1.240	0.239	7353	
		$year^2$	-0.022	0.018	-1.240	0.239		

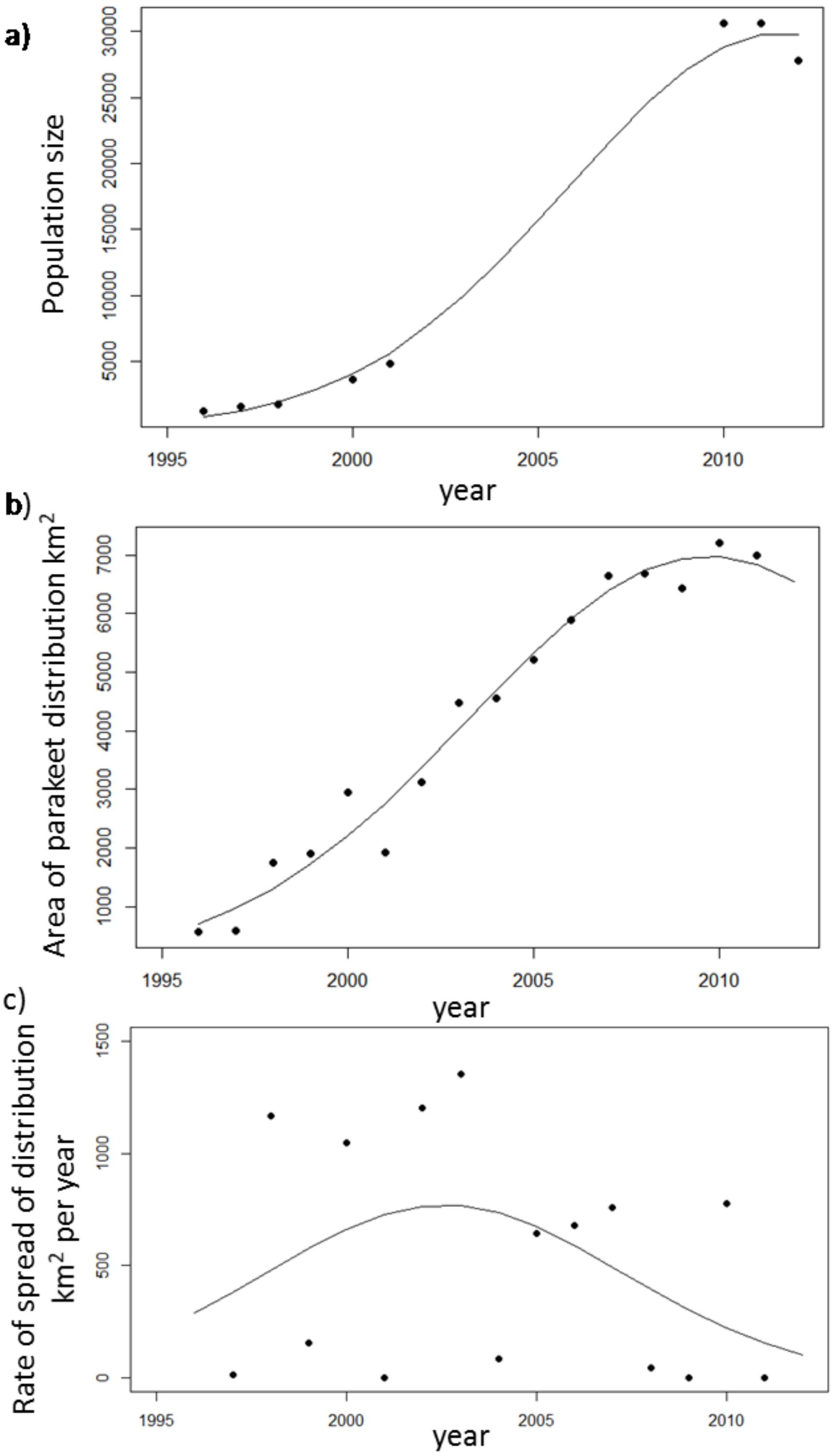

Figure 3.9. a) Population size (highest roost count totals) per year from 1996 to 2012, b) area km^2 of minimum complex polygon for BBS squares where parakeets were present (distribution area) per year from 1996 to 2011 and c) rate of spread km^2 of minimum complex polygon for BBS squares where parakeets were present (distribution area) per year from 1996 to 2011, negative values for change in distribution per year have been changed to zero to represent no spread. Lines are the predictions from fitting the quadratic models to the data.

Land use predictors of parakeet presence across South East England

Parakeet presence was negatively correlated with distance from the centre of the 1996 distribution (z= -5.711, p=<0.001) and with the proportion of green space in the local area (z=-2.286, p=0.022). Increases in the proportion of domestic housing in the local area did not influence parakeet presence on its own (z=1.190, p=0.234) but did have a positive effect when coupled with an increase in the proportion of green space (housing x green space, z=3.215, p=0.001 (GLMM results are summarised in Table 3.3 and correlation of fixed effects results Table S2.7). Proportion of domestic gardens in the local area was removed from the initial model due to collinearity with the proportion of housing area (correlation of -0.747).

Table 3.3. Results of the generalised linear mixed model analysing variation between location in parakeet 2011 presence and absence (0 and 1) with variables of land use 2005 (GLMM p-values, ***P<0.001, **P<0.01, *p<0.05). Location of BBS points within National Grid 10km squares as a random effect. N =669 (parakeet present =561, absent = 108), Random effect of 10km square location of BBS point, variance 0.233, s.d. 0.483. '**x**' refers to an interaction in effects between variables.

Variables	Slope difference	SE	z-value	P-value	
Intercept	3.384	0.995	3.399	<0.001	
Distance from centre 1996 distribution (km)	-0.103	0.018	-5.711	<0.001	***
Proportion green space	-2.470	2.080	-2.286	0.022	*
Proportion domestic buildings	-12.521	10.522	1.190	0.234	
Distance **x** domestic buildings	-0.768	0.414	-1.856	0.063	
Green space **x** domestic buildings	40.240	12.515	3.215	0.001	**

Discussion

This study provides an update on the status of South East England's parakeet population which shows rapid growth since the first census in 1996. I show that the population now comprises more than 30,000 individuals over an area of approximately 7000km^2 of the South East of England and grew at an average of 26% per year between 1996 and 2010. This comparison of the quarterly simultaneous roost counts indicates that although there has been high population growth since 1996, both the Greater London and Ramsgate populations show little evidence for growth between 2010 and 2012. These results suggest that the Greater London population may have reached carrying capacity and may be limited by availability of suitable urban habitat and breeding sites. I discuss what population processes might be limiting further growth in the parakeet population as indicated by the results, the possible ecological factors underpinning these processes and the implications this has for rose-ringed parakeets on a wider scale.

Rapid population growth

The population size of the rose-ringed parakeet has grown so rapidly size since 1996, it is faster than any other of the 125 most common bird species in the UK over the same period. This is not particularly surprising given that most of the native species will have already reached carrying capacity. This is supported by the fact that the other species with high growth rates are also invasive species (n=2 see Fig. 3.6) or species which had declined in the past but are now undergoing conservation management through breeding programmes and re-introduction (n=2 see Fig. 3.6) (Evans et al. 1999; Meek et al. 2003). This indicates that the rose-ringed parakeet has the ability to rapidly populate areas where they are introduced.

The pattern of the parakeet population growth over the last 15 years is typical of a logistic population growth to carrying capacity (Beeby 1995). Similar patterns of population growth and spread have been observed in many invasive bird species, where populations have undergone near exponential growth after establishment, but slower increases in geographic spread, resulting in high population densities (reviewed by Blackburn et al. 2009). Examples of invasive species in which this pattern of rapid growth, followed by stabilisation has been documented include the monk parakeet in North America and the house crow (*Corvus splendens*) in Singapore (Lim et al. 2003; Pruett-Jones et al. 2007; Blackburn, Lockwood, and Cassey 2009). For the rose-ringed parakeet, the growth appears particularly similar to that of the establishment of the non-native common waxbill (*Estrilda astrild*) in Portugal between 1964 to 1999 (Silva et al. 2002), which also had a ten year period of rapid population growth and expansion, which was then followed by reduced expansion rates as the suitable habitat became occupied.

<u>Explanations for the apparent slowing of population growth between 2010 and 2012</u>

These results show that population increase has levelled off, with no growth in population size between 2010 and 2012. It is possible that this is due to roost sites within the census area having gone undetected. However considering the extent of the publicity for information about roost sites to the general public and local birding groups it seems unlikely that I could have missed birds in such high numbers as the disparity suggests. An alternative is that there may have been an increase in mortality and/or emigration from the population in this period as a result of density dependent factors. This view is supported by the increasing disparity between the observed and predicted counts between 2010 and 2012. To the best of my knowledge, there are no records of long distance dispersal in rose-ringed parakeets in the UK and the occurrence of parakeets in other cities across the country are thought to be due to captive bird escapes (FERA 2009). Nonetheless long-distance emigration has been proposed as a possible reason behind the decline in sizes of non-native monk parakeet populations in North America (Pruett-Jones et al. 2011), where genetic evidence showed that individuals from the Florida population had dispersed as far as 100km to forage (da Silva et al. 2010). Therefore the long-distance migration hypothesis cannot be discounted entirely.

A stable number of breeding pairs and an increasing number of non-breeding individuals from 2010 to 2012 were estimated. This suggests that the reduced population growth is a result of something that is limiting breeding capacity. In order to determine whether this is the case, an extension study would be required to quantify the density of breeding cavities available as there is currently no evidence as to how limited cavity sites are within in the parakeet distribution (Newson et al. 2011). An alternative explanation for the stable population pattern seen over the last three years is that the particularly cold winters of 2009/2010 and 2010/2011 (Guirguis et al. 2011; Prior and Kendon 2011) caused fewer breeding attempts or higher breeding failure. There has been some limited evidence that the cooler climate in the UK reduces egg fertility in comparison to another introduced parakeet population in Israel and to its native range in India, both of which have warmer climates (Shwartz et al. 2009). A cold winter might particularly effect parakeets as they start breeding as early as February (Tayleur 2010). A study investigating the life history of avian introductions found that birds which invest in future reproduction rather than rapid current population growth, are more likely to be successful (Sol et al. 2012). The parakeet may fit this life-history well, as the bird is a long lived species and therefore the recent reduction in population growth may in fact be a strategy of some individuals forgoing breeding due to poorer environmental conditions, resulting in poorer body condition (Strubbe and Matthysen 2009) rather than due to density dependent factors. A study of rose-ringed parakeet introductions in Europe found populations failed if the area of introduction had over 50 days of frost, therefore showing the sensitivity of the species to cold climates (Strubbe and Matthysen 2009). However the winter of 2011/2012 was milder on average for the period 1971-2000, with +0.9°C above average (Met Office 2013) and so it would be expected that the 2012 breeding season would have been more successful if the winter temperature was a factor in the previous years' reduced success. The persistence of the parakeet in South East England for over 40 years and its ability to reach such a large population size demonstrates the ability of the species to withstand the cool temperate climate.

Although the population has been spreading from the Greater London area, the rate of spread has slowed down in a similar pattern to the change in population size. This suggests that not only is population increase limited within Greater London but that something is limiting range expansion as well. The analysis comparing parakeet presence and land use patterns, suggests that the stabilisation of the parakeet distribution and population may be due to an absence of suitable habitat outside the current distribution into which to expand. I found a negative relationship between the density of green space and the location of parakeet presence, showing that parakeets are less present in rural and agricultural areas. I suggest this is because parakeets are avoiding those areas. The density of green space was not collinear with the distance from the 1996 parakeet establishment area and therefore it appears that it is not simply because the distribution has not yet had enough time to spread far enough to high density areas of green space surrounding Greater London. The additional finding of a positive interaction between the density of green space and density of domestic buildings, indicates that where there is high density of housing and high density of green space, parakeets are more likely to be present and so it is specifically rural green space which the parakeets are not spreading to. This finding is supported by ecological niche modelling of the Belgian parakeet population which also found the distribution was correlated with older forest and parks near built up areas (Strubbe and Matthysen 2007; Strubbe and Matthysen 2008). This is likely to be due to parakeets preferring urban areas for foraging (Clergeau and

Vergnes 2011) but needing green space such as woodland or parkland nearby for breeding areas (Strubbe and Matthysen 2007). There is no certainty that parakeets will not move to more rural areas in the future and a previous study using a habitat suitability analysis found that there was suitable habitat within <7km in all areas of the South East of UK (FERA 2009). The abandonment and relocation of both small and large roosts over the last few years reveals that whole roost sites of over 1000 birds can relocate quickly in response to changes in the local environment and shows the high mobility of the parakeets. Despite this they have not rapidly spread into the rural areas outside of Greater London, highlighting their preference for urban areas. Overall the distribution of the parakeets and reduced rate of spread suggests that urban areas may have supported the parakeet growth but that the population is restricted to these areas.

It is also worth noting that the previous population growth is likely to have been partly driven by regular augmentation by captive parakeets escapes in to the wild (Fletcher and Askew 2007). A ban on the import of wild-caught birds was placed in January 2007; however the ease with which the parakeets can be bred in captivity means that their trade in the UK will not necessarily drop (Fletcher and Askew 2007; Lambert et al. 2009). As the population distribution reaches areas less densely populated by humans there is likely to be less augmentation occurring. However due to the large breeding population size of the current population, any effect of augmentation occurring from captive bred individuals is likely to be negligible.

<u>Predicting the future population trend</u>

The first records of breeding and establishing parakeets in the Greater London area are from the 1970s (Butler 2003), and therefore these findings suggest the population has taken around 40 years to stabilise. Their apparent preference for urban landscapes (Strubbe and Matthysen 2007), use of garden bird feeders (Clergeau and Vergnes 2011) and avoidance of agricultural fields (Strubbe and Matthysen 2008) suggests that the population growth may have been supported by the urban landscape and may be restricted by agricultural areas. This could mean that change in landscape since the establishment of the parakeet population forty years ago, with increased suburbanisation due to urban sprawl in Greater London (Stanilov and Batty 2011) in conjunction with increased provision of garden bird feeders in gardens (Jones and Reynolds 2008), may have improved the conditions needed for the population to spread. As the population expands out of Greater London it will be reaching more rural landscape types that may restrict its expansion. There is the possibility that parakeets could adapt to utilise resources in rural areas on a larger scale than found so far in the UK (FERA 2009), in particular using agricultural crops as a food source as shown in their native range (Iqbal, Khan, and Ahmad 2000; Khan et al. 2011; Patel 2011; Ahmad et al. 2012). However, so far there is little evidence that this has happened on a significant scale in the UK or elsewhere in Europe, apart from a few reports (Fletcher and Askew 2007; Strubbe, Shwartz, and Chiron 2011). Given the support that the urban landscape provides for populations of rose-ringed parakeets, it seems likely that if urbanisation increases in the land surrounding Greater London then the parakeet population will continue to expand. It also seems likely that further populations could establish and grow to similar densities in towns and cities across the country, and across Europe but that populations are likely to remain close to these urban areas.

Conclusions

These findings provide the first estimate of the parakeet population size in the UK since 2001, showing that rapid growth occurred resulting in the population reaching a high density in Greater London but that evidence suggests that the population size and distribution is now stabilising. Further investigation is needed in to what exactly may be limiting the population increase within the distribution area, such as whether breeding cavities are limited or if some other unidentified factor is playing a part. Further monitoring of the population size and distribution is also required to see if the halt in growth as seen between 2010 and 2012 continues or if the parakeets alter their use of resources within the landscape enabling expansion to outside the urban areas. These findings provide a basis on which to evaluate the consequences of any ecological and economic impacts found of the parakeet population and the potential for management. This also highlights the potential for dramatic population increase following establishment of parakeet populations in other cities in the UK and Europe.

Chapter 4

Experimental evidence of impacts of an invasive parakeet on foraging behaviour of native birds

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Abstract

Invasive organisms have the potential to affect native species through resource competition, but detecting such impacts can be difficult due to complex interactions of potential environmental drivers, particularly in urban environments. The rose-ringed parakeet (*Psittacula krameri*) is an increasingly common invasive species, predominantly associated with large urban centers. Using an experimental approach I test the behavioural responses of native garden birds in response to the presence of a rose ringed parakeet versus the presence of a similarly sized and dominant native bird, the great spotted woodpecker (*Dendrocopos major*). Parakeet presence significantly reduced feeding rates and increased vigilance among native birds compared to the control treatments. Of visits made by native birds in the presence of a parakeet, feeding was more likely to occur in sites within the parakeet range compared to sites outside, suggesting some habituation of native birds has occurred following prior exposure to parakeets, but overall foraging behaviour is still disrupted. This experimental approach reveals that non-native species can have complex and subtle impacts on native fauna, with these results showing that a non-native competitor can impact native species simply through their presence near resources.

Introduction

It is well documented that non-native species can have devastating impacts on biodiversity (Mack et al. 2000; Simberloff 2005; Shochat et al. 2010b; Vilà et al. 2010) but despite extensive research, a high degree of uncertainty still exists with regards to the mechanisms of these impacts on native fauna (Perrings et al. 2002; Vilà et al. 2010). Anecdotal evidence and a lack of understanding of the nature and dynamics of the invasion process have contributed to this uncertainty (Mack et al. 2000; Gurevitch & Padilla 2004). Knowledge of the behavioural impacts resulting from non-lethal interspecific competition between native and non-native species can, therefore, give insight in to the mechanisms and consequences of invasions (reviewed in Chapple, Simmonds & Wong 2012).

It is thought that non-native species that displace native species are likely to be better able to exploit resources and thus have strong interference effects on native species (Amarasekare 2002). For instance, increased interspecific competition can result in reduced foraging success of the affected individuals, increased time spent on vigilance, displacement to less high value resources and ultimately result in non-lethal fitness consequences with the potential to indirectly affect population level changes (Cresswell 2008). This type of interspecific competition is widely thought to play a role in the impact of non-native species (Probert & Litvaitis 1996; Kiesecker et al. 2001; Wauters et al. 2002; Dame et al. 2006; Soares & Serpa 2006) but may be difficult to demonstrate unambiguously (Blackburn et al. 2009) perhaps in part because the ecological impacts of non-native species can be difficult to distinguish from other potential environmental causes (Shochat et al. 2006; Dures & Cumming 2010). There is thus a need for experimental investigation to identify how interspecific interference might lead to behavioural changes driven by non-native species (Dame et al. 2006; Strubbe et al. 2011).

Another factor that requires consideration when studying the potential impact of invasive organisms on the behaviour of native species is habituation. It has been suggested that simply the novelty of the invasive species may disrupt normal behaviour in native species, by eliciting a neophobic avoidance response (McEvoy et al. 2008). Neophobic impacts can be reduced or altered by repeated exposure to the novel species, as shown in cases of habituation in predator-prey interactions (reviewed by Brown & Chivers 2005). However, there has been relatively little work investigating habituation of native species to invasive species and the effects of prior exposure on competitive interactions (but see Webb *et al.* 2008; Abril & Gómez 2009; Nelson, Crossland & Shine 2011). In this context, rapid ongoing range expansion by exotic populations therefore offer the opportunity to investigate whether native species do habituate to the presence of invasive species (Freidenfelds et al. 2012).

In this study I use an urban population of the rose-ringed parakeet, listed as one of the top 100 most invasive alien species in Europe (Vilà et al. 2009) and a common invasive bird species around the world (Feare 1996), to test for evidence of interference competition with native species and for habituation in the native species. This study system is ideal because, although invasive bird populations have been well studied (Duncan et al. 2003), there is little quantitative evidence of their impacts on native faunas (Blackburn et al. 2009; Strubbe et al. 2011).

The high density populations of the rose-ringed parakeet in urban centres, provides a situation in which interspecific competition for resources with native species might be expected (Tayleur 2010). This is the case for many other non-native bird invasions as urban feeding favours species invasions, by allowing rapid population growth, leading to positive correlations between non-native bird abundance and human population density (McKinney 2006; Daniels & Kirkpatrick 2006; Fuller et al. 2008; Strubbe & Matthysen 2009a).

Previous studies on rose-ringed parakeets have been limited to investigating competition for nest sites and have suggested that the impact of this form of competition is likely to be negligible (Strubbe et al. 2010; Czajka et al. 2011; Newson et al. 2011). However, the parakeet's highly varied diet (Feare 1996), its ability to eat non-native plants and human-provided food sources (Koutsosms et al. 2001), as well as the fact that individuals have been found to spend half their feeding time at artificial bird feeders (Clergeau & Vergnes 2011), means that it has potential to compete with a wide variety of native bird species for these resources and particularly with species found in urban gardens.

Here I use an experimental approach to address the following questions: i) Does the presence of a non-native competitor at a high value food source alter the foraging behaviour of native species? ii) Does the native species' response to the presence of the non-native competitor differ from that of a similarly dominant native species with which they have co-existed? iii) Is the strength of response to the presence of an establishing non-native competitor correlated with prior exposure to the non-native species? iv) If so, is this response indicative of reinforcement of avoidance behaviour of the non-native species, or of habituation to the non-native species?

Methods

Experimental procedure

Behavioural experiments were performed at standardised feeding stations in urban gardens, with the behaviour of free-living native birds being observed under a range of experimental and control conditions. In total, feeding stations were set up at 41 sites within a 70km radius of the centre of London, UK, using the London Natural History Society method of using St Paul's Cathedral as an approximate for the centre of London (Fig. 4.1). To test for potential habituation, gardens were classified as being either within or outside the current range of the invasive parakeet population. This was classified based on residents' information and verification by observations made during the experiment. Parakeet absence was also verified by British Breeding Bird Survey (BBS) parakeet presence and absence data for London and the Home Counties for 2009 (see Fig. 4.1).

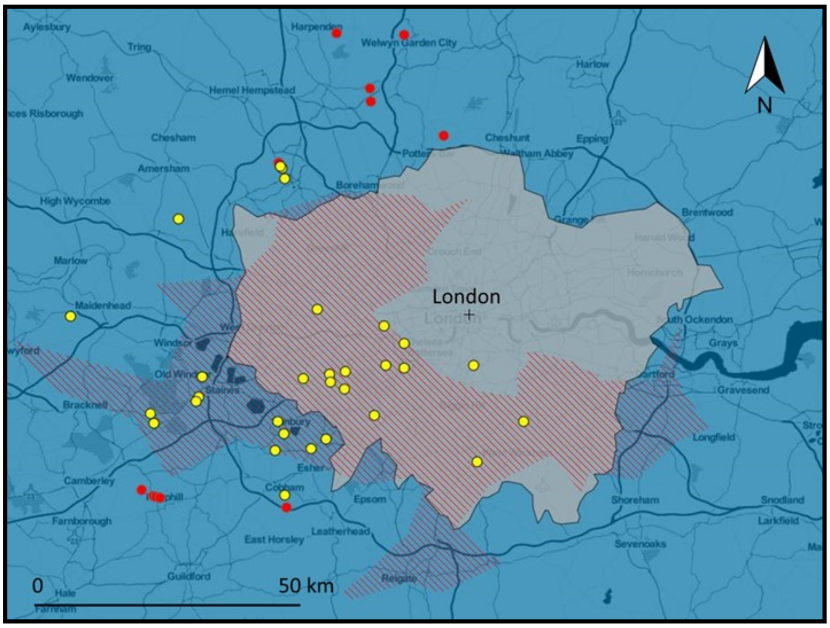

Figure 4.1 Experimental feeding site locations across London. Red circles represent parakeet free sites, yellow circles represent sites where parakeets were present, the grey area represents the area of Greater London, the red lined polygon represents the area of the 2009 parakeet range (this is the extent of the BBS 1km^2 squares where parakeets were recorded present in 2009). The cross represents the location of St Paul's Cathedral (sites were chosen within a 70km radius of this).

Sites comprised the gardens of members of the public who responded to advertisements made through the media, project website, local bird watching groups and word of mouth and therefore the location of sites used were constrained by those offered (see Chapter 2). Procedures for contacting members of the public were assessed and passed by Imperial College's research ethics committee in April 2010. Sites were at least 200m apart (closest distance between two sites 226m, see Fig. 4.1) to minimise the risk of repeating the experiment on same individual native birds. Feeding stations comprised two squirrel proof feeders (The Nuttery NT28 and NT22

ASIN: B0007LQ3WQ, dimensions 20.3 x 20.3 x 34.3 cm) hung on a steel shepherd hook pole Gardman (ASIN: B001F36RA8, height 218cm). The two feeders at each feeding station were supplied with peanuts and sunflower seeds respectively for two weeks before the experiment was conducted, allowing habituation of the local birds. These feeders represented a localised, high value resource that could be standardised across sites independent of season, and prevented interference from squirrels.

The behavioural experiments were conducted from May 2010 to February 2011 by H.L.P or H.E.P, using seven treatments that were designed to vary in the extent to which native birds were exposed the presence of parakeets and control treatments (see Table 4.1).

Table 4.1 Treatments used per site, 'cage' refers to whether an experimental cage was empty or had a live woodpecker or parakeet with in it and 'call' refers to whether there was no audio recording or if a recording of a woodpecker or parakeet call was played. The order of the seven treatments was randomised in each site.

			Cage	Call
Control 1	(C1)		Empty	none
Control 2	(C2)		Woodpecker	none
Control 3	(C3)		Woodpecker	Woodpecker
Treatment 1	(T1)		Parakeet	none
Treatment 2	(T2)		Parakeet	Parakeet
Control 4	(C4)		Empty	Woodpecker
Treatment 3	(T3)		Empty	Parakeet

Both a caged live parakeet and a recording of its call were used as treatments, as birds are known to be sensitive to both sight and sound (Sturkie 2000). In addition to the control of an empty cage with no recording it was necessary also to use native controls, making it possible to test for the strength of any effect of neophobia or habituation to the parakeet.

The great spotted woodpecker was chosen as a control species because it is the closest species in size that regularly feeds from hanging garden feeders, (rose-ringed parakeet: 400 mm length, mass 120g; great spotted woodpecker: 220 mm in length, mass 85g (Snow et al. 1998)) and its distribution overlaps with the study area (Balmer et al. 2013). Although smaller than the parakeet, this species has been observed to be aggressive at feeding stations in comparison to other birds and has been recorded successfully supplanting parakeets from feeding stations (Pithon 1998).

Seven treatments were presented in a randomised order for 20 minutes each (ie, a total treatment time of 140 minutes per site) generated through non-replacement sampling in R (R Core Development Team 2009) for each individual site. For all treatments the cages (Montana KT3001, GTIN 04038374320048 46 x 63 x 53 cm) were equipped with two metal bowls containing peanuts and water. For each treatment, the cage was placed on a stand at 0.3m from the feeder station at the same height as the feeder for 20 minutes. In the treatments involving sound, calls were played from a Ministry of Sound MOSMP020 MP3 player connected to two Skytronic speakers, at full volume, positioned on the ground directly below the cage. The great spotted woodpecker call was obtained from pre-recorded material (Sample 1996), while the parakeet call was recorded from a series of vocalisations of an adult male rose-ringed parakeet in a garden in Richmond, Surrey, specifically for the study using a Sony Dictaphone. Both calls were edited using Audacity 1.2.6 to minimise any background noise and repeated with intervals of random length (0-5 seconds) between calls to be of similar length (under 3 minutes). These were played on repeat for the duration of the treatment.

The rose-ringed parakeet and great spotted woodpecker pairs (a male and female of each) used in the experimental trials were caught from the wild using a standard mist net under license from the British Trust for Ornithology, and kept under Natural England (NE) licence (number 20101145) in an outside aviary between experiments. Aviaries were provisioned with nest boxes, ad libitum food and water, and provided sufficient room for flight (see Chapter 2). Each bird in a pair was used in alternate experiments in order to minimise stress and to control for any differences in behaviour of visiting birds in response to differences in appearance due to sexual dimorphism. After all experiments were completed, the woodpeckers were given a two week soft-release at the catching site with open access to the aviary for food, water and shelter. The parakeets were re-homed in captivity as required by the NE licence.

Data collection

The activity of native birds at the feeder was recorded using a small camcorder (Panasonic SDR-S156) mounted on a tripod 3m from the feeders. Video recordings of each trial were watched subsequently to record each visiting bird's species, duration of visit (in seconds), whether or not feeding occurred and which food was eaten (sunflower seed or peanut). For sites within the current range of the parakeet population, visits made by wild parakeets to the feeding station during the trials were removed from the data before analysis (this included 136 visits altogether and occurred in 12 out of the 30 sites within the parakeet range). Data were recorded by trained volunteer research assistants, using standardised methods. Error checking was carried out by double checking a random five minute sample of each video.

Environmental conditions of the feeder location for each trial were recorded to take in to account any variables that might affect foraging behaviour and visiting activity of birds with in each location. These included; feeder position in the sun or shade as direct sunlight can affect perception of risk and therefore foraging (Fernández-Juricic & Tran 2007), cloud cover and rain (cloudy, rain or clear sky) as rainfall can also affect foraging (Hilton et al. 1999), wind strength (0-3: no wind to strong wind) which has been found to affect visiting rates (Cowie & Simons 1991), time of year measured as months from May (1 to 10) to account for seasonal effects on feeding requirements (Chamberlain et al. 2005), time of day (am or pm) to account for changes in foraging activity during the day (Bonter et al. 2013), and distance of the feeding station to vegetation cover (<1m, 1-2m, >3m) as distance to cover is known to affect foraging in birds (Cowie & Simons 1991). Distance of the site from the centre of London (measured in km from St Paul's Cathedral) was also measured to account for any effect of urbanisation on species abundance, which might be confounded with parakeet distribution.

Data analysis

The data on the behaviour of native birds at the feeding stations were analysed to test for differences between experimental treatments in a number of dependent variables: model 1 tested the number of visits by native birds to the feeders; model 2 tested the proportion of visits that included a bout of feeding; model 3 tested the absolute time spent feeding within a visit; model 4 tested the proportion of time spent vigilant during a feeding visit. These were chosen to test whether parakeets inhibited birds from visiting (model 1) and then whether and how they affected foraging success (model 2 and 3) and the trade-off between foraging and vigilance (model 4). Vigilance is defined here as the proportion of time spent not feeding during feeding visits to peanuts and is an indication of risk perception. The absolute time feeding is likely to be correlated with the amount of food taken and therefore an indication of foraging success. The assumption was made that when birds are on the feeding station and not feeding then they were being vigilant. Birds visiting the feeders were not individually marked and so multiple visits by the same individual could not be accounted for but all sites were treated equally. In addition to the experimental treatments described in Table 4.1, I also tested for an effect of whether or not the site was within the range of the invasive parakeet population.

Data were analysed using generalised linear mixed effect models in R (R Core Development Team 2009), using the lme4 package (Bates et al. 2012). Models 1 and 3 were over dispersed so these included an observation-level random effect and were fitted using a Poisson lognormal error structure and a log link function (Elston et al. 2001). Models 2 and 4 were fitted using a binomial error structure and logit link function. Model 1 was analysed using a data subset of the summed total visits for each treatment per site. Model 2 was analysed using the full data set of each individual visit. Sunflower seeds were visited for such a short time per visit (median= 1 second, IQR= 1, n= 2117) regardless of treatment, that it was not possible to analyse differences in time spent feeding. Therefore only feeding visits to peanuts were analysed for differences in time feeding, so models 3 and 4 were analysed using a subset of only feeding visits where the bird fed on peanuts.

In models the experimental feeding site identification was added as a random effect. Variables measured in each site were added in to each model as fixed effects: inside or outside the parakeet range, cloud cover and rain, wind strength, sun or shade, time of day (am or pm), time of year (number of months from May), distance of the feeding station to vegetation, and distance (km) from central London. Inside or outside the parakeet range was categorised as binomial (absent or present), as preliminary analysis using a continuous measure of parakeet numbers in the site ranging from 0 to 5 found no difference in visits between the sites ranging from 1 to 5. The order in which each treatment took place were also added as a fixed effect to account for any interference that may result in a time-lag between exposure to a treatment and resumption of foraging (Sih 1992; Evans 2003). For models 2, 3 and 4 the species visiting the feeding station were also added as a fixed effect to account for differences in behaviour between species in response to the treatments. This variable could not be tested on Model 1 due to it being a measure of total visits and therefore excluding details of individual visits. No explanatory variables included in the full models were highly correlated ($r<0.249$ in all cases, see Appendix Table S3.1).

The minimum adequate models were reached by entering all fixed effects and dropping them sequentially until only those that explained significant variation remained (see site variable effect results in the Appendix Table S3.2). At each stage the reduced model was tested against the previous model to check that a significant amount of variation had not been lost using a Chi-squared statistic in an ANOVA.

Results

In total, at the 30 sites inside the current range of the parakeet population, the feeding station was visited 6872 times (median = 96, interquartile range = 42-252 visits per site) and in the 11 sites outside the parakeet range the feeding station was visited 4021 times (149, 72-311). Across these visits 18 native bird species were observed on the feeding stations, which were predominantly blue tits (*Cyanistes caeruleus*, 42% of visits) and great tits (*Parus major*, 41%) (a summary of visits made by each species, Appendix Table S3.3).

<u>Sites inside the current range of the parakeet population</u>

The analyses demonstrated that at sites inside the current range of the parakeet population, experimental exposure to caged parakeets resulted in a significant reduction in the number of visits by native birds to the feeders (Fig. 4.2a), a significant reduction in the number of visits that included a feeding bout (Fig. 4.2b), a significant reduction in the absolute time spent feeding (Fig. 4.2c), and a significant increase in the proportion of time spent vigilant (Fig. 4.2d), (Appendix Table S3.4). For all these behaviours, changes in the same direction were also observed in the presence of a woodpecker (Figure 4.2 and Appendix Table S3.4), but the changes in the presence of a parakeet were significantly greater than those in the presence of a woodpecker (Fig. 4.2 and Appendix Table S3.5).

A parakeet call alone reduced the proportion of visits resulting in a feeding bout and increased the proportion of time spent vigilant (Fig. 4.2 and Appendix Table S3.4). This effect was significantly greater from that of the woodpecker call for the proportion of time spent vigilant. But in all cases the effect of the parakeet call alone was less pronounced than that of the presence of a caged parakeet (Fig. 4.2 and Appendix Table S3.5) and the addition of a parakeet call to the presence of a parakeet had little additional effect for all response behaviours (Fig. 4.2 and Appendix Table S3.5).

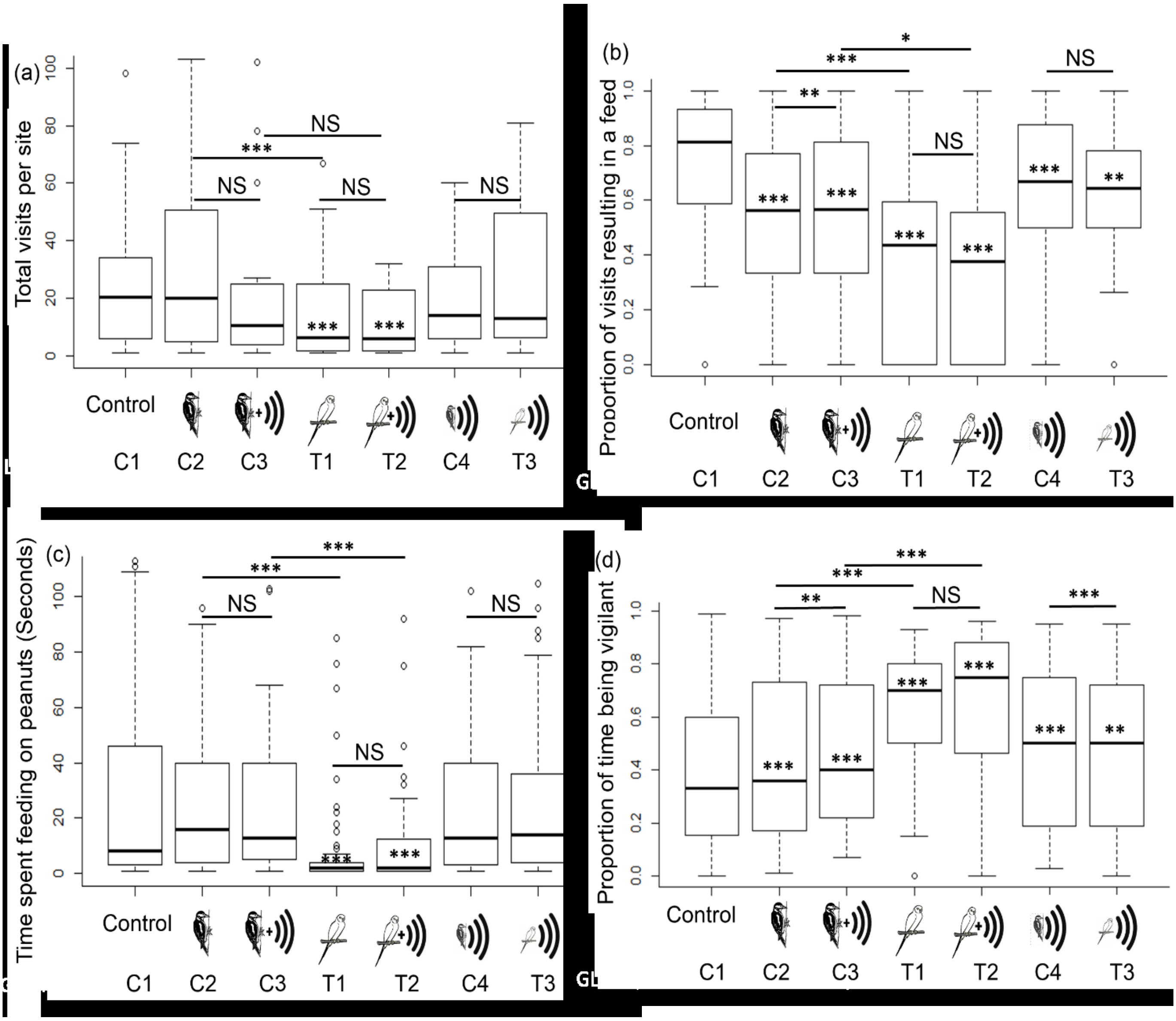

Figure 4.2. Box and whisker plots for (a) number of visits (n= 6826), (b) proportion of visits resulting in a feeding event (n= 6826), (c) time spent feeding (seconds) on peanuts per feeding visit (n=555), (d) vigilance (proportion of time spent not feeding (seconds) per feeding visit to peanuts) (n=555), per treatment for sites inside the parakeet range (n=30). Significant values within a box refer to the difference of the treatment from the control (C1), values outside a box and on a solid line refer to between treatments, (p-values, ***P<0.001, **P<0.01, *p<0.05).

Sites outside the current range of the parakeet population

Overall the patterns in response to treatments at sites outside the range were consistent with those inside the current parakeet range (Appendix Tables S3.4 and S3.5). The number of total visits to feeding stations was higher for three out of four of the control treatments (C1, C3 and C4) at sites outside the parakeet range compared to sites within (Fig. 4.3a). However, notably, parakeet treatments (T1 and T2) resulted in a lower proportion of feeding events outside of the parakeet range than inside (Fig. 4.3b and Appendix Table S3.6). During the two caged parakeet treatments there were so few feeding visits to peanuts, (T1 n=7, T2 n=3) that changes found for total feeding time and vigilance, in response to these two treatments could not be confidently compared (Appendix Tables S3.4, S3.5, S3.6). However, the parakeet call alone treatment (T3), which did have enough visits to compare (visits n=95 outside, n=63 inside), was shown to elicit a stronger vigilance response inside the parakeet range than outside (T3 outside range v T3 inside range; Appendix Table S3.5).

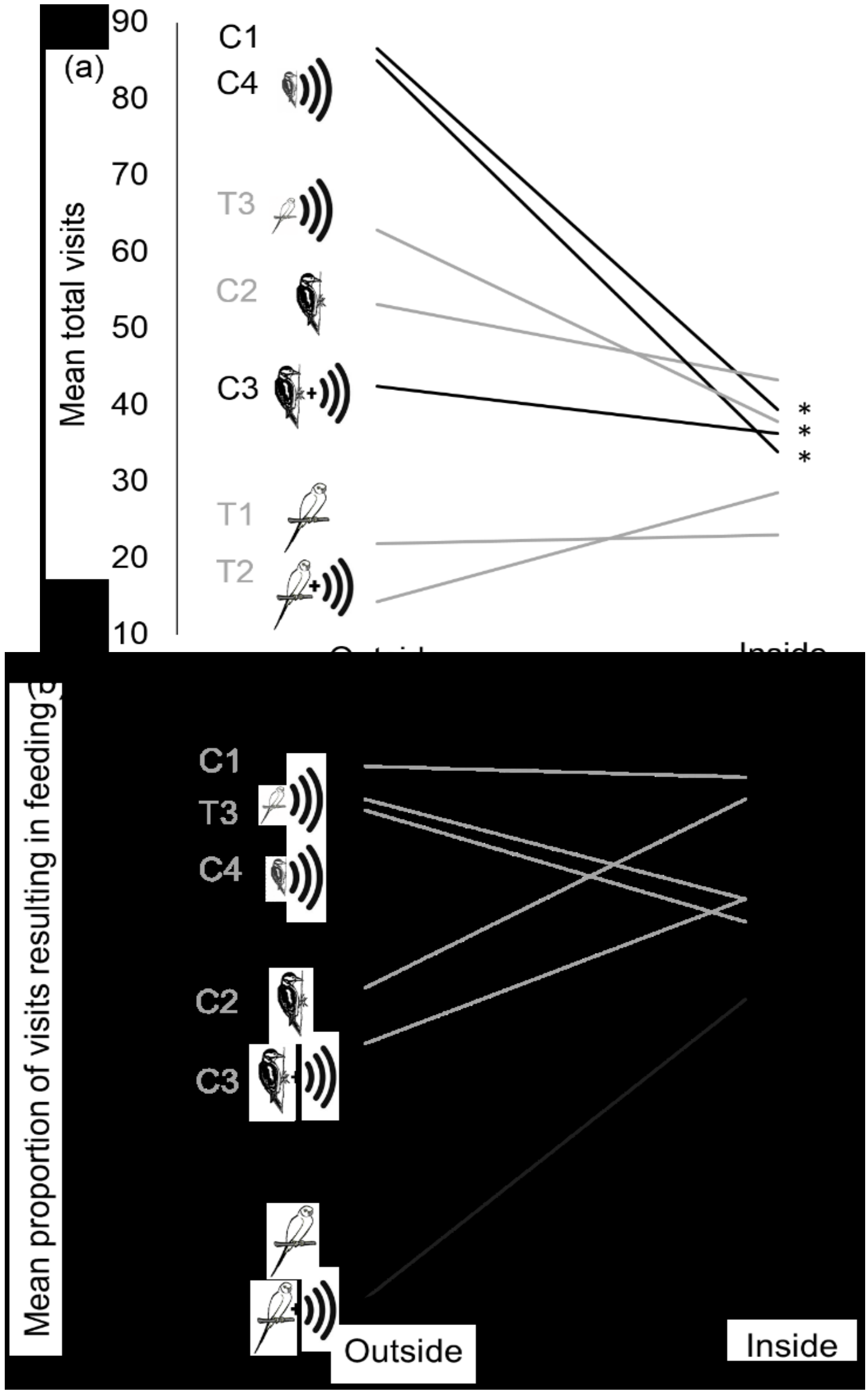

Figure 4.3 Differences between sites per treatments outside and inside parakeet range for (a) Mean total visits, and (b) the proportion of visits resulting in a feed (visits outside range n=4027, inside range n=6826). Significant difference refers to differences within treatments between sites outside and inside the parakeet range, grey lines denote differences between range sites within treatments which are not significant, black lines are significant (p-values, *P<0.05)

Discussion

These findings show that experimental exposure to parakeets influences the behaviour of native birds, resulting in reduced feeding and increased vigilance. These changes in behaviour are much more pronounced in the presence of a parakeet than in the presence of another dominant native species, the great spotted woodpecker. Whilst visit rates drop significantly both inside and outside the current parakeet range, visits that do occur are more likely to result in feeding inside the range. Taken together, these results suggest that interference competition between a non-native species and the native fauna does appear likely in this study system, and that some habituation may occur in the native populations.

Interference competition

Interspecific interference competition between native and non-native fauna is a concern as it may lead to reduced energy intake, and thus potentially lower the fitness of native birds (Gustafsson 1987; Cresswell 2008). Similarly, increased vigilance induced by the presence of non-native species can diminish the relative value of a food resource through increasing access costs (Cooper & Frederick 2007).

Interspecific competition between tit species in coniferous forest has been shown to cause displacement of individuals of less dominant species to lower quality food sources (Alatalo et al. 1987). The presence of parakeets may simply result in temporary displacement of native species from a food source, with minimal costs. For example a study found temporal niche shift behaviour in the case of foraging of an invasive mink (*Neovison vison*) in avoidance of two native mustalids (*Lutra lutra* and *Mustela putorius*) (Harrington et al. 2009). The analyses did, however, control for time of day and found it was not a significant predictor of the number of visits to the feeding station. This suggests that parakeets may induce a spatial, rather than, temporal shift in native bird foraging behaviour. Similar spatial shifts in response to environmental changes, such as loss of access to food resources, has been shown to lead to reduced population sizes (Durell et al. 2005, 2006; Stillman & Goss-Custard 2010). Consistent displacement of native birds from high quality resources may, therefore, be expected to have long-term implications for native species' populations.

There are very few examples in the literature of dominance over food sources by non-native species resulting in displacement of native species. Examples of this occurring with non-native vertebrates include an invasive gecko (*Lepidodactylus lugubris*) in Hawaii (Petren & Case 1996) and the invasive grey squirrel (*Sciurus carolinensis*) in the UK (Kenward & Holm 1993) but see (Wauters & Gurnell 1999). The subtle changes in feeding behaviour seen in response to parakeet presence may represent a mechanism for displacement, which to my knowledge would be the first case of such by a non-native avian species and therefore merits further investigation.

<u>Habituation</u>

The finding of a higher likelihood of feeding in the presence of a parakeet within the parakeet range compared to sites outside, suggests habituation to parakeets following prior exposure. This is particularly evident considering the overall lower mean total number of visits in the sites within the parakeet range compared to those outside. Without data on individual behaviour, it is not possible to distinguish whether this effect is due to an increased number of visits by bold individuals who have become accustomed to the parakeets, comparable to behaviour seen in several other bird species exposed to a predator (van Oers 2005; Quinn & Cresswell 2005; Minderman et al. 2010; Rockwell et al. 2012), but see (Couchoux & Cresswell 2011); or, if the perception of risk lowers for all individuals with continued exposure (Ellenberg, Mattern & Seddon 2009; Rodríguez-Prieto, Martín & Fernández-Juricic 2011). The former would suggest that some individuals may be disproportionately impacted by non-native species' presence, whereas the latter would indicate population-wide adjustment to the presence of a non-native species, and potentially lower overall impact.

In contrast to habituation to the presence of the parakeets, I also found some evidence of reinforcement behaviour, such that native birds within the parakeet range were more vigilant when exposed to a parakeet call, which suggests that prior exposure to parakeet calls has an influence on behaviour. This finding is consistent with previous studies demonstrating this initial lack of response of prey to the calls of a novel avian predator (Reudink et al. 2007; Elmasri et al. 2012) and studies demonstrating learned association of predator cues (reviewed by Griffin, Blumstein & Evans 2000).

It is possible differences in native bird behaviour between sites within and outside the parakeet range are due to differences associated with urbanisation (Lowry et al. 2012), however I did control for this in the analysis, by testing for an effect of distance from the city centre, which was not found to be of importance. Regardless of the causes for the differences in response of birds inside and outside the parakeet range, the higher proportion of feeding visits at sites inside the range in the presence of a parakeet was still lower than the control treatments and therefore foraging visits were still less successful across all sites in the presence of a parakeet at a food source, despite the prior exposure. This indicates that the inhibition of foraging in the presence of a parakeet is a permanent effect and not just a case of neophobia.

Ecological implications

It should be noted that wild rose-ringed parakeets often forage gregariously and therefore monopolise a feeding site (Pithon 1998). During the experiment, 95 out of 136 visits by wild parakeets to the experimental feeding station were when one of the captive parakeets was present in the cage, further demonstrating parakeets' gregarious nature. Given this I would expect that the impacts demonstrated here are a conservative estimate of those that would be seen with free living parakeets.

It has been hypothesised that optimal foraging in urban settings can alter the community structure and result in biodiversity loss (Shochat et al. 2004). It is also common for invading species to establish where competition among the resident species is low (Crawley et al. 1986) and so the dominance of non-native species can also be increased by the provision of artificial feeding stations in gardens (Chace & Walsh 2006; McKinney 2006; Jones & Reynolds 2008; Cannon 2010). The link between garden feeding and the success of invasive species is seen directly in Chicago, where the persistence and growth of the monk parakeet (*Myiopsitta monachus*) population is attributed to the generalist diet of the non-native species and its sole use of bird feeders in winter (South and Pruett-Jones, 2000). Clearly garden food provisioning plays a major role in the persistence of invasive populations, which in tandem with the temporally stable climate and homogenisation of the environment makes the urban landscape favourable to non-native species (Garden *et al.*, 2006). Given the evidence for foraging disruption at artificial food sources and the potential reliance of the parakeets on garden bird feeders (Clergeau & Vergnes 2011), an interesting implication is that the exclusion of parakeets from access to garden bird feeders might benefit native species through reducing the interference competition, whilst simultaneously reducing the foraging benefits of urban areas for the parakeets, which may in turn limit the persistence of the parakeet populations.

In conclusion, I have shown that the presence of a non-native bird can disrupt foraging behaviour in native birds. These findings are the first to my knowledge to demonstrate interference foraging competition between non-native and native birds. Whilst this study does not provide proof of any population level change as a result of the disrupted foraging, it does demonstrate a mechanism by which non-native birds could potentially impact native species at the population level and shows a need for further investigation. The increased establishment of rose-ringed parakeets in the UK (Tayleur 2010) and across Europe (Strubbe & Matthysen 2008) as well as other non-native bird species in urban areas across the world (Peacock et al. 2007; Blackburn et al. 2009; Bonter et al. 2010), highlights the potential for widespread occurrence of similar effects of foraging behaviour on urban birds.

Chapter 5

Evidence of direct competition for food between the non-native rose-ringed parakeet (Psittacula krameri) and native birds in urban gardens

Abstract

Non-native rose-ringed parakeets (*Psittacula krameri*) are increasingly found in gardens in cities across Europe but little is known about their impacts on native wildlife despite their broad diet and use of garden bird feeders, meaning they have the potential to be competing with a wide range of garden birds. Using a year-long experimental study with bird feeders in urban gardens in London, the UK, I test how much wild parakeets are depleting common food sources used by native garden birds and whether this effects native species' overall food consumption. I demonstrate direct competition between parakeets and native birds at supplemental food sources in gardens where parakeets are present daily, with consistent displacement of all native species, resulting in a significant reduction of food consumed by great tits. At this high level, parakeets have the potential to be depleting food resources twice as fast as would occur without their presence. These findings indicate that for native birds, the interference of foraging behaviour caused by presence of parakeets at a food source results in reduced food consumption and continuous displacement from shared food sources.

Introduction

Non-native species have been increasingly establishing in urban areas (Peacock et al. 2007; Blackburn et al. 2009; Bonter et al. 2010), where introductions are more frequent, but also where the disturbed landscape and abundance of human-provided resources can help support establishment (McKinney 2006; Garden et al. 2006). Under these conditions, competition for resources between non-native species and native species can play a large role in the establishment success of non-native species and in some cases may cause the competitive exclusion of native species (Shochat et al. 2010). Resource competition between non-native and native species is not inevitable as non-native species can also utilise resources which native species do not and therefore assist successful invasion. For example, the common waxbill *(Estrilda astrild*) in SW Europe (Batalha et al. 2013) and five species of small non-native birds in urban areas in NSW Australia (Sol et al. 2012), were found to forage opportunistically by exploiting under-utilised food resources and therefore avoid competition with native species.

If resource competition does occur, theoretically it can happen through exploitation competition whereby the non-native species does not directly inhibit feeding by the native species but indirectly affects them by depleting a limited resource, or by interference competition, when the invasive species directly excludes the native species from utilising the same resource (Amarasekare 2002). Interference by a competitor does not necessarily result in reduction of food consumed. It could be that the food source is so abundant that the effect of interference does not impact food consumption. For example the invasive cane toad (*Chaunus [Bufo] marinus*) in Australia has been shown to suppress activity of the native frog (*Cyclorana australis*), but despite this did not influence food intake or diet composition (Greenlees et al. 2007), due to the high abundance of the food source. It could also be that temporary displacement of the native species (spatial or temporal) occurs but no overall reduction in total consumption of the resource, as food can be consumed at another time or place.

It is important to distinguish between these possible processes of interference competition, because if temporary displacement is occurring but overall food consumption is unaffected then the fitness of individuals should be maintained and the population unaffected. For example the coexistence of the invasive American mink (*Neovison vison*) with the native otter (*Lutra lutra*) despite dietary overlap, was found to occur because of an apparent temporal shift in foraging of the mink to avoid foraging at the same time as the otter (Harrington et al. 2009). But if there is reduction in total consumption of the food source, and/or depletion of the food source, then fitness may be reduced. For example, displacement due to interference through aggression at a food source was found to be the mechanism behind competition between the invasive black rat (*Rattus rattus*) and the endemic Santiago rice rat (*Nesoryzomys swarthi*) on a Galápagos island, resulting in decline in the endemic population (Harris & Macdonald 2007).

Given that population declines can occur under resource competition, it is possible that species diversity can be affected as a result. For example, Argentine ants (*Linepithema humile*) have been found to reduce diversity of native ant species in areas that they have invaded through both aggressive encounters and reduced foraging success (Human & Gordon 1996).

Evidence for or against effects occurring on native birds through competition by non-native birds is lacking (Blackburn et al. 2009), with assumptions about potential impacts on native species made without scientific evidence (Strubbe et al. 2011). This may partly be due to cases where impacts of competition by non-native birds are neutral or negligible being more likely to have gone unreported than those that have caused negative (or positive) impacts, and being under represented in the literature (but see Poling & Hayslette 2006; Sol et al. 2012). Even when correlative studies have shown changes in abundance of native species associated with non-native species competition, evidence is lacking for the resource competition mechanisms causing these changes (Strubbe et al. 2011). This may be because evidence for direct, over indirect, competition for resources can be difficult to detect (Eguchi & Amano 2004). This difficultly may be, in part, because disentangling the effects of resource limitation due to indirect competition, from those due to the impacts of habitat disturbance from urbanisation, can prove difficult (Parsons et al. 2006). Particularly as variation in ecological parameters make the changes in resource availability and species abundance difficult to compare (Shochat et al. 2004; Sax et al. 2007). These difficulties highlight the need for experimental studies, allowing these various confounded factors to be controlled, to investigate whether this is an impact of non-native species through direct interspecific competition.

The altered landscape and resource availability in urban areas can alter the diversity and abundance of native birds species (Clergeau et al. 2002; Møller 2009). In particular food supplementation through provision of bird feeders has been shown to increase abundance of wild birds in urban areas (Parsons et al. 2006; Fuller et al. 2008; Chamberlain et al. 2009), suggesting artificial food sources may support bird species in establishing and expanding in urban areas where natural food sources are less available (Parsons et al. 2006; McKinney 2006; Pruett-Jones et al. 2007). It has been hypothesised that native species which are abundant in urban areas are those that are most adaptable and able to utilise resources in a disturbed environment, making these species more resistant to competition from non-native species (Lowry et al. 2012). However, this adaptability may also benefit invasive species as a mechanism of establishment as they tend to have broad diets and high behavioural flexibility (Sol et al. 2002). These characteristics are likely to increase their potential to compete for food with a variety of native species, particularly at supplementary feeding stations (Shochat et al. 2010). In addition, supplemental feeding using garden bird feeders is widespread in many urban and particularly suburban areas; for example, it has been estimated that 51% of households with gardens in the UK feed birds (Davies et al. 2009). Consequently, supplementary feeding in urban areas presents an important resource for which to study competition between native and non-native species (Shochat et al. 2004).

A non-native species that is known to utilise urban resources and particularly garden bird feeders is the rose-ringed parakeet (*Psittaculla krameri*). The parakeet's highly varied diet (Feare 1996), its ability to eat non-native plants and human-provided food sources (Koutsosms et al. 2001; Clergeau & Vergnes 2011) and the fact that individuals have been found to spend half their feeding time at artificial bird feeders (Clergeau & Vergnes 2011), means that it has potential to compete with a wide variety of native bird species in urban gardens. Also, its relatively large size in comparison to many other garden bird species which use feeders in the UK (rose-ringed parakeet: 400 mm length, mass 120g, (Snow et al. 1998)), is generally thought to give it an advantage in interspecific interactions (Alatalo & Moreno 1987; Schro et al. 2009; Robinson et al. 2013) but see (Poling & Hayslette 2006).

The current distribution of established parakeet populations across Europe has so far been in urban or semi-urban areas, which highlights its ability to thrive in these landscapes (Strubbe & Matthysen 2007, 2009) and the potential for it to increase in abundance and distribution in urban areas elsewhere (Strubbe & Matthysen 2009). Despite its increasing presence and establishment, there have been few studies exploring its impacts on native fauna. These studies have focussed on competition for nest sites and found negligible impacts (Strubbe et al. 2010; Newson et al. 2011). This lack of investigation has led to concerns being raised about the lack of scientific evidence to support claims of the detrimental potential of the rose-ringed parakeet to native wildlife (Strubbe et al. 2011).

Chapter 4 provides experimental evidence that parakeet presence at a food source interferes with the foraging behaviour of native birds, resulting in reduced number of visits and feeding time of native birds and increased their vigilance time, particularly in the blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*). Given that parakeets are known regularly to use garden bird feeders, this suggests that parakeets may be directly competing with native birds through interference competition at the common food source, however there is no evidence as to how much the parakeets are actually depleting the food available for the native species. In addition, it is not known what the overall impact of interference of foraging is on the total consumption of the food source by native species. It could be that there is temporary displacement of the native birds, either spatially or temporally, but no overall reduction in total consumption of the resource. Or it could be that the birds are consistently displaced resulting in reduction in total consumption of the resource and potentially population level effects. It also not known if the interference to foraging (as shown in Chapter 4) varies between different native species using the food source or if the effect is the same across species. It is important to quantify the competitive impact that this is having in order to determine the broader implications for the impact of parakeets on native species.

By manipulating parakeets' access to standardised bird feeders in parakeet-frequented gardens in London, UK, I aim to establish: i) if use of garden bird feeders by parakeets is reducing food availability for native birds and if so by how much, ii) whether this competition with parakeets is simply temporarily displacing native birds or if their overall use of garden bird feeders is reduced, and iii) whether the effects of this competition differs between two common garden native bird species: blue tits and great tits. See Table 5.1 for more details of the hypotheses tested.

Table 5.1 Summary of hypotheses and statistical models used in this chapter to explore the impact of parakeet use of garden bird feeders on foraging behaviour of native birds. The statistical models described in the table were fitted separately to data from weeks where no parakeets were observed and where parakeets were observed every day. See methods for more model fitting details.

Hypothesis	Tests	Explanatory variables
i) Food availability Parakeets' use of garden bird feeder depletes food available for native birds.	Generalised linear mixed effects model (GLMM) of weekly food consumed	- Feeder type (parakeet accessible or restrictive) - Parakeet presence during observations (0/1) - Blue tit presence during observations (0/1) - Great tit presence during observation (0/1) - Other native species presence during observations (0/1) - Interaction of feeder type and each species presence (parakeet, blue tit, great tit or other species) - Season - The order in which the treatment (restrictive feeder) was placed (1st or 2nd six months) - The garden identity as a random effect
ii) Effects of parakeet competition Native birds alter their use of garden feeder to periods when parakeets are not using them (temporal displacement) Native birds alter their use of garden feeder in response to the feeders' accessibility to parakeets (spatial displacement)	GLMM of visits during observation by - All species - Blue tit - Great tit	- Feeder type - Parakeet presence in observation (0/1) - Season - Time of day (hour) - The order in which the treatment (restrictive feeder) was placed (1st or 2nd six months) - The garden identity as a random effect
iii) Species-specific effect The effect of parakeet use of bird feeders will vary between great tits and blue tits.	Tested by including presence/absence of each species (blue tit and great tit) in i) and by fitting separate models for the number of visits made by each species in ii).	

Methods

<u>Experimental procedure</u>

Standardised feeding stations were set up at 33 garden sites in London and Ramsgate, UK where the garden owners reported parakeets as regular visitors to garden bird feeders (see Fig. 5.1). Garden owners were recruited through advertisements made through the media, project website, local bird watching groups and word of mouth (see Chapter 2), and therefore the location of sites used were constrained by those offered. Procedures for contacting members of the public were assessed and passed by Imperial College's research ethics committee in April 2010. Sites were at least 500m apart (closest distance between two sites 566m) to minimise the risk of repeating the experiment on the same individual birds.

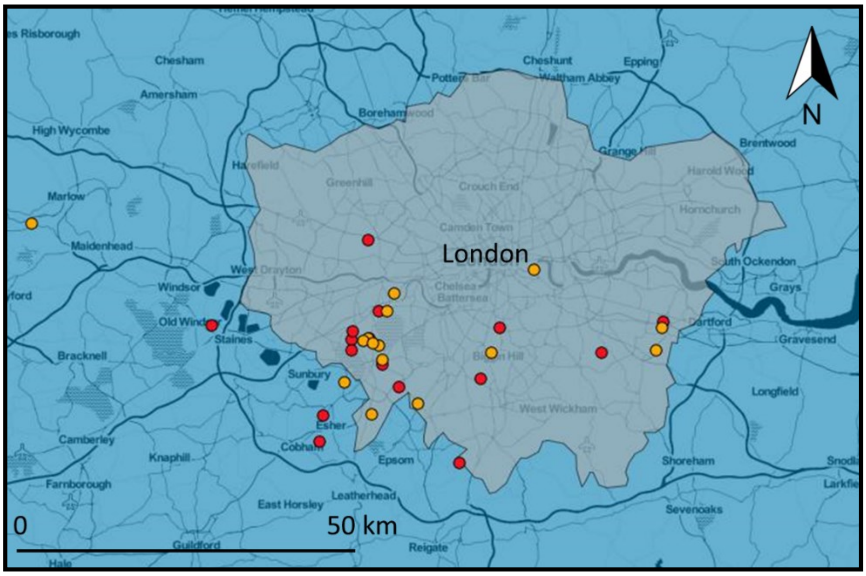

Figure 5.1. Garden locations in South East England. Orange dots are gardens in Group A, red dots Group B. An additional garden in Group A is in Ramsgate Kent, approximately 100km to the South East. The grey shaded area represents the boundary of Greater London.

Two types of feeding stations, 'accessible' and 'restrictive' garden bird feeders, were installed at these sites for six months each, both were designed for seed and had metal mesh cages surrounding them to prevent access by squirrels (see Chapter 2). The 'Accessible feeders' (dimensions 20.3 x 20.3 x 34.3cm, size of mesh squares 5.2cm x 2.8 cm, distance from mesh cage to food 6 cm)could be accessed by all garden birds including parakeets. The 'Restrictive feeders' had smaller mesh size and further distance from the mesh to the seed dispenser to restrict access to the food by larger birds, in particular parakeets (dimensions 21.2 x 21.2 x 23.2 cm, size of mesh squares 2.6cm x 3.55cm, distance from mesh cage to food 6.5cm). Sites were divided in to two groups, A and B by alternating between the two as each garden was recruited. Each site in group A had an accessible feeder installed in their garden for 6 months from December 2011 till June 2012, and a restrictive feeder from June 2012 till December 2012. Sites in group B had a restrictive feeder for the first six months and an accessible feeder for the second six months.

All existing bird feeders were removed from the gardens, and the single standardised feeder introduced. Each feeder was marked to show the food level that represented c.220g of black sunflower seeds and was refilled ad libitum by the volunteer. Black sunflower seed was chosen as it proved popular for both parakeets and native birds in a previous experiment (see Chapter 4), is used commonly in garden bird feeders and has a high nutritional value for birds (Ewald & Rohwer 1982), making it an attractive food. The feeders, therefore, represented a localised, high value resource that could be standardised across sites independent of season.

The 'accessible' and 'restrictive' bird feeders, were tested for their effectiveness by placing them in a garden for three weeks where parakeets and other garden birds visited throughout the day. During this time groups of up to eight parakeets were observed attempting to feed from the restrictive feeder daily but without success, while other garden birds were observed feeding from both feeders successfully. Post hoc analysis of the yearlong data found the restrictive feeder was accessed by a parakeet (ie. the parakeet was able to feed) on 50 occasions out of 583 observations, whereas parakeets accessed the accessible feeder on 632 occasions out of 564 observations.

Data collection

Each of the volunteers conducted weekly 20 minute observations of the feeders from December 2011 to December 2012 (n=30). An additional three gardens had data available for only six months or fewer preventing treatment comparisons. Volunteers varied the time of day they made these observations from week to week. This was in order to capture a more representative sample of the species using the feeders and the numbers of visits they made. The information recorded during the observation included the date and start time, the amount of seed refilled per week, e.g. 2.5 refills, this was later transformed to approximate grams of seed, the total number of visits by each species and the maximum number of birds of each species on the feeder at once.

In each week volunteers also recorded number of days parakeets visited the garden (0 to 7) and the maximum number of parakeets seen in the garden. For the second six month period, the volunteers also recorded whether a parakeet visit to the feeder resulted in feeding and the time (minutes and seconds) the parakeet spent feeding.

The volunteers were trained individually by HLP using standardised methods and given an instruction booklet and bird species identification and methods information online. Observations were recorded on identical observation sheets (see Chapter 2) and copied to an online survey site or sent directly to HLP. Error checking was carried out on a weekly basis by HLP by scanning through the observations for a sign of any unusual information and the volunteer was contacted by email or telephone to verify unusual observations. Where inconsistencies were found the methods were clarified again and observations deemed incorrect were removed from the data. Where the volunteer continued to follow the methods incorrectly all observations from the garden were removed from the data.

Data analysis

Feeder effectiveness at restricting parakeets

Prior to the main analyses (see Table 5.1), preliminary analyses were conducted to confirm that the restrictive feeder did effectively restrict parakeets' access to food. Generalised linear mixed effects models (GLMMs) were used to test whether the feeder design effectively restricted parakeets. The following three measures were fitted as response variables with feeder type as the explanatory variable and garden identity as a random intercept: a) whether a parakeet visited during the observation, b) whether a visiting parakeet fed from the feeder during an observation, c) the number of days over the week that parakeets were observed in the garden. Models a and b were fitted using a binomial error structure with a logit link function and model c was fitted using a Poisson error structure with a log link function.

Number of visits and seed consumed

Data for number of visits and the amount of seed consumed were analysed using GLMMs (see Table 5.1). Analyses were divided into two categories of contrasting parakeet presence levels:

1) No parakeet presence defined as 0 observations of parakeets in the past week (83 observations of the accessible feeder across 17 gardens and 136 observations of the restrictive feeder across 22 gardens); The purpose of this analysis was to confirm that the differences in feeder design between the restrictive and accessible feeder did not affect native bird foraging behaviour, and so the results of the analysis of the next data set (high parakeet presence) were due to differences in parakeets' ability to access food rather than differences between the accessible and restrictive feeder design.

2) High parakeet presence defined as daily observations of parakeets in the past week (263 observations of the accessible feeders across 23 gardens and 166 observations of the restrictive feeders across 20 gardens), to test for any difference in feeder-type effects that occurred at high parakeet presence.

Data representing low levels of parakeet presence (observations during weeks where parakeets were observed for 1-6 days) were also analysed in the same way to these two data sets (see Appendix S4)

Models were fitted with an observation-level random effect and using a Poisson lognormal error structure with a log link function to account for over-dispersion (Elston et al. 2001) and with the garden identity code added as a random effect. Season (spring: April–May, summer: June-August, Autumn: September–November, winter: December–February) was included as a fixed effect to account for seasonal effects on feeding requirements (Chamberlain et al. 2005). In addition the order in which the treatment took place per garden (the restrictive feeder put up for the 1st or 2nd six months) was added as a fixed effect to account for the possibility of a time-lag between the feeder type being changed and parakeets adjusting their feeding behaviour accordingly (Sih 1992; Evans 2003). Time of day (hour of the day 6am to 8pm) was included in models of number of visits to account for changes in foraging activity during the day (Bonter et al. 2013). In each case minimum adequate models were reached by entering all fixed effects in the full model and dropping them sequentially until only those that explained significant variation remained. At each stage the reduced model was tested against the previous model to check that a significant amount of variation had not been lost using a Chi-squared statistic in an ANOVA. Details specific to each model in each analyses are provided below.

Number of visits

Generalised linear models of weekly observations of number of visits of native birds were run to test for differences between numbers of visits to the two feeder types (see Table 5.1). These included models of each of the two data sets (no parakeets and high parakeet presence) run separately for three response variables describing the number of visits during the weekly 20 minute observations by, a) all native species (i.e. excluding parakeets) b) blue tits and c) great tits. Blue tits and great tits made up 89% of all species observed and analysing their visits separately allowed us to test for any differences between the two species (see Table 5.1). Each of the models, was fitted as described above and also included feeder type (restrictive or accessible) as a fixed effect. Models run with the high parakeet presence data set also included whether a parakeet visited the feeder during the observation (0 or 1) as a fixed effect, to account for any effect of presence of a parakeet at the feeder on the number of visits made by native birds.

Seed consumed

The amount of seed refilled per week was taken as an indication of the amount of seed eaten by visiting birds and was analysed as approximate quantity of food (g) eaten per week (see Table 5.1). Ad libitum observations of parakeet feeding visits to the feeders found parakeets fed for a median of 6 minutes at a time (IQR 3-10, 114 observations). Observations of blue tit and great tit visits made during a previous experiment to the same parakeet accessible feeders and seed, found feeding visits lasted for 1 second or less (see Chapter 4). Therefore, for analysis of species effects on food consumed, whether or not each species visited the feeder during an observation was used for comparison of species effects on weekly food consumption rather than visit numbers per species per observation.

Separate models using the two data sets (no parakeets and high parakeet presence) were fitted. Both models included the total seed eaten (g) from the feeder each week as the response variable, and whether a visit occurred from a blue tit (0,1), great tit (0,1) and all other species (0,1) during the weekly observation, feeder type (restrictive or accessible) as fixed effects and an interaction between feeder type and each species presence.

All analyses were conducted in R (R Core Development Team 2009) using the lme4 package to fit GLMMs (Bates et al. 2012).

Results

Parakeet presence in gardens

The median maximum number of parakeets seen in the gardens (n=33) at a time was 3 (IQR 1-5). 19% of observations were in weeks where no parakeets were seen in the garden, 43% were when parakeets were seen from one to six days during the week and 38% were during weeks when parakeets were seen in the garden daily. Although all gardens had parakeets present at least once over the year, two gardens never had parakeets use either of the feeders during observations.

Feeder type effectiveness at manipulating parakeets' ability to access food

The likelihood of a parakeet visiting the feeder during the observation was reduced from 36.3% (205 out of 564 observations) when gardens had the parakeet accessible feeder to 8.7% (51 out of 583 observations) when they had the parakeet restrictive feeder (binomial GLMM, coefficient (± s.e.) = -2.42 (±0.21), z= 11.3, $p<0.001$). The likelihood of parakeets that visited the feeder going on to feed from it was reduced from 98.0% (201 out of 205 observations in which a parakeet visited) when gardens had the parakeet accessible feeder to 43.1% (22 out of 51 observations in which a parakeet visited) when they had the parakeet restrictive feeder. (binomial GLMM, coefficient (± s.e.) = -4.70 (0.69), z= 6.79, p<0.001).

The number of days during the week that parakeets were seen in the garden was lower in weeks when the restrictive feeder was in the garden (median number of days = 3, IQR 1-7, n=571 observations) compared to weeks when the accessible feeder was in the garden (median number of days = 6, IQR 2-7, n=554 observations; Poisson GLMM, coefficient (± s.e.) = -0.26 (±0.03), z=8.4, p<0.001).

Number of visits

Of the 564 observations of parakeet accessible feeders, a total 16,497 native bird visits occurred (median 11, IQR 3-36 per observation) and of the 583 observations of the parakeet restrictive feeders, 15,785 native bird visits occurred (median 10, IQR 3-30 per observation). Other than parakeets, 23 species were recorded visiting the feeders. 54% of visits were from blue tits and 35% from great tits. The other 21 species made up only 11% of total visits. (see Appendix Table S4.1 for visit numbers for each species to each feeder type). Blue tit visits occurred in 69% of observations to the parakeet accessible feeder and 77% of observations to the parakeet restrictive feeder. Great tit visits occurred in 65% of observations to the parakeet accessible feeder and 63% of observations to the parakeet restrictive feeder.

Weeks where parakeets were absent from gardens

To test for the effect of differences in the two feeder designs on the number of visits by native species (rather than those due to the effect that the feeder types had on parakeets' ability to access food), I analysed data for just weeks where no parakeets were seen in the garden. There were no differences between feeder types in the number of visits made by all native birds, blue tit and great tits (Table 5.2) indicating that the feeder designs do not influence the number of visits by native species.

Table 5.2 Results of the generalized linear mixed models analysing factors effecting number of visits per observation to the bird feeders when parakeets were not seen present in the garden for at least a week prior to the observation, for visits by: all species, just blue tits and just great tits (NS: no significant difference, ** p<0.01-0.005, ***p<0.005). Garden identity is included as a random effect.

	species visits (excluding parakeets)				blue tit visits				great tit visits			
Feeder	total visits	median visits	IQR		total visits	median visits	IQR		total visits	median visits	IQR	
Accessible	2006	9	1-31.5		1164	2	0-11		459	1	0-9	
Restrictive	2261	8.5	3-21.5		1440	4	1-9.5		559	1	0-4	
	estimate	s.e.	pvalue		estimate	s.e.	pvalue		estimate	s.e.	pvalue	
Intercept†	1.132	0.489	0.021		0.780	0.537	0.146		0.231	0.669	0.729	
Restrictive	0.183	0.255	0.473	NS	0.461	0.271	0.089	NS	-0.478	0.334	0.152	NS
Summer	0.963	0.300	0.001	**	0.851	0.324	0.009	**	0.487	0.417	0.244	NS
Autumn	1.356	0.293	<0.001	***	1.005	0.315	0.001	**	1.440	0.388	<0.001	***
Winter	0.747	0.196	<0.001	***	0.879	0.211	<0.001	***	0.484	0.283	0.087	NS
Hour	-0.004	0.027	0.869	NS	-0.053	0.030	0.083	NS	-0.023	0.040	0.557	NS

† the intercept is the parakeet accessible feeder in spring

Weeks where parakeets were seen every day (high level of parakeet presence)

To test for the effect of restricting parakeets' ability to access food on bird visits where parakeets were present high levels, I analysed data from weeks where parakeets were seen in gardens every day. Native birds (all species, blue tit and great tit models) visited the parakeet accessible feeder less than the restrictive feeder (Table 5.3 and Fig. 5.2). For these weeks with a higher level of parakeet presence, occurrence of a parakeet visit on the feeder during the twenty minute observation had a significant negative effect on number of visits in all cases (Table 5.3). (See Appendix Table S4.2 for corresponding results for weeks where parakeets were observed between 1-6 days, i.e. lower parakeet presence).

Table 5.3 Results of the generalized linear mixed models analysing factors affecting number of visits per observation to the bird feeders for weeks of high parakeet presence, for visits by: all species, just blue tits and just great tits (NS: no significant difference, * p<0.05** p<0.01, ***p<0.005), garden identity is included as a random effect.

	species visits (excluding parakeets)				blue tit visits				great tit visits			
Feeder	total visits	median visits	IQR		total visits	median visits	IQR		total visits	median visits	IQR	
Accessible	9977	15	6-49		5199	5	0-23		3105	3	0-16	
Restrictive	7091	17	4-61		3319	5	1-29		3216	7	0-27	
	estimate	s.e.	pvalue		estimate	s.e.	pvalue		estimate	s.e.	pvalue	
Intercept†	2.445	0.349	<0.001		1.045	0.414	0.011		0.828	0.484	0.088	
Restrictive	0.257	0.128	0.046	*	0.343	0.156	0.028	*	0.566	0.157	<0.001	***
Parakeet	-0.557	0.125	<0.001	***	-0.604	0.152	<0.001	***	-0.482	0.150	0.001	**
Summer	0.025	0.174	0.884	NS	0.298	0.217	0.171	NS	0.146	0.211	0.488	NS
Autumn	0.647	0.168	<0.001	***	1.109	0.208	<0.001	***	0.614	0.202	0.002	**
Winter	0.831	0.155	<0.001	***	1.368	0.193	<0.001	***	0.702	0.186	<0.001	***
Hour	-0.033	0.017	0.060	NS	-0.023	0.021	0.277	NS	-0.040	0.021	0.060	NS

† the intercept is the parakeet accessible feeder in spring.

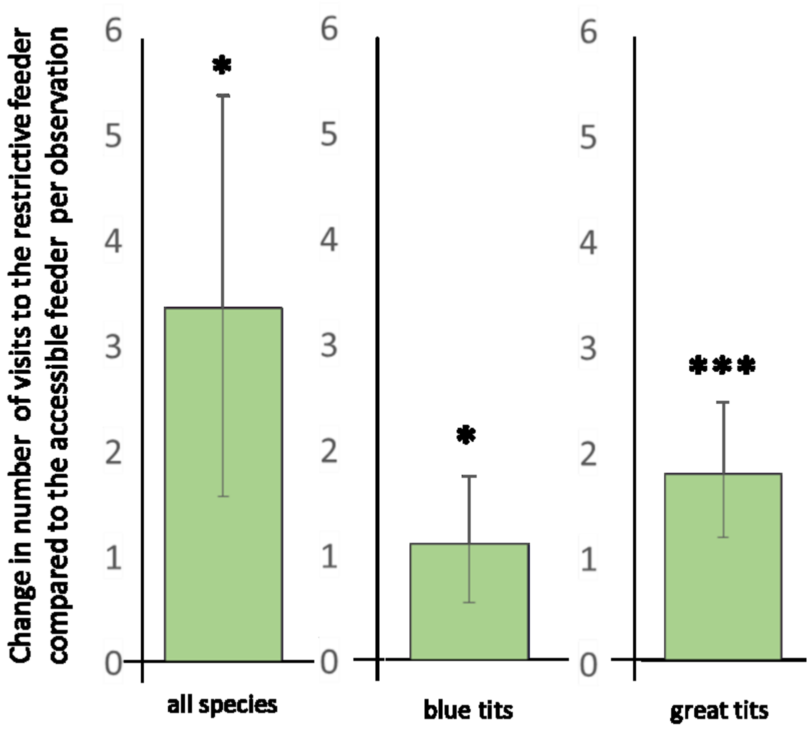

Figure 5.2. The predicted change in the number of visits per observation for the restrictive feeder compared to the accessible feeder, for observations in weeks of high parakeet presence (Significant difference in visits to the restrictive feeder compared to the accessible feeder: * = p<0.05, *** = p<0.001).

Seed consumed per week

Weeks parakeets were absent

Blue tits were observed in 73% of observations in parakeet absent weeks (161 out of 219 observations), great tits were observed in 54% of observations (119/219) and other species were observed in 43% of observations (95/219).

To test for the effect of differences in the two feeder designs on the amount of seed consumed, we analysed data for weeks where no parakeets were seen in the garden. A median of 220g per week was consumed from both feeder types, parakeet accessible (IQR 33-660) and parakeet restrictive feeders (IQR 0-413). Overall no difference was found in the amount of food eaten between feeder types (Table 5.4). More food was eaten from both feeders when blue tits visited during the observation while when species other than blue tits and great tits visited during the observation more food was eaten from the accessible feeder than from the restrictive feeder (Table 5.4). Whether great tits visited during the observation did not explain a significant amount of variance in seed eaten and so did not remain in the minimal model.

Table 5.4 Results of the generalized linear mixed model analysing factors affecting the amount of seed eaten per week in parakeet absent weeks (NS: no significant difference, * $p<0.05$** $p<0.01$, ***$P<0.005$), garden identity is included as a random effect.

	estimate	s.e.	p-value	
Intercept †	0.690	0.774	0.373	
Blue tits visited	1.178	0.513	0.022	*
Other sp. visited (accessible feeders)	2.258	0.734	0.002	**
Restrictive feeder	0.731	0.595	0.219	NS
Other sp. visited: restrictive feeders	-1.78	0.861	0.039	*
Summer	1.819	0.633	0.004	**
Autumn	1.873	0.645	0.004	**
Winter	0.547	0.501	0.274	NS

† the intercept is the parakeet accessible feeder in spring.

High parakeet presence weeks

Blue tits were observed in 77% of observations in high parakeet presence weeks (330 out of 431 observations), great tits were observed in 71% of observations (306/431) and other species were observed in 49% of observations (211/431).

To test for the effect of restricting parakeets' ability to access food on the amount of seed consumed by native birds where parakeets were present at higher levels, I analysed observations from weeks where parakeets were seen in gardens every day. Overall less food was eaten from the parakeet restrictive feeder (Table 5.5), with a median of 330g (IQR61-880) eaten per week from the restrictive feeder compared to 660g (IQR 220-1540) from the accessible feeder. Great tit presence increased the amount of food eaten but only from the parakeet restrictive feeder (see Table 5.5), with a predicted increase of 162g compared to when they were not present (see Fig. 5.3). Blue tit or other species presence did not predict any significant difference in the amount of seed consumed and did not remain in the minimal adequate model. (See Appendix Table S4.3 for corresponding results for weeks where parakeets were observed between 1-6 days, ie lower parakeet presence).

Table 5.5 Results of the generalized linear mixed model analysing factors effecting the amount of seed eaten per week for just weeks of high parakeet presence (426 observations and 26 gardens) (NS: no significant difference, * p<0.05** p<0.01, ***p<0.005) , garden identity is included as a random effect.

	estimate	s.e.	p-value	
Intercept †	5.799	0.455	<0.001	
Great tit visited (accessible feeder)	-0.104	0.217	0.631	NS
Restrictive feeder	-2.002	0.326	<0.001	***
Great tit visited: restrictive feeder	1.638	0.375	<0.001	***
Summer	-0.477	0.229	0.038	*
Autumn	-0.388	0.222	0.081	NS
Winter	-0.337	0.206	0.102	NS

† the intercept is the parakeet accessible feeder in spring.

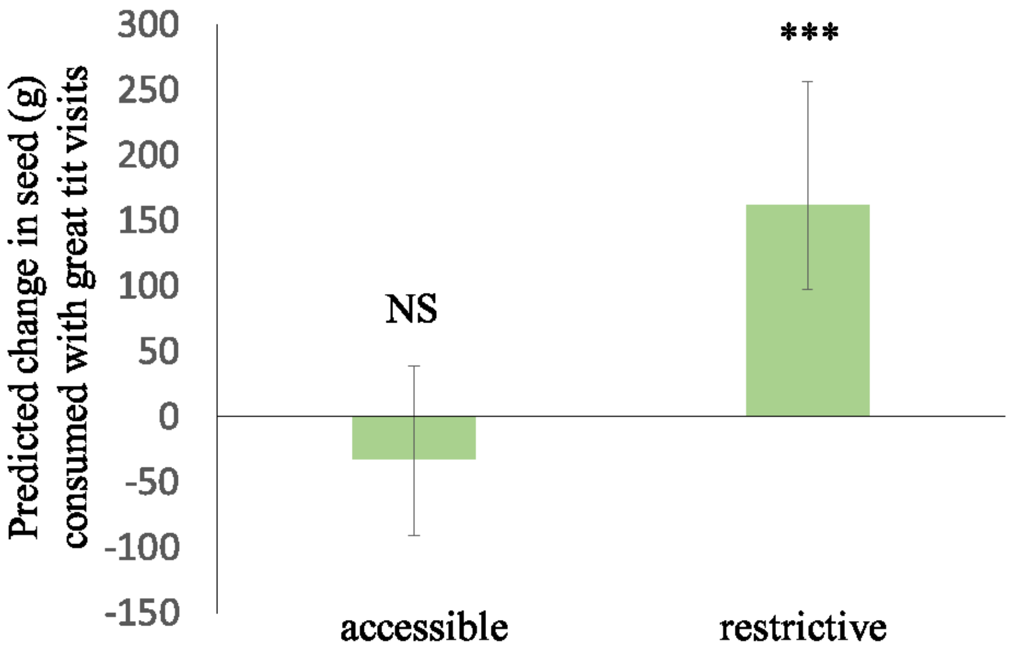

Figure 5.3. Predicted change in seed (g) consumed per week by great tits between feeder types for weeks of high parakeet presence (error bars: +/- predicted standard error, ***p<0.001: significant difference in seed consumed between feeder types).

Discussion

I found that the parakeet restrictive feeder did effectively restrict parakeets from feeding. There was a reduction in the likelihood of parakeets visiting the restrictive feeder compared to the accessible feeder. When parakeets did visit, feeding from the restrictive feeder did not occur on almost all occasions. In addition when the restrictive feeder was in the gardens, parakeet visits reduced, therefore indicating that once parakeets had learned that they could not access food from the feeder, they stopped attempting to. I therefore conclude that parakeets are depleting a common food source resulting in reduced consumption of food by other species. This interspecific competition is occurring through interference competition as a result of direct exclusion of birds, shown by reduced visits of birds to feeders which were also accessed by parakeets compared to feeders which had restricted access for parakeets. Differences in effect on species of parakeet use of feeders was found between great tits and blue tits, with great tits able to feed more once parakeet access was restricted whereas the restriction of parakeet access had no significant effect on seed consumption by blue tits.

Effects of parakeet feeder use on visits by native species

For both feeders parakeet presence on the feeder reduced visits by all species. This is consistent with my previous experiment (Chapter 4) which showed that a parakeet's presence near a feeder interferes with native birds' foraging behaviour. However, the results also extend Chapter 4's findings by showing that interference results in overall reduced food intake by native birds, demonstrating that interference competition is occurring.

In observations in weeks of high parakeet presence, all species visited the restrictive feeder more than the accessible feeder. This suggests that the high presence of parakeets in the garden was inhibiting birds from feeding from the accessible feeder, leaving less opportunity for feeding by other birds. This therefore shows that native birds are not simply displaced temporarily but that visits are overall reduced at high levels of parakeet presence. This effect was not seen for observations in weeks when parakeet presence was lower, showing that the effect of parakeets on native birds' foraging only becomes apparent above a certain threshold of parakeet presence. This finding may be because as parakeet presence increases in an area, the number of food sources relatively free from parakeets is likely to reduce. In periods of high parakeet presence the parakeet restrictive feeder is likely to have been one of the few resources in the area which was relatively free of parakeets, leading to native birds utilising it more. This is consistent with studies showing increased use of food sources with reduced interspecific competition. For example removal of a dominant tit species in coniferous forest led to expansion in foraging niche for the remaining subordinate species into areas which were previously used by the dominant species (Alatalo et al. 1987).

Effects of parakeet feeder use on native species' seed consumption

For weeks where parakeets were present at higher levels, the fact that restricting parakeets' access to feeders resulted in half as much seed being consumed suggests that when parakeets can access the feeder they are consuming at least as much as all the other species. This difference in food consumed is highly likely to be due to consumption by parakeets as opposed to other birds, because this difference was not found for seed consumption in weeks where no parakeets were present. I therefore show that parakeets are competing directly for a high value food source, with the potential for food sources to be depleted at least twice the rate as normal. One consequence of this high resource use by non-native species is that there is the potential to affect native species' fitness. Exploitation of a food source by an invasive species in an urban environment has been seen with invasive gecko *Hemidactylus frenatus* in competition for insect food with a native gecko *Lepidodactylus lugubris*. This was found to result in the invasive species depleting the food source to a lower level than normal resulting in reduced fecundity and survivorship in the native species (Petren & Case 1996).

I also show that this direct competition between parakeets differs in its effects between species. The great tit is shown to consume more food from the restrictive compared to the accessible feeders in gardens where parakeets are present daily, while no difference was found for great tit food consumption between feeder types for gardens where no parakeets were present for the week of the observations. Whereas blue tits were found to have no effect on seed consumed from the feeders in observations of high parakeet presence but did consume more food from both feeder types where no parakeets were present.

It is interesting that these differences in foraging behaviour are found as the two tit species' use of the bird feeders are generally so similar compared to between other species. A mechanism behind the reduced consumption of seed by great tits at the accessible feeder could be due to inhibition from feeding in the presence of parakeets on the feeder (as also shown in chapter 4). Whereas the fact that no significant effect of blue tit presence on seed consumption from either feeder type occurred at the high levels of parakeet occurrence suggests that blue tits may have been inhibited from feeding altogether by the higher overall parakeet presence irrespective of parakeets' ability to access the food source. An alternative explanation could be that the lack of effect of blue tits on food consumption is due to there being fewer blue tits during observations with higher levels of parakeets, however this is not the case as blue tits were actually observed visiting more than great tits (blue tit 77% and great tits 71% present during observations) in weeks of higher parakeet occurrence.

It could be that there are differences in behavioural adaptation to the presence of a dominant competitor between the two species. This could result in a shift in balance of competition between the two tit species under the presence of parakeets, because of differences in the behavioural effect of the parakeet presence on the two species. For example behavioural adaptation of bird species living in rural areas compared to behaviour of birds in urban areas due to differences in potential predators in urban areas has been demonstrated (Møller & Ibáñez-Álamo 2012). However a study investigating the effect on feeding behaviour of tit species in the presence of model birds of prey at a sunflower seed feeder found no difference in the effects of the predator presence on the feeding visits and feeding duration between blue tits and great tits (Tvardíková & Fuchs 2010). It could therefore be that the two species differ in their ability to distinguish predators and large competitors.

Personality differences between species have also been increasingly highlighted as important in the outcome of interspecific competition (Sih et al. 2004; Moller 2010; Lowry et al. 2012). It might be that great tits are just generally bolder than blue tits, resulting in the presence of a dominant non-native competitor having less effect. Or it could be that great tits are more adaptable to variation in threats, learning when a situation is not risky (Carter & Feeney 2012). This highlights the value of testing for species level effects of invasive species on native species.

Implications

Here I show competition with blue tits and great tits for sunflower seed. As parakeets have a very broad diet (Clergeau & Vergnes 2011) they are likely to be competing over other food sources which are fed on by other species. Therefore it might be that other species in urban gardens which are reliant on other food sources may be affected. However any species affected are likely to be smaller than parakeets. For example bird species inhibited by a native dominant urban –adapted bird, the noisy miner (*Manorina melanocephala*), in urban areas in Queensland, Australia, were all small compared to those unaffected (Kath et al. 2009) and a study of non-native birds in New South Wales, Australia, found the small non-native species of birds which succeeded did so through utilising other resources and therefore avoiding competition with the larger and more aggressive native species (Sol et al. 2012).

This study has shown that direct competition is occurring between parakeets and native garden birds and reducing food intake for great tits. It is yet to be understood if the parakeet is actively excluding the native birds through aggression or if the competition effect is simply the inhibition of the smaller native birds from feeding next to a large, exotic bird. Anecdotal observations of interspecific interactions at the garden bird feeders recorded during this study did suggest that aggression was occurring, however this appeared to be extremely rare with only four aggressive incidents recorded out of 1207 observations (aggression defined as the parakeet observed forcing other birds away), however as these records were not an essential part of the twenty minute observation, it is not clear how often aggressive incidents went unrecorded. A study of a large dominant non-native bird, the common myna (*Acridotheres tristis*) in Australia, which was widely thought to be aggressive, found unexpectedly that it posed no aggressive threat to wild birds (Haythorpe et al. 2012). Rigorous observation of interspecific interactions at food sources would be needed to determine the part that aggression plays in interspecific competition of parakeets with native birds. Either way the reduction of visits and food consumption demonstrates that competitive exclusion of great tits and blue tits is occurring through interference competition with parakeets.

For this study the food resource was unlimited as the bird feeders were kept topped up with seed daily but under normal circumstances garden bird feeders can be left empty for long periods (Davies et al. 2009) and for the majority of natural food sources, availability is likely to be limited with season. Therefore the effects of competition with parakeets is likely to be greater in gardens where food sources are more limited than shown here. If due to the lack of natural food sources in urban areas, garden bird feeders provide an integral part of the diet of urban bird populations, thus helping support native species populations (Chamberlain et al. 2005) and increase abundance (Fuller et al. 2008), then it is possible that fitness consequences may occur as a result of the high competition with parakeets.

The popularity and abundance of garden bird feeders in cities across Europe does present a circular conundrum as the provision of the supplemental food allows some native species to survive at higher abundance (Fuller et al. 2008) but in doing so it is also likely to be supporting the parakeet population (Clergeau & Vergnes 2011) which in turn competes with native species. Restricting parakeets' food access was shown to reduce the days the parakeets were seen in the garden. This shows that restricting parakeets from garden bird feeders could help reduce parakeets from coming to gardens. The question is whether parakeets are competing over natural resources with native birds as well, resulting in greater depletion of natural food sources. If this is the case, removal of access of garden bird feeders to parakeets may result in parakeets foraging from natural food sources more and therefore simply moving the competition, resulting in exacerbated competition for natural food sources. On the other hand the removal of access to supplemental food could result in parakeets being unable to persist at such high numbers. Therefore it may be possible to use this as a mitigation strategy to reduce competition for supplementary food in gardens.

Conclusions

In summary these findings show that parakeets compete directly with native species for food at garden bird feeders. Evidence for this competition was found specifically at high levels of parakeet presence for all species. Under these conditions species' visits to feeders were increased when parakeets' access was restricted, demonstrating that displacement of birds is not simply temporary, but results in species' use of the bird feeders reducing overall. Direct competition through interference was demonstrated to differ in effect between the two common native species, as great tits consumed considerably more seed when parakeets' access to the food was restricted, while blue tits' had no significant effect on seed consumption at high levels of parakeet occurrence. This shows at high levels parakeets may reduce blue tits from feeding altogether, even when parakeets are restricted. In addition, restricting parakeets' access to feeders halved the overall food consumption in periods of high parakeet presence. These results demonstrate that at high levels of presence, parakeets have the potential to cause food resources to be depleted twice as fast as they would otherwise, and results in direct competition with native species, through reduced food consumption in gardens. Although this study was investigated using bird feeders it demonstrates that this direct competition for food could be occurring for other food sources in gardens and green spaces in urban areas and so has the potential to affect native species on a broader scale than shown here.

Chapter 6

Discussion

In this thesis I have investigated aspects of the population ecology of the rose-ringed parakeet in South East England using variation in roost use and changes in the population size and distribution over time (Chapter 3). I have also addressed some of the gaps in our knowledge of the ecological impacts of the parakeet on native wildlife, specifically the impact of foraging competition, through investigating behavioural impacts and quantifying resource loss through competition (Chapters 4 and 5). I have discussed each of these findings separately within each data chapter but now discuss three common themes which run through the three data chapters. These are: i) the importance of the urban environment for parakeets, ii) the importance of the impact of parakeets on native species' foraging behaviour , iii) the use of citizen science for invasive species research. Under each of the theme headings I discuss how I have found the theme to be important, what the implications of this thesis's findings are and how future research might build on this. Finally in light of the overall findings and taking into account policy proposals set by the European Commission, I make recommendations for policy and management of the rose-ringed parakeet in the UK.

i) **The importance of the urban environment for parakeets**

Invasive species establishment is determined by introduction events and therefore is constrained by where these take place. For invasive birds, this has been found to predominantly occur in temperate and island locations (Blackburn & Duncan 2001). As rose-ringed parakeets are popular pets, escapes or releases resulting in introduction events into the wild are most likely to occur in

urban areas (Strubbe & Matthysen 2009a) and therefore establishment of rose-ringed parakeets is also more likely to occur in urban areas due to propagule pressure (Lockwood et al. 2005).
In Chapter 3 I show that the rose-ringed parakeet appears not only to establish initially in urban areas with green space, but also to preferentially stay in the urban landscape rather than distributing elsewhere. This has also been found to be the case for the parakeet population in Belgium with evidence from ecological niche modelling and radiotelemetery (Strubbe & Matthysen 2008, 2011). In addition, comparison of introduction and establishment success of rose-ringed parakeets in Europe found that taking into account the propagule pressure in areas of high human density, establishment was still positively correlated with urban areas (Strubbe & Matthysen 2009a). Therefore it seems plausible that the success of parakeet establishment is governed by conditions created by human modification of the landscape.

A likely contributor to this establishment success is the provision of supplemental food in gardens, through the popular use of bird feeders and the wide variety of garden plant species available. Chapter 5 shows that parakeets were found to consume at least as much as all other species using the feeders, therefore suggesting a considerable part (if not the majority) of their diet is provided by bird feeders. This is also supported by observations of foraging at garden bird feeders in Paris, which found the parakeets spent half their time on garden bird feeders (Clergeau & Vergnes 2011). This study of wild parakeets in Paris also showed that they feed from a wide variety of exotic plant species. It may be that the variety of plant species found in urban areas, particularly gardens and parks (Loram et al. 2008), provides extra variety of foods than are not available in more rural areas. This may provide some release from competition with native species as non-native bird species may be able to utilise exotic plants more that native birds species, as shown with non-native birds in suburbs in Tasmania (Daniels & Kirkpatrick 2006).

As well as year-round stability in the abundance of food sources, urban areas are known to retain heat better than rural areas and therefore have a higher mean temperature throughout the year (Costanza et al. 2001; McCarthy et al. 2010). It therefore seems possible that urban areas could also be preferred by parakeets due to having warmer climate. This has been suggested as a factor in the parakeets' establishment in urban landscapes as climate-matching analyses found the parakeets positively associated with warmer areas (Shwartz et al. 2009).

The establishment and population growth of the rose-ringed parakeet demonstrates that human modified landscapes provide an environment in which invasive species are more likely to establish compared to less disturbed habitats. This has also been found with many widespread invasive bird species, for example: the house crow (*Corvus splendens*), which has been found to only invade areas close to human habitation (Nyari et al. 2006), the Eurasian collared-dove (*Streptopelia decaocto*) in North America (Bonter et al. 2010) and the house sparrow (*Passer domesticus*) in West Mexico (MacGregor-Fors et al. 2009). A particularly pertinent example due to the species' similarity to the rose-ringed parakeet, is a study of the monk parakeet (*Myiopsitta monachus*) in Chicago. This study found that during the winter months the monk parakeets' diet consisted of 100% bird seed from garden bird feeders and so demonstrated the likely dependence of the species on the supplemental food source (South & Pruett-Jones 2000).

It is not only non-native species that can become invasive in urban areas. The abundance of anthropogenic food in urban areas is thought to be the driving force behind increases in abundance of some native species which dominate in urban areas, and therefore a driver of ecological change in avian populations (Robb et al. 2008). For example the feral pigeon (*Columba livia*) has adapted to live in urban areas, relying almost entirely on anthropogenic food sources (Rose & Nagel 2006); and the abundance of corvid species in urban areas is thought to be particularly driven by anthropogenic food sources (Marzluff & Neatherlin 2006). Some native species have adapted to urbanisation and thrived in the human modified landscape when previously they had had not been associated with urban landscapes. For example over the last century the red fox (*Vulpes vulpes*) (Harris & Rayner 1986) has become increasingly abundant in cities across the UK, but before the 1940s had been rarely seen in cities; and the European black bird (*Turdus merula*) is abundant in cities across Europe but before the 19th Century was only found in forest areas (Luniak 2004).

The implications of the adaptation of a few species to urban areas, resulting in high abundances compared to other less well-adjusted species, means that the species composition is altered in urban areas in a way that results in the dominance of urban-adapted species (McKinney 2006; Shochat et al. 2006). Establishment of invasive species such as the rose-ringed parakeet appear to be fitting this trend. Urban environments are predicted to increase in the future, with the growth of human population, and so more investigation is needed into the impacts of invasive species associated with the urbanisation on native wildlife and the adaptation of wildlife to urban environments (Shochat et al. 2010b). With increased knowledge of these species impacts and adaptations, management and urban planning can be better informed to reduce invasive species' impacts on native wildlife.

In order for predictions to be made about the future use of different environments by invasive parakeet populations, their use of the urban and non-urban environment needs to be better understood. This could be achieved by tracking individuals over long periods to measure daily through to annual patterns of movement. This would allow landscape-level patterns of foraging, roosting and breeding landscape to be analysed and so allow predictions to be made about the potential for growth in distribution, and possible conflicts that may occur such as resource competition. Radio-telemetry tracking has been used on five rose-ringed parakeets in Belgium but this was only for approximately ten days due to the low battery life and so only allowed a short period of tracking (Strubbe & Matthysen 2011). Therefore long-term tracking is still needed. In order to further understand potential for spread of the distribution it is also important to know whether parakeets are totally reliant on gardens for foraging or if they forage further afield for parts of the year. Therefore details of parakeet movement such as daily distances travelled and in particular any long distance dispersal to new areas are needed. The status of the rose-ringed parakeet in its native range as “one of the worst vertebrate pests” due to the damage it causes to agricultural crops (Ahmad et al. 2012), highlights the potential of parakeets adaptating to living in less urban areas and to start utilising areas of agriculture as foraging sites and means it is also important to monitor any changes in its use of the landscape. If this were to occur the parakeet would potentially be able to become more widespread across the UK.

ii) The importance of the impact of parakeets on native species’ foraging behaviour

Behaviour is known to play an essential role in both the establishment of invasive species and their impacts on native species (reviewed in Holway & Suarez 1999). It is also known that behavioural adaptation can play an important role in the establishment and persistence of species in urban environments (Sol et al. 2013**.** Here I discuss the importance of behaviour in the establishment and persistence of the rose-ringed parakeet populations and in its impacts on native species and how further investigation into the influence of behaviour in the invasion process is needed.

Chapters 4 and 5 show that the parakeets are able to dominate native species at garden feeders, consuming more than all other birds and disrupting the foraging behaviour of native birds through inhibition. Chapter 4 also showed that the impacts of parakeets on foraging of native birds are complex due to the subtle effects of the presence of the parakeet on native species behaviour, resulting in some possible habituation of native species to parakeet presence but also increased vigilance and overall reduced foraging. Given that habituation could result in the parakeets having less of an impact on native species' foraging behaviour, it warrants further investigation to see if it is occurring, particularly as there is relatively little work that has been carried out into habituation of native species to other invasive species (but see Webb et al. 2008; Abril & Gómez 2009; Nelson et al. 2011; Spicer Rice & Silverman 2013). In order to do this identification of individual birds is required to test for changes in behaviour at the individual-level rather than general species effects. Studies which have individually marked native species have revealed both species- and individual-level patterns and drivers of behaviours such as foraging, for example using passive integrated transponder (PIT) tags (for example Aplin et al. 2013) or unique colour-band combinations (for example Toms 2013). By employing these individual marking techniques in studies of invasive species' impacts it would be possible to identify which behavioural traits make native species and individuals more susceptible to competition from invasive species (as reviewed by Sih et al. 2012).

As discussed earlier, it is clear from Chapters 4 and 5 and from the distribution in urban areas shown in Chapter 3, that parakeets utilise the food resources made available in the urban environment. As with other successful urban species, behavioural adaptability to resources in the human modified landscape has allowed parakeets to succeed (Sol 2002; Sol et al. 2012a). For example, across an urban gradient in Australia the non-native common myna (*Acridotheres tristis*) was found to modulate its foraging behaviour depending on its environment's level of urbanisation (Sol et al. 2011). The success of the rose-ringed parakeet appears to be partly due to the adaptability of the species to the use of food sources found particularly in urban gardens and parks (Clergeau

& Vergnes 2011) and similar behavioural adaptations to urban areas has been seen in several other species (as reviewed in Sol et al. 2013).

The adaptability of invasive species to food source does not always result in negative competition effects. For example non-native game birds in high-elevation Hawaiian shrub land have been found to forage on native plants that were once eaten by, now extinct, native species and therefore not be competing with native birds, and also has the potential to benefit the degraded ecosystem through facilitating seed dispersal of native plants which have lost their natural dispersers (Cole et al. 1995). In addition small invasive bird species in New South Wales, Australia, have been found to use opportunistic foraging to exploit food sources which native species are not utilising (Sol et al. 2012a). It might be that the broad diet of the parakeet means that it utilises parts of plants that other species do not. Further investigation into the similarities and differences between parakeets and native birds in the plant species, and specific parts of these plants, each utilises is needed to explore this possibility.

In order to further investigate the mechanisms behind feeding competition and use of urban food sources, tracking of individual birds would allow more detailed collection of foraging behaviour and provide insight into patterns of resource use over the year, and across the landscape, for example through long term radio tracking, pit tagging or colour banding. Given the large quantities of seed that the parakeets consumed compared to the native species at garden bird feeders and given the knowledge that parakeets eaten a wide variety of plant species in gardens (Clergeau & Vergnes 2011) it seems possible that competition may be occurring over more natural food sources as well. As plants can be more variable resources than garden bird feeders, (which are re-filled) then competition from parakeets could have effects on native bird species that are reliant on certain plant species during the year. For example mistle thrush (*Turdus viscivorus),* defend individual fruit bearing trees such as Holly (*Ilex aquifolium*) throughout the winter suggesting they are reliant on the berry crop for winter survival (Snow & Snow 1984). Therefore further investigation is required to investigate if the behavioural impacts of parakeets found at bird feeders (Chapters 4 and 5) are also found on other food sources, in particular more natural food sources. This is particularly important to investigate because bird feeders are an unusual food source in being predictable and so densely concentrated in a small area (Chamberlain et al. 2005), whereas food from plants is likely to be more variable over space and time (Keane & Morrison 1999). Two studies have previously looked at the effect of how invasive species foraging impacts may differ between clumped and scattered food sources. These looked at food competition between native-red-legged frogs (*Rana aurora*) and introduced bullfrogs (*R. catesbeiana*) (Kiesecker et al. 2001) and between the invasive black rat (*Rattus rattus*) and native rice rat (*Nesoryzomys swarthi*) (Harris & Macdonald 2007). Both studies found the distribution of food to be extremely important in determining the level of impact on the native species, with scattered food resulting in little effect of competition, shown by little difference in each species' food consumption, while clumped food sources resulted in native species' foraging behaviour being disrupted due to time spent avoiding the non-native species. These studies indicate the need for further investigation into the effect of parakeets on native species' foraging behaviour at natural food sources compared to bird feeders. Given that food sources on vegetation are likely to be more scattered than bird feeders, it may be that the impact of parakeet presence on foraging of native birds is weaker in comparison. Knowledge gained about how the placement of food influences the foraging competition effects of parakeets may be useful for mitigation strategies to reduce their competitive impacts on native birds.

It is also worth noting that it is not just adaptability to food sources but also to breeding sites that may make the parakeet a successful invasive species. For example there are increasing reports of parakeets utilising loft insulation in domestic buildings for nest sites in Germany (Braun 2007) and four reports in South London in 2012 (personal communications Martin J., 2012; Thomas R., 2010; Abrahams N., 2012; Sweetland J., 2012). They have also been seen to nest in the spire of a church with wooden tiles in South East London (personal observation H.L.Peck). In addition, parakeets are highly gregarious, as shown by the formation of communal roosts consisting of 1000s of birds (Chapter 3) and foraging in social flocks as seen during observations in the experiments in Chapters 4 and 5, where birds were observed foraging in groups on bird feeders and plants (personal observation H.L.Peck and see Fig 6.1).

Figure 6.1. Group of foraging rose-ringed parakeets a) on a bird feeder in a London garden (photo credit Colin Farrant), b) on a *Pyracantha* bush, Ramsgate Kent (photo credit Richard Kinzler).

Although the role that communal roosts play in the establishment success of parakeets in the UK is unknown, communal roosts in general are thought to provide social benefits. These include improved efficiency in locating food sources through providing a centre for information sharing and dispersal of foraging flocks (Ward & Zahavi 1973; Chapman et al. 2007). The sociality of the rose-ringed parakeet may also give it an advantage in foraging in a new environment and in generally aiding establishment success. For example of the sixteen invasive bird species found to have invaded South East Asia from 1981 to 2000, all were found to behave sociably, through behaviour such as group foraging and communal roosting (Yap & Sodhi 2004). Consequently the role that sociality plays in the establishment success and potential spread of parakeets requires investigation.

Overall Chapters 4 and 5 demonstrated that behavioural impacts of non-native species on native species are a potential mechanism for wider effects at the population level. They also highlight the general need to investigate the more subtle impacts of invasive species presence on behaviour of native species, where impacts and the mechanisms behind them may not have been identified. This has consequences for conservation of native species as by understanding the mechanisms behind invasive species impacts, the development of mitigation strategies may be more effective.

iii) The use of citizen science for invasive species research

Citizen science is the partaking by members of the public in scientific research. It has been utilised by scientists for centuries to collect observational data (reviewed by Miller-Rushing et al. 2012)). But with the advances over the last twenty years in communication technology, in particular the internet, cheap and fast communication to limitless numbers of people and the ability to send digital files has made the potential for use of citizen science for ecological research boundless (Dickinson et al. 2012).

For all three data chapters, the collection of data was dependent on volunteers through data collection in the field, or through crowdsourcing of field sites and maintenance of the experimental equipment. In Chapter 3 members of the public provided information on the roost locations, on changes in roost use over the study period and by taking part in the quarterly simultaneous roost counts. These would not have been possible without the over one hundred volunteers which took part. In addition to this roost data, the distribution data used in Chapter 3 came from BTO's

Breeding Bird Survey (BBS) which is also carried out by volunteers (Risely et al. 2013). Both garden bird feeding experiments (Chapters 4 and 5) could not have taken place without the crowdsourcing of members of the public for use of their gardens. Public space would have proved too difficult to acquire and to maintain without disruption. The data collection for Chapter 5 was entirely done by each garden volunteer, this would have been extremely time consuming to do alone, as it allowed forty, twenty minute observations to be carried out each week across the South East of England at various times of day and week over an entire year. Chapter 5 used video recordings of the birds feeding at the garden bird feeders. The quantity of footage required to extract the data was too time consuming to be able to do alone and so volunteers were used to help extract the behavioural data and enter it into spreadsheets. Therefore citizen science enabled the use of anecdotal information on the study species (such as roost locations) which was not available in scientific or even grey literature, and also provided a means to collect data on a much larger scale (both in geographic location and quantity) than would be possible by a lone researcher.

Chapters 4 and 5 used field experiments to test for effects of parakeet competition on foraging behaviour and food consumption by native birds. This allowed effects across a range of parakeet abundance levels to be found over a short time span compared to observational data which would require the existence of data before the expansion of the parakeet population so that comparisons can be made. These sort of short-term field experiments have been widely used in the study of invasive species' impacts (for example Human & Gordon 1999; Gurnell et al. 2004; Griffen et al. 2008; Sol et al. 2012a). They are particularly beneficial because once invasive species have spread it is extremely difficult to eradicate or control them, and therefore research into potential impacts of new species introductions need to turn out results quickly.

In the majority of cases citizen science research in ecology is used to collect purely observational data and the use of citizen scientist for experimental research is less common (but see for example Jones et al. 1998; and Trumbull et al. 2000). The use of volunteers to collect observations from experimental set ups, as used in Chapter 5, shows that it is possible to combine rigorous experimental work with the use of citizen science.

Using field rather than lab-based experiments so that data can be collected under natural conditions is important to avoid unexpected outcomes caused by variation in environmental conditions and interactions with other species. It must be considered that although short-term experimental research in the field provides the most effective means to collect data quickly, only long-term monitoring where effects at the population level can be found provides a sure way of knowing the long-term impacts of an invasive species. For example a field study of the impact of invasive cane toad (*Bufo marinus*) on native Australian snake species, found that field experiments did not match the findings from time series analysis of data over 11 year period (Brown et al. 2011). In addition long-term monitoring is also vital for monitoring long-lived invasive species and the use of citizen science can particularly benefit in this monitoring. For example the British Trust for Ornithology's (BTO) bird ringing scheme, is a citizen science project which has been running for over 100 years (Balmer et al. 2008). The long-term data collection provides information such as mortality values which otherwise would be difficult to obtain. For example in Chapter 3 mortality values of different age classes of wild living rose-ringed parakeet were required but the average life span of the rose-ringed parakeet in the UK is currently unknown (requiring the use of mortality estimates from the monk parakeet instead), and it is only through long-term monitoring that mortality values for wild individuals can be gained.

Therefore for invasive species such as the rose-ringed parakeets where establishment is already widespread, the combination of both long-term monitoring and experimental field research provides the most thorough means to investigate ecological impacts. But for species that are newly introduced, experimental field research can provide an effective way to test for impacts so that mitigation strategies can be designed before it is too late. In both cases, long-term monitoring and field experiments, is likely to be a potentially useful and important tool.

Although there were huge benefits in using citizen science to collect the field data, these must be weighed up with the drawbacks. These included the time it takes to correspond with volunteers, whether by email, telephone or in person, the resources and time required to recruit volunteers, the requirement to provide adequate information on the data collection to an audience that does not necessarily have a scientific background and the need for data quality checks and editing. Bias in data collection also needs to be accounted for, for example in Chapter 5 the time of weekly observations was determined by the volunteer. This meant there was a possibility that the volunteer could choose a time specifically when parakeets were seen feeding, in preference to time without parakeets. This could result in an overestimation of the use of the feeders by parakeets and therefore bias the results. Measures were taken to avoid this bias by specifically explaining that observations were required for a variety of bird activity and so to vary observations to different times of day. But without dictating specific times to volunteers it would be difficult to reduce this sort of bias. However requiring volunteers to be free at specific times to carry out observations every week for a year would considerably reduce the numbers of people able to take part.

A further drawback that may hinder the possibility of crowdsourcing volunteers for experimental sites, was that many of the volunteers were not comfortable with changing the bird feeder food and type in case it affected the abundance and diversity of species using their garden.

Volunteers were often worried about specific species being affected, for example several volunteers were not happy about removing other supplemental food sources such as niger seed feeders put out specifically for goldfinches (*Carduelis carduelis*). This proved to be a particular difficulty in recruiting volunteers due the need to keep strict experimental controls as much as possible, and did result in approximately 10 out of 50 potential garden sites being lost due to volunteers being unwilling to alter their bird feeding regime. These types of drawbacks are general to the use of citizen science for ecological research (Dickinson et al. 2010), but are particularly important for the use of citizen science in ecological experiments. For example a review of the use of three citizen science projects to collect data on ladybird species in the UK, found that the accuracy of data collection was reduced in comparison to verified data, however overall the benefits of the ability to collect larger samples sizes compensated for the error (Gardiner et al. 2012).

Since the start of this research at the end of 2009 there has been a noticeable increase in sophistication of smart phones including developments in mobile apps, automatic GPS locations and social networking technology (Newman et al. 2012; Roy et al. 2012). This means that time required for researchers to develop, collect and correct error in volunteer collected data is reducing. The possibilities of using citizen science for monitoring invasive species have therefore increased as the potential data collection techniques have become more sophisticated and user friendly. For example the development of data quality filters as used for eBird and FeederWatch in the USA allows over a million observations to be automatically reviewed for error (Dickinson et al. 2010). The use of mobile phone technology could have benefited this parakeet research, for example in Chapter 3 the location of roost sites was largely facilitated by reports from members of the public. However this was through emails sent with descriptions of potential roosts locations and therefore required verification through a site visit to check characteristics of the site location and to check

that the site was a true roosts rather than a pre-roost or day time foraging site. This resulted in over thirty visits being undertaken to sites across South East England. If mobile phones had been used by the members of the public to take photos or video of the roost, with a GPS location, travel hours and costs would have been saved by not having to verify each potential roost location.
Citizen science also provides an avenue through which to engage the public in conservation issues (Jordan et al. 2012; Pandya 2012). Therefore by using citizen science for research in to invasive species, it is possible to promote mitigation and management strategies which the public can apply, such as taking steps to limit the release of non-native species into the wild or to limit resource access for invasive species and simply to report sightings to research organisations.

Given the wide distribution of the rose-ringed parakeet, the high profile of the species and advantages of collecting large quantities of data, the use of citizen scientists in parakeet research seems invaluable. This demonstrates the potential for use of citizen science to research ecological impacts of other invasive species, particularly if experimental studies can be combined with long-term monitoring.

Conclusions of the three broad thesis themes

The current distribution of the established populations of the rose-ringed parakeet is predominantly in urban areas. This may be due to the reliance on the density of resources found in urban areas, in particular food from garden bird feeders. By establishing in urban areas parakeets are adding to the dominance of synanthropic species in urban areas and therefore may be contributing to reductions in species diversity (McKinney 2006a; Shochat et al. 2010a). Parakeets can also dominate native species at food sources, such as urban bird feeders, through the impacts of their presence on native bird behaviour. It also appears that the behavioural adaptability, and possibly sociability, of the parakeets gives them a foraging advantage and therefore warrants further research. The need for increased knowledge of the potential for competition of parakeets with native birds for other resources would be benefited by detailed tracking of individual parakeets in the landscape and by behavioural studies investigating individual behaviour of native species affected. The fact that this thesis' research was made possible through the use of citizen science, shows that there is huge potential for using citizen science in invasive species research more widely, and that combining both observations made by volunteers with field experiments is a relatively untapped and valuable tool which has potential to be utilised more, particularly with advances in technology.

Policy and mitigation suggestions for limiting ecological impacts of the rose-ringed parakeet population in the UK

Here I will discuss the implications for policy of this thesis' findings in the context of the current European Commission's invasive alien species policy proposals (European Commission 2013). I will then discuss additional implications other than ecological impacts of the parakeet presence in the UK which may also influence the need for policy and mitigation. Taking these factors, the European Commission proposals and examples from other species control schemes into account, I will make suggestions for possible mitigation strategies that could be used to reduce ecological impacts of the UK's rose-ringed parakeet populations.

Applying the European Commission 2013 proposal for regulation on the prevention and management of the introduction and spread of invasive alien species to the management of the UK's parakeet population

The released proposal in September 2013 by the European Commission for regulation on the prevention and management of the introduction and spread of invasive alien species (IAS) (hereafter 'the proposal'), aims to establish a framework for action to prevent and mitigate adverse impacts of invasive alien species on biodiversity and ecosystem services (European Commission 2013). The proposal was produced because there is currently no EU framework for a general approach to address the occurrence of IAS (European Commission 2013). The proposal is structured in five main sections: 1) the prioritisation of IAS of concern based on risk and scientific evidence, 2) prevention measures for the introduction of IAS, 3) early detection and eradication, 4) management of IAS that are already widely spread, 5) reporting obligations and review of measures. I will discuss just the proposals which might be relevant to policy and management of the UK's parakeet population under each of these sections in turn.

1) *The prioritisation of IAS of concern based on risk and scientific evidence*

An IAS is considered a risk if through scientific evidence it is found to be capable of establishing and spreading anywhere in the European Union. It is clear from Chapter 3 that the rose-ringed parakeet is therefore an IAS of risk concern as it has established a large population of over 32,000 in the UK in addition to other established populations across Europe (Strubbe & Matthysen 2009a). In addition, it seems that from the evidence of ecological impacts on native species in the UK, such as through foraging competition (Chapters 4 and 5) and potential nest site competition (Strubbe & Matthysen 2009b; Strubbe et al. 2010), that the parakeet would also be classed as IAS of concern due to its potential impacts on biodiversity. However there is no evidence as yet that this competition for resources has resulted in population level impacts on native species and whether it will in the future. For example, a study specifically investigating population-level impacts of parakeet presence on native cavity nesting bird species found no significant evidence (Newson et al. 2011). Therefore further investigation and ongoing monitoring is needed to assess potential ecological impacts of the parakeet population, and identify whether these impacts lead to population-level effects on native species.

2) Prevention measures for the introduction of IAS

The general conclusion made for policy on invasive alien species by the European Commission was that "prevention is generally more environmentally desirable and cost-effective than reaction and should be prioritised". As the parakeet population in the South East UK and in cities across Europe are already well established, prevention is not an option for those areas. However the prevention of further spread of the parakeets to new areas is a possibility. Therefore the emphasis on managing routes of parakeet introduction as a priority strategy is still relevant. This no tolerance approach for newly introduced non-native species, with eradication of individuals as soon as they are discovered has also been proposed specifically for non-native species of birds as a more effective approach, as by waiting for the population to grow enough to cause significant ecological (or economic) impacts the process of control then becomes too costly and in many cases too difficult (Edelaar & Tella 2012).

Article 11 of the proposal suggested that to address the action plan on introduction pathways, there needs to be raised awareness by the public and regulatory measures. Consequently there needs to be public engagement in the risks associated with escapes or deliberate release of parakeets from captivity into the wild, and regulatory measures could be enforced if escapes or release are found to have occurred. Action on the introduction pathways for parakeets in the UK have already been partly addressed though a ban on the import of wild-caught birds which was put in place in January 2007; however the ease at which the parakeets can be bred in captivity means that their trade in the UK will not necessarily drop (Fletcher & Askew 2007; Lambert et al. 2009). This means there is high potential for future introductions across the UK and therefore a need for higher public awareness of the risk of captive parakeets ending up in the wild.

The proposal highlights that early detection and rapid eradication are a priority and that this should be done at an early stage of the invasion, preferably within three months of detection. The high visibility of the parakeets' bright feather colours, distinctive tail feathers in flight and loud squawking call means that they are easily distinguishable from native species and early detection in new areas should not be difficult. The effectiveness of this has already been shown by the use of members of the public to report parakeet roost sites in Chapter 3, indicating that public surveillance of parakeets can be effective. In order for this to occur, surveillance needs to be put in place to detect new introductions. The use of public engagement could be used to promote the need for surveillance and therefore result in members of the public reporting any sightings to an online database. This would mean there could be widespread coverage across the UK without the need for concerted efforts by government bodies to carry out surveillance themselves. This is already happening through the use of online reporting projects such as BirdTrack (http://blx1.bto.org/birdtrack) and the BTO's Breeding Bird Survey (Risely et al. 2013) but efforts to specifically increase awareness of the need to report the parakeet and other invasive species could be made.

3) Early detection and eradication

Article 16 of the proposal states that exemption from the obligation for rapid eradication can be due to a) the eradication not being feasible due to environmental constraints or b) that the cost would be too high or c) that there were no methods available. All three reasons could apply to problems with eradication of the parakeet population. a) The urban distribution of the parakeet population, as shown in Chapter 3, means that the environment in which eradication could take place would be constrained by being near human activity, such as in gardens and therefore posing a safety risk or requiring access to private property. b) The cost of eradication of newly established populations of parakeet is unknown but the eradication of a small population of the monk parakeet species in London is reported to have cost the Department for Environment, Food and Rural Affairs (DEFRA) £192,000 since 2008 (Whalen 2013) to control approximately 60 birds in London (The Non-native Species Secretariat 2011). This shows that eradicating even small numbers of birds can be costly, however this might be outweighed by the greater costs of impacts if the population is left to expand. For example spending on research and control of the ruddy duck (*Oxyura jamaicensis*), a widespread non-native species in the UK which had a population size of an estimated 5946 in January 2000 (Smith et al. 2005), has cost DEFRA £3,700,000 on research and policy and a further £1,350,000 for control research between 1999 and 2009 and through various parties, approximately £350,000 has been spent in addition on eradication efforts since 1991 (Williams et al. 2010). Finally, c) the methods available for eradication of rose-ringed parakeets may not yet be available. As they are found in urban areas, shooting of the birds may prove unsafe, and other urban control programmes, such as the eradication of the common myna (*Acridotheres tristis*) in urban area in the Seychelles, found that the birds rapidly developed gun shyness making it unfeasible as a control method (Canning 2011).

4) Management of IAS that are already widely spread

The most relevant policy proposals by the European Commission for the established parakeet populations in the UK are those in in Article 17. This proposes policy for management of IAS that are widely spread. This states that methods must have “due regard for human health and the environment and that when animals are targeted, they are spared any avoidable, distress or suffering”. As far as I am aware no methods have been developed that would be effective for eradicating the parakeets in South East England without affecting other wildlife or human health and/or creating suffering for the parakeets. However a trial of a contraceptive drug, Diazacon, in a captive population of rose-ringed parakeets has been carried out to see if reduced fertility could be a feasible means to reduce the population size in the wild (Lambert et al. 2010). This found that fertility could be reduced without suffering to the birds but that a feasible application method and formulation of the drug for wider-scale use needs to be produced. However the ability to repeatedly administer a non-species specific contraceptive drug to thousands of parakeets across the South East of England without other species also managing gain access to it seems extremely difficult and even implausible.

Article 17 also proposed the need for a surveillance program to determine how effective management is. This could easily be achieved for the current population in the South East UK, through the same simultaneous roost count methods used in Chapter 3. Finally, article 17 proposed that the possibility of the IAS spreading to another European member state must be considered and the member state immediately notified. Given that parakeet populations are already widespread across Europe, this is not currently a relevant issue (see European distribution (see European distribution Strubbe & Matthysen 2009a)).

5) Reporting obligations and review of proposed measures

Article 19 proposes that reports should be produced of each IAS within the member state. This includes reporting on the surveillance system put in place, the distribution of the IAS, the action plan for management and any relevant information gained on the IAS. There are already surveillance bodies in place that monitor the distribution of parakeets (and other species) across the UK, for example the British Trust for Ornithology's British Breeding Bird Survey (Risely et al. 2013) and Bird Track (http://blx1.bto.org/birdtrack). Chapter 3 should provide relevant information to these bodies on the current parakeet distribution within the UK, and highlight how members of the public might be integrated into surveillance systems. All data chapters (3, 4 and 5) provide information on the ecology of the rose-ringed parakeet in the UK and the findings in chapters 4 and 5 about their negative impacts on native species' foraging behaviour and access to supplementary food provide a useful contribution to assess the risks posed by the parakeet population to native wildlife. Finally, Article 21 proposes that public participation in the IAS management should be gained. Given the use of citizen science throughout the parakeet research in this thesis it is clear that public participation in the management of the rose-ringed parakeet in the UK has already occurred and there is huge potential for its use in the future as discussed earlier in the use of citizen science for invasive species research.

Concluding remarks on the possibility of management of the UK's rose-ringed parakeet population fitting the EU Commission proposals

In summary, applying the 2013 proposals set out by the European Commission for management of IAS to the UK's population of parakeets produces three major considerations:

1. There is potential for increased use of public participation for surveillance of the UK's population of parakeets, particularly for reporting newly establishing populations elsewhere in the UK.
2. The eradication of parakeets in South Eastern UK appears to be unrealistic due to the lack of available strategies for the eradication of high numbers of birds distributed widely over an urban area.
3. Ongoing research is needed to monitor ecological impacts and to develop feasible mitigation methods, given the constraints of the urban distribution of the current parakeet population.

Further implications to be considered in UK parakeet policy and mitigation

The high public profile of the parakeet in the UK

Although the European Commission proposals highlighted the need for public participation and awareness in the mitigation strategies for IAS, the huge influence that public opinion can have on management success was not addressed. This is particularly relevant for the rose-ringed parakeet in the UK because of their high profile to the public: they are highly visible, highly vocal, they are sociable birds and so are often found in large numbers, both foraging in small flocks and roosting communally, and their distribution is in urban areas. Therefore any management scheme that occurs is likely to be highly conspicuous to the public.

The recruitment of over 200 volunteers for this thesis' research demonstrates the interest the public has in the species, and the media interest in the project (as discussed in Chapter 2) demonstrates the high public profile of the parakeet. A questionnaire based survey carried out on 671 members of the general public in London and residents living close to parakeet roost sites, found that public awareness of the parakeet population was very high and that public opinion was highly variable (Baker 2010). Strong and variable public opinion of parakeets was also highlighted by the variation in volunteers' motivation for taking part in the research for this thesis, from being interested in and enjoying watching the parakeets to being concerned about the impacts of parakeets on the other garden birds, on garden plants and on the costs incurred by the amount of seed that was consumed from the bird feeders. This high public profile and varied opinions therefore increases the need for public support for any management strategies for the parakeets compared to species with less public profile, because public opinion can be extremely influential on the implementation of mitigation and management strategies of non-native species (McNeely 2001). For example, culling of a small population of less than fifty monk parakeet (*Myiopsitta monachus*) in Hertfordshire, UK by the Food and Environment Research Agency (FERA) was prevented due to a petition set up by residents, which resulted in the local council stopping the cull of the birds (Thain 2011). Also a more recent report in the media shows that public disapproval of culling of monk parakeets is now causing problems for control methods in South London (Whalen 2013). It has been found that public opinion varies considerably on invasive species issues (García-Llorente et al. 2008), but that awareness and education can increase support for control and eradication programmes (Bremner & Park 2007). This shows the importance of engaging the public in the scientific research and policy on the rose-ringed parakeet.

Social and economic impacts of the parakeet population

As well as the potential ecological impacts of the parakeets on native species there are also some social, economic and health risks that can occur as a result of their high numbers, particularly due to their aggregation at communal roosts. The noises and droppings produced by thousands of parakeets roosting at the same sites every night have resulted in some residents living next to roosts sites becoming anxious about the presence of these roosts (personal communication Thomas R., 2010). On two occasions I received reports of air guns or catapults being used on the roosts to scare away the birds, and for one roost this resulted in the whole roost being temporarily displaced elsewhere. This highlights the impact that the parakeets can have on local residents and the strong negative opinion that this can cause. The location of a roost within a few hundred metres of a major airport (the roost at Long Lane, Stanwell is next to Heathrow airport, see Chapter 3 Fig 3.3) has also resulted in concerns from the aviation industry that parakeet roosts located near to airports pose risks to aeroplanes at dawn and dusk as the birds arrive and depart. This is supported by reports of parakeet strikes by aeroplanes. In 2005 one bird strike at Heathrow was a parakeet (out of 54), and in 2006, 2 strikes were parakeets (out of 44), with the average cost of a bird strike being in excess of £20,000 (Fletcher & Askew 2007). In addition some incidents of damage to properties have been due to parakeets, for example in all cases of the reports of parakeets utilising loft insulation in domestic buildings for nest sites in South London in 2012, members of the public were concerned about damage to their lofts by pairs of breeding parakeets (personal communications Martin J., 2012; Thomas R., 2010; Abrahams N., 2012; Sweetland J., 2012). In addition, a windmill in Shirley, South London, reportedly required £45,000 of repairs after parakeets damaged its wooden sails (Whalley 2010).

Despite the status of the parakeets as severe agricultural pests in their native range (Dhindsa & Saini 1994; Khan et al. 2006), so far there have been few reports of parakeet damage to UK agriculture. However these publicised reports do highlight the potential for the parakeets to become agricultural pests in the future. For example, Painshill Park vineyard in Surrey has reported up to 200 parakeets regularly visiting and eating the grape crop, resulting in a loss of crop and a need for preventative control measures, costing an estimated £5000 in damage annually and an additional £2000 per year for bird scarers (FERA 2009; Williams et al. 2010). In addition, Osterley

Park, a National Trust property in Middlesex, has had rose-ringed parakeets feeding from a field of barley (personal communication Jeremy Dalton, Head Warden Osterley Park). These reports highlight the potential for damage to vegetation by the destructive feeding behaviour of parakeets as discussed in the Chapter 1 (and see Fig. 1.4) and is supported by an extensive literature review by FERA on agricultural impacts by parakeets which found repeated reports of parakeets being wasteful feeders and damaging fruit but only eating a small part of it before moving on to the next (FERA 2009). This highlights that the impacts of parakeet foraging can be economic as well as ecological (as shown in Chapters 4 and 5), and so emphasises the potential need for strategies that mitigate these foraging impacts.

Management suggestions

It seems that the most economical and viable strategy for the management of rose-ringed parakeets in the UK would be to focus on limiting establishment of new populations before those populations increase to the unmanageable numbers as seen in London. The high numbers of this species in the pet trade will result in further augmentation of the species in the wild, requiring continuous monitoring and management into the future. Regardless of the scale and significance of any impacts, the population is so high in South East England and spread across such a large and densely populated urban area that it would be very difficult to eradicate the London parakeet population. Therefore it might be more realistic here to manage serious problems caused by parakeets in areas where they are already established, such as damage to properties, on a case-by-case basis at a local scale, rather than attempting to remove all parakeets from the area. This strategy has also been identified as the most viable option for management of the monk parakeet population in the United States. Here, as in this thesis' conclusions, eradication methods were considered to require impractically large amounts of effort to be worth attempting (Pruett-jones et al. 2007).

In South East England a strategy more feasible than eradication that might help reduce the impacts of competition for food between native birds and the parakeets would be for people to replace existing bird feeders in their gardens with bird feeders which prevent access of the parakeets to the food while still allowing access to other species. For example the parakeet 'restrictive' feeder used in Chapter 5 provided some mitigation of parakeets' resource use in favour of native species, particularly in area of high parakeet abundance. However, given the highly flexible and adaptable foraging abilities of the rose-ringed parakeet (Demery et al. 2011) it may be that they are able to adapt to this restrictive feeder type over time (indeed, by some parakeets did manage to access the restrictive feeder seed by the end of Chapter 5's study period by squeezing their heads through the tight gap in the feeder mesh). To reduce dimensions of the gaps in the mesh any further would risk seriously restricting other species access to the food. An alternative method might be to use a spring weighted mechanism where the weight of the parakeet (ie. around 120g) causes the access to the seed to close. This would prevent bird species of the same weight or heavier of also getting to the seed but this would only prevent a few species which use garden bird feeders from access as only corvid and columbidae species are likely to be heavier (eg. Woodpigeon (*Columba palumbus*) 450g, Jay (*Garrulus glandarius*) 170g (Snow et al. 1998)). Any method used to restrict parakeet access to food would also be reliant on support from the public to implement the change in resource accessibility and need to be cost effective.

The use of members of the public to implement invasive species management has been demonstrated with an approach for American mink (*Neovison vison*) eradication used on the mainland in Eastern Scotland which used volunteers to help trap the minks for eradication. This proved highly successful and the authors proposed that the use of volunteers for similar mink eradication programmes should be tried elsewhere. It was noted however that a considerable effort was made to raise public awareness of the impacts of the mink on native wildlife in order to gain support for the project (Bryce et al. 2011). This shows that the use of citizen science for implementing mitigation schemes can be effective but that public awareness schemes are critical for success.

Conclusion

The research in this thesis has shown that there are extremely high numbers of parakeets in the South East of England (over 32,000) particularly in urban areas of London and that they could be reliant on anthropogenic resources in the urban landscape, particularly garden bird food. This shows the potential for parakeets to reach high number in urban areas across the UK, and potentially in cities globally where similar resources can be found and where temperatures remain high enough for survival. However the halt in growth of the population in South East England over the last few years suggests that population may have reached capacity here. This means that any ecological impacts in South East England are unlikely to worsen, unless the parakeets' behaviour or some other environmental factor were to change.

This thesis has also provided evidence of competition for food between parakeets and native birds, causing negative impacts on native bird foraging behaviour and resulting in a reduction garden bird species' ability to access food. This shows that parakeets are having a significant effect on the behaviour of native birds with the potential for broader impacts at the population level. This adds to knowledge of ecological impacts of the rose-ringed parakeets and provides further insight into the impacts that non-native species can have on native wildlife. It particularly highlights the fact that behavioural impacts of invasive species on native species need to be considered, and that these behavioural impacts can occur simply through an invasive species being present.

So far there is no evidence that the impacts demonstrated here are having a significant effect on native species abundance and so further long-term monitoring is required. Given that rose-ringed parakeets have been present in the South East UK for the last decade in high numbers without yet causing noticeable changes in abundance of native species, it seems that control of the species in its established distribution is not urgent. The use of citizen science provides an efficient means by which to monitor the population across the UK in the long-run, combined with experimental field research to investigate further potential impacts and the mechanisms behind them.

The numbers of parakeets are too high in South East UK for current methods of control to be possible, particularly as the high public profile of the species increases the likelihood of public disapproval of control strategies which involve culling, as demonstrated by the reaction of the public to the culling of the monk parakeet. However where impacts are found it seems sensible that these are addressed on a case-by-case basis in combination with mitigation strategies carried out by members of the public, such as changes to supplemental feeding practices. The most important strategy is to focus on reducing the likelihood of establishment of parakeet populations elsewhere in the UK, as the management of non-native species, such as the rose-ringed parakeet, becomes extremely difficult once the population has established and grown.

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Appendix S1

Supporting Information for Chapter 2

20th May 2012 **Parakeet direct feeding competition experiment**

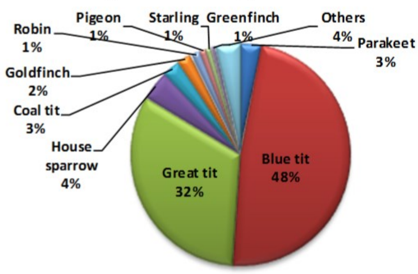
Here's a summary of results so far…. **Half way there!**

We have 43 parakeet frequented gardens taking part in the experiment.
Half the gardens have parakeet proof feeders half have parakeet 'friendly' feeders.
So far we have 6 months of weekly feeding observations, this totals a fantastic 486 weekly observation sessions.

Visits overall:

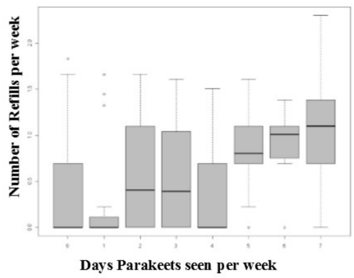
Altogether 19 different species have visited the gardens, with a total of 12,994 visits. An average of 3 species and 27 visits per observation. The rarest bird to visit a feeder so far is the lesser spotted woodpecker. Interesting species which didn't visit the feeder but were recorded in the gardens, include: redpoll, fieldfare, siskin, heron, goldcrest, sparrow hawk and a tortoise!

% Species visiting the feeders



Total visits and species per feeder type:
There was found to be no difference in number of visits per observation between parakeet proof and parakeet 'friendly' feeders.

Total species per feeder type: Other than the loss of parakeet visits to the 'proof' feeders, the numbers of species visiting was found to be the same for both feeder types.



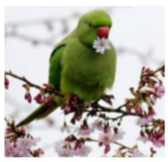
Results for seed consumed: The parakeet 'friendly' feeders required filling significantly more often than the parakeet proof feeders. A positive relationship was found between numbers of parakeets observed in the garden during the week and an increase in the number of refills, suggesting that the parakeets are consuming proportionally more seed than the other species.

Weather: Colder weather reduced the bird visits. This is surprising as it would be expected that birds would rely on the garden feeders more in colder weather for energy to keep warm. Cloud cover, precipitation and wind appeared to have no effect on the visits but further data will allow us to investigate this in more detail.

Parakeets in the garden

The record for maximum number of parakeets on the feeder during an observation so far is **9**!

Parakeets were reported to eat a range of garden plants, including: the pollen, buds, young leaves, flowers, fruit and seeds from, cherry tree, silver birch, almond, horse chestnut, buddleia, pyracantha, apple and crab apple. No doubt this list will increase over the summer.



Conclusions so far…

- Parakeet abundance and frequency of visits in the garden has not been found to have a significant effect on species or numbers of visits to the feeders, however further anaylsis with results over the whole year may prove otherwise.
- We have shown that parakeets are eating more seeds than the other birds.

What do we need the next 6months data for?

- The main reason for the experiment is to compare how the access of food for parakeets within each garden effects the amount of food consumed and the species that use the feeders. Therefore the most exciting results will come at the end of the whole year.
- It will also allow us to examine how the feeder use by both parakeets and other species changes with the seasons and will provide twice as much data to support the results so far, strengthening the findings.

Thank you so much for all your help so far. I look forward to being able to give you conclusive results at the end of the year! Hannah Peck, Imperial College London

Figure S1.1 'Half-way there' 6month report for volunteers taking part in the parakeet feeding restriction Chapter 5

Appendix S2

Supporting Information for Chapter 3

Table S2.1: Historical roost counts 1996 to 2006, * refers to a missed count.

	Year	W.London						S.E.London			Kent				
Source	* is missed count	Walton-on-thames	Esher	Coronation	Thames Ditton	Stanwell	Maidenhead	Hither Green/ Lewisham	Foots Cray	Red hill	Ramsgate Station	Ellington Park, Ramsgate	**Totals London**	**Total Kent**	**Over all total**
Pithon & Dytham	Sep-96	1120						*	*	0	299	0	1120	299	1419
"	Oct-96	1123	0	0				85	35	0	265	0	1243	265	1508
"	Nov-96	0	1000	0				*	*	118	*	*	1118	0	1118
"	Dec-96	0	875	0				75	11	0	0	200	961	200	1161
"	Jan-97	0	775	0				75	1	123	208	0	974	208	1182
"	Feb-97		775	0				75	4	94	192	0	948	192	1140
"	Mar-97	0	680	0				100	1	*	150	0	781	150	931
"	Apr-97	0	0	150				40	1	0	0	100	191	100	291
"	Jun-97	0	0	200				70	0	*	80	0	270	80	350
"	Aug-97	0	0	1346				220	0	0	314	0	1566	314	1880
"	Sep-97	0	*	*				275	0	*	275	0	275	275	550
"	Oct-97	0	0	0	500+			*	*	*	280	0	0	280	280
"	Nov-97	0	0	0	965			210	0	*	139	0	1175	139	1314
"	Dec-97	0	*	*	0			160	0	*	232	0	160	232	392
"	Feb-98	0	*	*	*			100	0	*	155	0	100	155	255
"	Mar-98	0	1100	0	0			*	*	*	138	0	1100	138	1238
"	Apr-98	0	550	0	0			*	*	40	50	0	590	50	640
"	May-98	0	920	0	0			*	*	*	*	*	920	0	920

	Year	W.London						S.E.London			Kent				
Source	* is missed count	Walton-on-thames	Esher	Coronation	Thames Ditton	Stanwell	Maidenhead	Hither Green/ Lewisham	Foots Cray	Red hill	Ramsgate Station	Ellington Park, Ramsgate	**Totals London**	**Total Kent**	**Overall total**
"	Aug-98	0	1460	0	0			95	*	75	320	*	1630	320	1950
"	Sep-98	0	1530	0	0			210	0	0	320	0	1740	320	2060
County recorders (Butler 2003)	1998	*	1704	*	*			210	*	75	437	*	1989	437	2426
"	1999	*	250	*	*			*	*	*	480	*	250	480	730
"	Nov-00	*	2672	*	*		*	*	*	*	*	*	2672	0	2672
Counts from Butler C. (2003)	Dec-00	*	2999	*	*		*	625	*	*	435	*	3624	435	4059
"	Jan-01	*	3080	*	*		*	626	*	*	*	*	3706	0	3706
"	Feb-01	*	*	*	*		*	550	*	277	*	*	827	0	827
"	Mar-01	*	*	*	*		*	502	*	*	293	*	502	293	795
"	Apr-01	*	2327	*	*		*	408	*	*	205	*	2735	205	2940
"	Nov-01	*	*	*	*		116	867	*	350	*	*	1333	0	1333
"	Dec-01	*	3894	*	*		118	842	*	*	*	*	4854	0	4854
"	Jan-02	*	4096	*	*		*	803	*	*	540	*	4899	540	5439
"	Feb-02	*	*	*	*		*	708	*	*	*	*	708	0	708
"	Mar-02	*	3154	*	*		*	580	*	*	*	*	3734	0	3734
"	Apr-02	*	3078	*	*		*	529	*	*	317	*	3607	317	3924
Kent Ornithological Society (KOS)	2003										850		0	850	850
KOS A & F. Simpson	2004		2750								1050		4754	1050	5804
P.Cropper (pers comms)	2005					2700	*				300		2700	300	3000
KOS	2006					*	*				224		0	224	224

Table S2.2: Roost Locations (Latitude and Longitude), South East UK. Including old roosts since the counts 1996 to 1998 (Pithon & Dytham 2002) and new roosts located for this study 2010-2012.

Historical Roosts still in use	Latitude	Longitude
Hither Green , Lewisham	51°26'8.95"N	0° 0'35.33"E
Ramsgate Station , Kent	51°20'24.91"N	1°24'16.03"E
New roost sites		
Alpine Rd, Redhill	51°14'58.40"N	0° 9'44.37"W
Long Lane, Stanwell	51°27'5.98"N	0°28'1.49"W
*Perivale Park	51°31'51.56"N	0°20'19.21"W
Mitcham Common	51°23'30.17"N	0° 7'58.87"W
Wormwood Scrubs	51°31'17.09"N	0°14'25.63"W
Hersham Gravel Pits	51°23'0.42"N	0°22'55.31"W
West Ewell	51°21'41.88"N	0°16'23.74"W
Slough M4 jct 7	51°30'33.15"N	0°38'33.01"W
*Brockwell Park	51°26'57.30"N	0° 6'36.82"W
*Sutcliffe Park	51°27'17.95"N	0° 1'47.97"E
Abandoned Roosts (after 1998)		
Esher Rugby Club, Hersham	51°22'54.04"N	0°23'21.04"W
Coronation Rec. , Hersham	51°22'25.56"N	0°23'46.13"W
Elmbridge Leisure Centre, Walton on Thames	51°23'56.27"N	0° 24' 45.78"W
Batts Hill, Redhill	51°14'31.31"N	0°10'40.29"W
Ellington Park, Ramsgate	51°20'15.01"N	1°24'28.03"E
Bray gravel pits, Maidenhead	51°30'1.36"N	0°42'8.39"W

*New roosts sites abandoned since 2011

Table S2.3: Calculations for missing count estimates

Mitcham missing July 2010

July as proportion of	April 2011	April 2012	Av proportion
	2.170	2.863	= 2.516

Previous available count is April 2010 = 400

July av. proportion of Aprils 2011 and 2012 x April 2010
2.52 x 400 = **1007**

Mitcham missing Oct 2010

October as proportion of	April 2013	April 2012	Av proportion
	3.373	1.443	= 2.408

Previous available count is April 2010 = 400

Oct. av. proportion of Aprils 2011 and 2012 x April 2010
2.408 x 400 = **963**

Hersham missing Jan 2010

January as proportion of	April 2011	April 2012	Av proportion =
	1.371	1.584	1.478

Subsequent available count is April 2010 = 3444
January av. proportion of Aprils 2011 and 2012 x April 2010
1.478 x 3444 = **5090**

a)

$$\begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{F_1} \\ \mathbf{S_0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{S_1} & \mathbf{S_2} \end{bmatrix}$$

b)

$$\begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{1.16} \\ \mathbf{0.61} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0.81} & \mathbf{0.81} \end{bmatrix}$$

Figure S2.1. The structure (a) and values (b) of the Leslie matrix used by Butler (2003) to model the rose-ringed parakeet population. As in my population parameter model (Fig. 3.3), Butler's Leslie matrix is spilt into three age-classes: 0 to 1 year olds (juveniles), 1 to 2 years old (yearlings) and 2 years and above (adults). Juveniles have an annual survival rate (S_0) of 0.61. Both yearlings and adults have a survival rate (S_1 and S_2) of 0.81. Only adults reproduce with a fecundity (F_1) of 1.16. Survival rates are taken from those estimated in monk parakeets (Spreyer & Bucher 1998). The stable age-structure calculated from this matrix (the dominant eigenvector) was used to provide a starting age structure for my model (Fig 3.3) of 39% juveniles, 20% yearlings and 41% adults.

Table S2.4. Total roost counts January 2010 to October 2012

Roosts site	Jan-10	Apr-10	Jul-10	Oct-10	Jan-11	Apr-11	Jul-11	Oct-11	Jan-12	Apr-12	Jul-12	Oct-12
North London												
Scrubs	1036	750	1577	4500	3343	1319	5841	4166	2569	2510	4835	3716
Perivale	1150	776	3632	0	130	437	0	0	0	0	0	0
West London												
Hersham	*(5090)	3444	15353	8560	7806	5693	8092	929	7038	4442	7222	0
Ewell	1599	0	0	(2112)	0	0	0	0	0	0	0	(200)
Stanwell	4264	2475	0	4749	3877	1778	3900	7008	2815	2951	3591	7574
Slough	*	*	*	*	*	*	*	*	582	500	(1372)	500
South East London												
Hither	3500	1961	8346	5839	3400	1711	9729	8291	5750	2942	6456	2863
Sutcliffe	567	400	0	0	0	0	0	0	0	0	0	0
Mitcham	(1000)	(400)	*(1007)	*(963)	(1400)	(800)	1736	2698	4200	1537	4400	2218
Brockwell	311	12	0	0	0	0	0	0	0	0	0	0
Reigate area												
Redhill	550	302	709	734	540	407	1306	1402	901	413	1257	870
Kent												
Ramsgate	1154	765	1061	1475	1596	793	1563	1880	940	813	1487	1658
Totals	15131	11285	30678	27969	22092	12938	32167	26374	24795	16108	30620	19599
with estimates of predicted missing	20221	11285	31685	28932	22092	12938	32167	26374	24795	16108	30620	19599
with estimates –(Ramsgate + Slough)	19067	10520	30624	27457	20496	12145	30604	24494	23273	14795	27761	17441

Note: * roost was yet to be discovered by us, ***(xxxx) =** missed count estimate calculated from proportional average of the of April counts in 2011 and 2012**,** (xxxx) = count from the same month but different day.

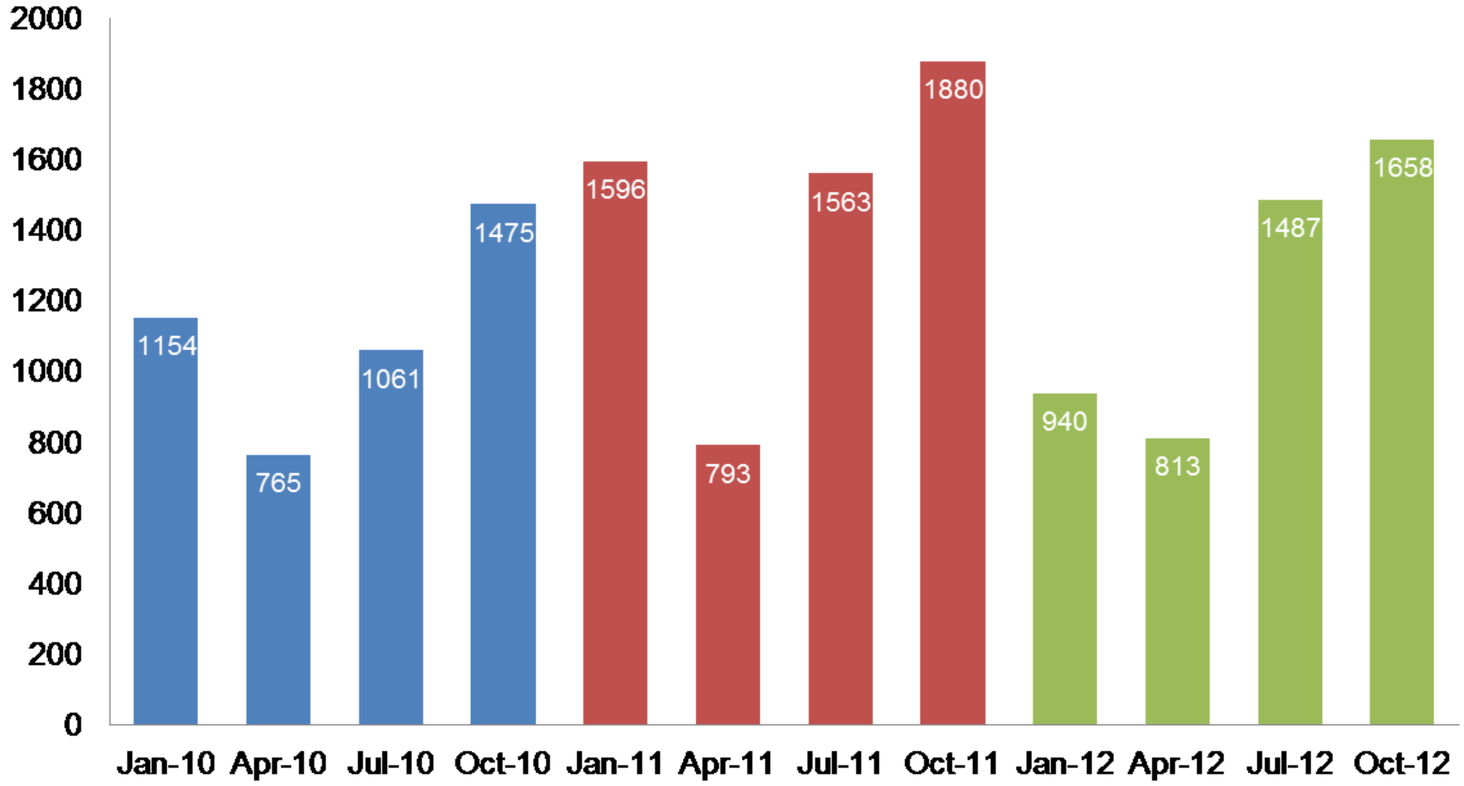


Figure S2.2 Quarterly count totals January 2010 to October 2012 for the Ramsgate roost, showing high October count sizes.

Table S2.5: Population parameter estimates for 2010 to 2012 extrapolated from variance in the quarterly roost counts. ‘Predicted’ is the estimated population size of the age class given the observed count and the age structure. ‘Expected’ is the population size given the previous quarter’s population size under the estimated mortality. ‘Est’ and ‘prop’ are abbreviations of estimated and proportion.

Mortality per quarter juveniles (<1yr)	**Mortality per quarter yearlings and adults (>1yr)**
0.116	**0.0513**

	Obs total count	**Est. total mortality**	**Expected total**	**Expected number juvs**	**Expected number yearlings**	**Expected number adults**	**Est. prop. juvs**	**Est. prop. Yearlings**	**Est. prop. adults**	**Predicted number juvs**	**Predicted number yearlings**	**Predicted number adults**	**Est. juv mort.**	**Est. yearling mort.**	**Est. adult mort.**	**Number breeding females**	**Number non-breed**	**Annual Fecundity**	**Discrpency between observed and expected total in Oct.**
2010																			
Jan	**19067**	NA	NA	NA	NA	NA	0.39	0.20	0.41	7436.13	3813.40	7817.47	NA	NA	NA				
Apr	**10520**	1459.25	17607.75	6573.54	3617.77	7416.43	0.37	0.21	0.42	6573.54	743.33	7416.43	862.59	195.63	401.04	7087.75	3432.25		
July	**30624**	755.82	16851.93	13772.07	6236.32	7035.97	0.45	0.20	0.23	13772.07	6236.32	7035.971	337.22	38.13	380.46			1.94	
Oct	**27457**	2278.43	28345.57	12174.51	5916.39	6675.03	0.43	0.21	0.24	11792.87	5730.93	6465.778	1597.56	319.92	360.95				**888.6**
2011																			
Jan	**20496**	1993.66	25463.34	10424.90	5436.93	6134.08	0.41	0.21	0.24	8391.23	1160.89	4937.459	1367.97	294.00	331.69				
Apr	**12145**	1286.23	19209.77	7417.85	1101.34	4684.17	0.39	0.06	0.24	7417.85	1101.34	4684.167	973.38	59.55	253.29	7064.77	5080.23		
July	**30604**	677.33	18532.44	12071.56	7037.31	5488.71	0.39	0.23	0.18	12071.56	7037.31	5488.71	380.54	56.49872	240.30			1.71	4066.1
Oct	**24495**	2042.89	28561.11	10671.26	6676.30	5207.14	0.37	0.23	0.18	9152.04	5725.82	4465.823	1400.30	361.01	281.57				
2012																			
Jan	**23273**	1584.47	22910.53	8090.40	5432.09	4236.73	0.35	0.24	0.18	8218.40	5518.03	4303.756	1061.64	293.73	229.10				
Apr	**14796**	1457.19	21815.81	7265.07	5234.95	4082.97	0.33	0.24	0.19	7265.07	5234.95	4082.973	953.33	283.07	220.78	7019.81	7776.19		
July	**27761**	850.71	20965.10	6795.90	6892.37	8839.92	0.24	0.25	0.32	6795.90	6892.37	8839.918	372.70	268.55	209.46			0.97	
Oct	**17441**	1595.39	26165.61	6007.58	6538.79	8386.43	0.23	0.25	0.32	4004.42	4358.51	5590.075	788.32	353.58	453.49				8724.6

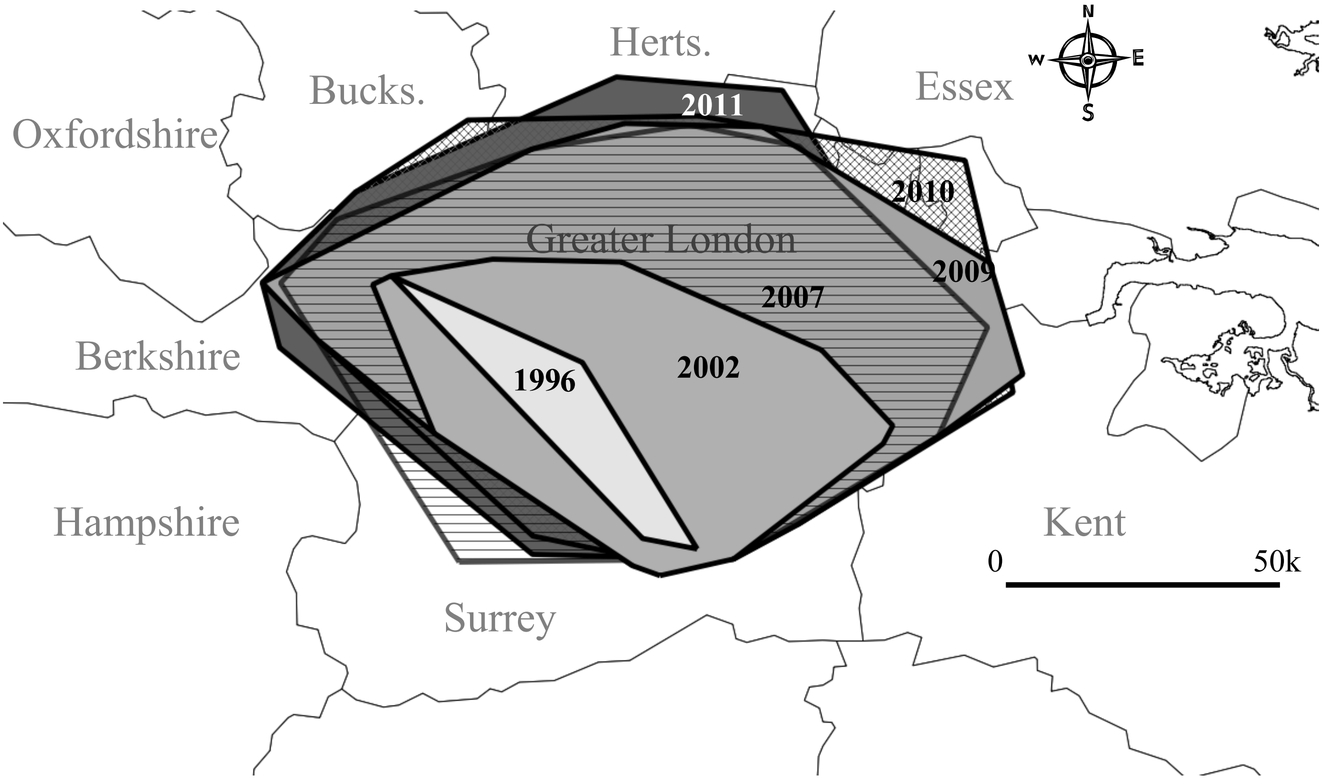


Figure S2.3. Distribution polygons of British Breeding Bird survey presence 1km squares for *Psittacula krameri* in Greater London and the Home Counties (excluding the Ramsgate population) for 1996, 2007, 2009, 2010 and 2011.

Table S2.6: Distribution area km^2, population size, rate of spread per km^2 and density per km^2 of London parakeet population between 1996 and 2012 (population size is determined by the roost counts and distribution by area polygons estimated from BBS $1km^2$ parakeet presence sites).

Year	Area km^2	Population size	Rate of spread km2/year	Density/km^2
1996	568.5	1243	NA	2.19
1997	580.4	1556	11.9	2.68
1998	1748.2	1740	1167.8	0.10
1999	1902.2	NA	154.0	NA
2000	2946.8	3624	1044.7	1.23
2001	1926.2	4854	-1020.6	2.52
2002	3128.5	NA	1202.3	NA
2003	4479.5	NA	1350.1	NA
2004	4565.5	NA	86.0	NA
2005	5209.9	NA	644.4	NA
2006	5889.0	NA	679.07	NA
2007	6648.0	NA	759.0	NA
2008	6690.5	NA	42.5	NA
2009	6434.8	NA	-255.7	NA
2010	7212.0	30624	777.2	4.25
2011	6988.5	30604	-223.5	4.38
2012	NA	27761	NA	NA

Table S2.7. Correlation of fixed effects for the generalized linear mixed model variation in parakeet presence and absence location against variables of land use

	Intercept	distance	Density green space	Density dom. building	Distance: buildings
Distance (km)	-0.371				
Density green space	-0.812	-0.171			
Density domestic buildings	-0.625	0.452	0.379		
Distance: domestic buildings	0.255	-0.594	0.092	-0.841	
Green space: domestic buildings	0.093	0.132	-0.133	0.115	-0.305

Appendix S3

Supporting Information for Chapter 4

Table S3.1. Collinearity scores for all continuous fixed effect variables in the full models, < 0.5 are considered highly correlated.

Model	Measured behaviour	Fixed effects	order	month	to London
1	total visits	order (1-7)			
		month (May to February, 1-10)	0.034		
		distance to London (km)	0.003	-0.072	
		wind strength (0-3)	-0.034	-0.223	0.064
2	proportion of visits resulting in feed	order (1-7)			
		month (May to February, 1-10)	-0.013		
		distance to London (km)	-0.004	-0.158	
		wind strength (0-3)	-0.033	-0.3	0.146
3	time feeding	order (1-7)			
		month (May to February, 1-10)	0.001		
		distance to London (km)	0.004	-0.311	
		wind strength (0-3)	0.048	-0.327	0.249
4	vigilance	order (1-7)			
		month (May to February, 1-10)	-0.013		
		distance to London (km)	0.004	-0.195	
		wind strength (0-3)	-0.005	-0.126	0.078

Table S3.2. Variables (other than treatment and site distribution outside or inside the parakeet range) remaining in the minimal adequate models as fixed effects. The effect of each variable was tested by dropping it from the final model and comparing the final and reduced model by comparing their log-likelihoods. Variables which did not remain in any of the minimal adequate models include: distance to cover (m), wind strength, station in shade or sunlight, distance to centre of London (km).

Model	Measured behaviour	Fixed effects	d.f	chi-squared	p-value
1	total visits	month (May to February, 1-10)	17	4.21	0.040
		time of day (am/pm)	17	30.82	<0.001
2	proportion of visits resulting in feed	order (1-7)	35	47.37	<0.001
		time of day (am/pm)	35	315.35	<0.001
		Species	17	1985.30	<0.001
3	time feeding	time of day (am/pm)	25	17.17	<0.001
		month (May to February, 1-10)	25	14.36	<0.001
		Species	18	63.01	<0.001
4	vigilance	order (1-7)	26	96.87	<0.001
		time of day (am/pm)	26	56.14	<0.001
		weather (cloudy, sun, rain)	25	25.71	<0.001
		Species	19	644.99	<0.001

Table S3.3. Total number of visits and percentage of total visits of each species that visited the feeding stations within and outside the parakeet range. Visits by 16 of the species were too rare to confidently compare foraging response, but it was found that greats tits spent less time feeding (median = 4 seconds; IQR = 1- 19; z = -7.58, p < 0.001) and more time being vigilant (median proportion of time = 0.566 seconds; IQR = 0.255-0.822; z = 16.47; p < 0.001) on peanuts than blue tits (time feeding: median = 18seconds; IQR = 3 – 58.5, proportion of time vigilant: median = 0.393; IQR = 0.157 -0.750).

Species	Visits within parakeet range	% total	Visits outside parakeet range	% total
Great tit	2876	41.85	1665	41.41
Blue tit	2950	42.93	1634	40.64
Blackbird	4	0.06	0	0
Chaffinch	3	0.04	0	0
Coal tit	170	2.47	92	2.29
Carrion Crow	1	0.01	0	0
Goldfinch	43	0.63	0	0
Greenfinch	33	0.48	7	0.17
Great spotted woodpecker	43	0.63	52	1.29
House sparrow	1	0.015	41	1.02
Jay	0	0	5	0.12
Long tailed tit	0	0	7	0.17
Magpie	2	0.03	6	0.15
Nuthatch	21	0.31	6	0.15
Pigeon	10	0.15	0	0
Robin	17	0.25	11	0.27
Woodpigeon	16	0.23	3	0.07
Unidentified	682	9.92	492	12.24
Total	6872		4021	

Table S3.4 Mean values for measured response behaviours per treatment for sites outside the parakeet range (n=11) and sites inside the parakeet range (n=30) and corresponding differences between each treatment and control one (C1) (GLMM z-values, with significant p-values, ***P<0.001, **P<0.01, *p<0.05). # denotes results which are unreliable due to too few data points to make a comparison.

Model	Behaviour	Treatment	Sites outside parakeet range mean	±SE	n	z and p values	Sites inside parakeet range mean	±SE	n	z and p values
1	Total visits	C1	86.55	17.99	952		39.4	11.59	1117	
		C2	53.18	10.82	585	-1.68	43.25	11.52	1226	0.043
		C3	42.45	7.92	467	-1.960 *	36.24	11.08	1030	-1.846
		T1	21.82	7.45	240	-5.288 ***	23	7.98	616	-3.691 ***
		T2	14.27	5.35	157	-6.546 ***	28.5	14.74	733	-3.634 ***
		C4	85	21.63	935	-0.632	33.9	9.69	1012	-0.394
		T3	62.82	15.5	691	-1.602	37.82	10.20	1092	-0.31
2	Proportion feeding visits	C1	0.73	0.014	952		0.72	0.013	1117	
		C2	0.53	0.021	585	-7.858 ***	0.7	0.013	1226	-5.788 ***
		C3	0.48	0.023	467	-8.613 ***	0.61	0.015	1030	-8.586 ***
		T1	0.25	0.028	240	-12.222 ***	0.52	0.02	616	-12.119 ***
		T2	0.25	0.035	157	-9.755 ***	0.36	0.018	733	-10.676 ***
		C4	0.7	0.015	935	-3.871 ***	0.61	0.015	1012	-3.065 ***
		T3	0.69	0.018	691	-3.332 ***	0.59	0.015	1092	-5.076 **
3	Time feeding	C1	63.12	6.66	104		36.43	6.1	83	
		C2	41.22	7.55	37	-2.183 *	30.65	4.29	86	-0.612
		C3	87.24	19.49	38	-1.748	27.18	4.93	45	-0.438
		T1	30.43	17.32	7	#-2.330 *	5.75	1.36	105	-6.161 ***
		T2	11.33	10.33	3	#-2.802 **	14.24	4.61	55	-4.732 ***
		C4	51.24	7.17	75	-1.285	35.31	6.2	86	-1.309
		T3	52.32	7.06	63	-2.114 *	29.12	4.4	95	-1.309

4	Proportion time vigilant	C1	0.31	0.028	104		0.397	0.031	83	
		C2	0.481	0.052	37	16.96 ***	0.428	0.032	86	11.582 ***
		C3	0.394	0.051	38	9.85 ***	0.453	0.042	45	13.366 ***
		T1	0.694	0.124	7	#32.06***	0.63	0.024	105	21.069 ***
		T2	0.7	0.115	3	# 5.78 ***	0.643	0.038	55	18.622 ***
		C4	0.448	0.036	75	20.15 ***	0.494	0.032	86	12.358 ***
		T3	0.407	0.041	63	5.44 ***	0.474	0.030	95	18.146 ***

Table S3.5 Differences in response behaviours between treatments other than C1 for both sites outside (n=11) and inside (n=30) the parakeet range (GLMM z-values, with significant p-values, ***P<0.001, **P<0.01, *p<0.05). # denotes results which are unreliable due to too few data points to make a comparison.

Model	Behaviour	Treatment	Sites outside range z and p values	Sites inside range z and p values	Model	Behaviour	Treatment	Sites outside range z and p values	Sites inside range z and p values
1	Total visits	C2 v T1	-3.650***	-3.725***	3	Time feeding	C2 v T1	-1.211	-5.888***
		C3 v T2	-4.648***	-1.796			C3 v T2	-2.204*	-3.852***
		C2 v C3	-0.273	-1.874			C2 v C3	0.335	0.087
		T1 v T2	-1.280	-0.017			T1 v T2	#-1.106	0.634
		C4 v T3	-0.967	0.077			C4 v T3	-0.925	-0.170
		T1 v T3	3.712***	3.336***			T1 v T3	#1.445	5.353***
		C2 v C4	1.047	-0.435			C2 v C4	1.097	-0.713
2	Proportion of feeding visits	C2 v T1	-6.608***	-7.391***	4	Proportion of time vigilant	C2 v T1	18.864***	12.163***
		C3 v T2	-3.970***	-2.323*			C3 v T2	3.665***	5.936***
		C2 v C3	-1.384	-3.081**			C2 v C3	-7.490***	2.912**
		T1 v T2	0.512	1.711			T1 v T2	#-5.910***	-1.487
		C4 v T3	0.341	-1.925			C4 v T3	-12.169***	5.595***
		T1 v T3	9.784***	7.640***			T1 v T3	#-28.160***	-8.069***
		C2 v C4	-4.280***	-2.666**			C2 v C4	-1.938	0.094

Table S3.6 Differences in response behaviours between sites outside (n=11) and inside (n=30) the parakeet range (GLMM z-values, with significant p-values, **P<0.01, *P<0.05). # denotes results which have too few data points to be confident in the comparison.

Model	Behaviour	Treatment	Difference	SE	z-value	P-value		Model	Behaviour	Treatment	Difference	SE	z-value	P-value	
1	Total visits	C1	-1.183	0.460	-2.571	0.010	*	3	Time	C1	-0.387	0.298	-1.299	0.194	
		C2	-0.642	0.468	-1.371	0.170			feeding	C2	0.067	0.341	0.198	0.843	
		C3	-0.963	0.472	-2.041	0.041	*			C3	-0.024	0.383	-0.062	0.951	
		T1	-0.260	0.482	-0.54	0.589				#T1	-0.555	0.621	-0.894	0.371	
		T2	0.182	0.487	0.373	0.709				#T2	0.762	0.925	0.824	0.410	
		C4	-1.066	0.463	-2.304	0.021	*			C4	-0.414	0.307	-1.349	0.177	
		T3	-0.742	0.466	-1.593	0.111				T3	-0.198	0.309	-0.641	0.522	
2	Proportion	C1	-0.167	0.228	-0.735	0.462		4	Proportion	C1	0.292	0.399	0.730	0.465	
	of feeding	C2	0.216	0.227	0.953	0.341			of time	C2	0.063	0.399	0.158	0.874	
	visits	C3	0.069	0.236	0.291	0.771			vigilant	C3	0.766	0.401	1.910	0.056	
		T1	0.607	0.271	2.241	0.025	*			#T1	-0.971	0.408	-2.380	0.017	*
		T2	0.700	0.296	2.365	0.018	*			#T2	0.398	0.466	0.854	0.393	
		C4	-0.042	0.227	-0.187	0.852				C4	0.186	0.398	0.467	0.641	
		T3	-0.307	0.229	-1.340	0.180				T3	1.106	0.398	2.777	0.005	**

Appendix S4

Supporting Information for Chapter 5

Table S4.1 Visits for all species per feeder type over the entire year, ('Acc' refers to accessible feeders, 'Res' to restrictive feeders, IQR: interquartile range).

	visits to Acc	visits to Res	% visits Acc	% visits Res	median Acc	median Res	IQR 1 Acc	IQR 3 Acc	IQR 1 Res	IQR 3 Res	mean Acc	mean Res
Parakeet feeding visit	632	50	3.69	0.31	2	2	1	4	1	2	3.113	2.273
All parakeet visits	634	100	3.70	0.63	2	0	0	1	0	0	1.124	0.172
Blue tit	8799	8552	51.	53.8	3	4	0	15	1	13	15.6	14.67
Great tit	5309	6050	31.0	38.09	3	2	0	13	0	12	9.41	10.38
Coal tit	701	663	4.09	4.17	0	0	0	0	0	0	1.243	1.137
House sparrow	781	75	4.56	0.47	0	0	0	0	0	0	1.385	0.129
Nuthatch	135	127	0.79	0.80	2	0	0	0	0	0	0.652	0.218
Robin	368	52	2.15	0.33	4	0	0	0	0	0	0.193	0.089
Greenfinch	109	29	0.64	0.18	1	0	0	0	0	0	0.239	0.050
Goldfinch	103	46	0.60	0.29	2	0	0	0	0	0	0.183	0.079
Chaffiinch	55	14	0.32	0.09	1	0	0	0	0	0	0.098	0.024
Pigeon	33	33	0.19	0.21	2	0	0	0	0	0	0.095	0.056
Marsh tit	11	62	0.06	0.39	5.5	0	0	0	0	0	0.020	0.104
Magpie	7	16	0.04	0.10	1	0	0	0	0	0	0.012	0.027
Starling	4	32	0.02	0.20	2	0	0	0	0	0	0.007	0.054
G.S. woodpecker	28	5	0.16	0.03	1	0	0	0	0	0	0.050	0.001
Jackdaw	0	4	0.00	0.03	0	0	0	0	0	0	0	0.007
Dunnock	28	3	0.16	0.02	1	0	0	0	0	0	0.050	0.005
Longtailed tit	16	1	0.09	0.01	2	0	0	0	0	0	0.028	0.001
Jay	2	6	0.01	0.04	2	0	0	0	0	0	0.004	0.010
L.S. woodpecker	0	4	0.00	0.03	0	1	0	0	0	0	0	0.007
Sisikin	3	0	0.02	0.00	1.5	0	0	0	0	0	0.005	0
Wren	3	6	0.02	0.04	1.5	0	0	0	0	0	0.005	0.010
Squirrel	1	5	0.01	0.03	1	0	0	0	0	0	0.002	0.009
Bullfinch	1	0	0.01	0.00	1	0	0	0	0	0	0.002	0
Total native species visits	**16497**	**15785**										
Number of observations	564	583										

Results of weeks where parakeets were seen from one to six days (low level of parakeet presence)

Table S4.2. Results of the generalized linear mixed models analysing factors effecting numbers of visits per observation to the bird feeders for low parakeet present weeks, for visits by: all species, just blue tits and just great tits (NS: no significant difference, * p<0.05** p<0.01, ***p<0.005), garden identity is included as a random effect. Low parakeet presence is defined as observations of parakeets on 1-6 days in the past week (207 observations of the accessible feeders across 26 gardens and 268 observations restrictive feeders across 28 gardens, observations for: 1day n=96, 2 days n=154, 3 days=97, 4 days n=115, 5 days n=97, 6days n=48).

	species visits (excluding parakeets)				blue tit visits				great tit visits			
Feeder	total visits	median visits	IQR		total visits	median visits	IQR		total visits	median visits	IQR	
Accessible	16497	7	2-27		8799	3	0-11		5309	1	0-12	
Restrictive	15785	9	2-28		8552	4	1-12		6050	2	0-11	
	estimate	s.e.	pvalue		estimate	s.e.	pvalue		estimate	s.e.	pvalue	
Intercept†	1.303	0.366	<0.001		-0.102	0.414	0.805		0.224	0.375	0.551	
Restrictive	-0.28	0.125	0.023	*	-	-	-		-0.519	0.169	0.002	**
parakeet	-	-	-		-	-	-		-0.488	0.255	0.056	NS
Summer	0.002	0.179	0.991	NS	0.333	0.212	0.115	NS	0.070	0.231	0.762	NS
Autumn	0.946	0.178	<0.001	***	1.306	0.212	<0.001	***	1.248	0.22	<0.001	***
Winter	0.605	0.159	<0.001	***	1.162	0.186	<0.001	***	0.407	0.209	0.052	***
Hour	0.041	0.021	0.052	NS	-0.043	0.024	0.081	NS	-	-	-	

† the intercept is the parakeet accessible feeder in spring, dashes represent terms that dropped out of the minimal model.

Results of factors effecting the amount of seed consumed during observations in low parakeet presence weeks

Table S4.3. Results of the generalized linear mixed model analysing factors effecting the amount of seed eaten per week (207 observations for the accessible feeder in 26 gardens, 268 observations for the restrictive feeder in 28 gardens) for weeks where parakeets were seen one to six days but not every day (NS: no significant difference, * p<0.05** p<0.01, ***P<0.005), garden identity is included as a random effect. A median of 220g per week was consumed from both feeder types, parakeet accessible (IQR 0-646) and parakeet restrictive feeders (IQR 0-440).

	estimate	s.e.	p-value	
Accessible feeder (in spring)	2.108	0.542	<0.001	
Blue tit visited	0.559	0.315	0.075	NS
Great tit visited	0.988	0.303	0.001	**
Other sp visited	0.733	0.267	0.006	**
Restrictive feeder	-0.466	0.257	0.070	NS
Summer	0.356	0.352	0.312	NS
Autumn	1.096	0.356	0.002	**
Winter	0.278	0.319	0.383	NS