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Bird densities at recreational parks within the species' native and introduced ranges

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Abstract Many bird species have been successfully introduced beyond their natural range, some becoming more abundant in their new environment than in their country of origin. In this study, bird density was measured at 2 study areas comprising a total of 48 recreational parks in northern England and Canterbury, New Zealand, for 10 focal species (native to the former, introduced to the latter). Site characteristics and presence of other bird species were also recorded and investigated as potential explanatory factors for differences in density between the 2 study areas. Common redpoll, common starling, European greenfinch and house sparrow had significantly higher densities at the New Zealand sites. Analysis using generalised linear models revealed a negative relationship between common starling density and proportion cover of trees and shrubs, and a positive relationship between common redpoll, common starling and European greenfinch densities and site species richness. However, since there were no significant differences in site characteristics or site species richness between study areas, these relationships could not account for higher densities at the New Zealand sites. There was an apparent negative relationship between densities of common starling and house sparrow and foraging guild diversity, suggesting that interspecific competition may contribute to differences in density between study areas. The proportion of variation explained by the models was relatively low, suggesting that there may have been missing variables that influenced species density. More detailed study of a wider range of variables is required to investigate this further.

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Keywords: species richness; foraging guild; habitat; interspecific competition

INTRODUCTION

Introduction of species beyond their natural range is a global phenomenon and has been the subject of a number of studies (*e.g.,* Case 1996; Davis 2003; Duncan *et al.* 2003; Cassey *et al.* 2004). The distribution of some species has expanded well beyond the natural geographical limits, as a result of intentional or accidental human assistance.

In New Zealand, acclimatisation societies organised numerous introductions in the latter half of the 19th Century (Long 1981), resulting in widespread establishment of various species, including many British birds. These were particularly successful in heavily modified urban and agricultural habitats (MacLeod *et al*. 2009), whereas many birds native to New Zealand were unable to occupy these post-settlement environments (Williams 1969). Birds were introduced for biological pest control (to reduce crop damage), as game birds or as reminders of the colonists' home countries (King 1984; Wodzizki & Wright 1984; Wilson 2004).

Some species were so successful in their new environment that they became more abundant than in their country of origin. MacLeod *et al*. (2009) demonstrated that a number of British bird species had considerably higher densities at farmland sites in New Zealand than at sites of equivalent habitat

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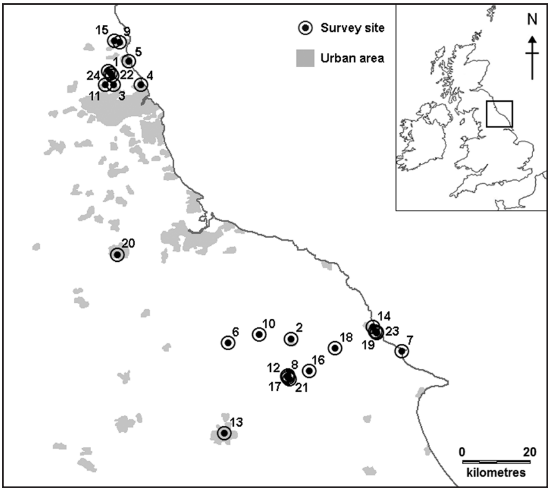

Fig. 1. Locations of survey sites in northern England: 1. Alexandra Park, Cramlington; 2. Beacon Park, Pickering; 3. Burradon Community Recreation Ground; 4. Churchill Playing Field, Whitley Bay; 5. Croft Park, Blythe; 6. Duncombe Park, Helmsley; 7. Filey Brigg; 8. Highfield Lane Recreation Ground, Malton; 9. Hirst Park, Ashington; 10. Kirkbymoorside Sports Field; 11. Lockey Park, Wideopen; 12. Malton Cemetery; 13. Museum Gardens, York; 14. Peasholme Park, Scarborough; 15. Peoples Park, Ashington; 16. Rillington Playing Field; 17. Norton Road Riverbank, Norton; 18. Snainton Recreation Ground; 19. South Bay, Scarborough; 20. South Park, Darlington; 21. St. Peter's Cemetery, Norton; 22. Valley Park, Cramlington; 23. Valley Park, Scarborough; 24. Westfield Park, Cramlington.

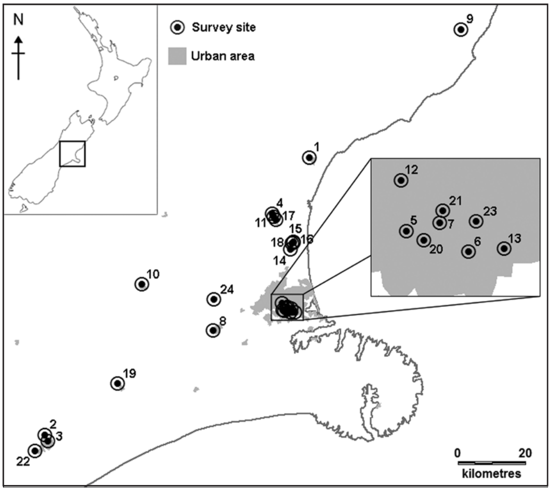

Fig. 2. Locations of survey sites in Canterbury, New Zealand: 1. Amberley Domain; 2. Argyle Park, Ashburton; 3. Ashburton Recreational Reserve; 4. Ashgrove Park, Rangiora; 5. Barrington Park, Christchurch; 6. Beckenham Park, Christchurch; 7. Bradford Park, Christchurch; 8. Brookside Park, Rolleston; 9. Cheviot Domain; 10. Darfield Domain; 11. Dudley Park, Rangiora; 12. Hagley Park South, Christchurch; 13. Hansen Park, Christchurch; 14. Hinemoa Park, Kaiapoi; 15. Kaiapoi Domain; 16. Kaiapoi Park; 17. Matawai Nature Park, Rangiora; 18. Murphy Park, Kaiapoi; 19. Rakaia Domain; 20. Somerfield Park, Christchurch; 21. Sydenham Park, Christchurch; 22. Tinwald Domain; 23. Waltham Park, Christchurch; 24. West Melton Domain

in Britain. Their study investigated habitat and climate as potential explanatory factors to predict bird densities. Although the variables measured could not explain differences in densities, it was suggested that in New Zealand specific habitats may provide introduced species with higher quality resources and birds may be subjected to fewer or less extreme adverse weather events.

In addition to habitat and climate, interactions with other organisms (*e.g.*, predation, parasitism and competition) can also influence population density (Krebs 1985). The effects of interspecific competition have been the subject of several studies, including for example song sparrow (*Melospiza melodia*) in North America (Yeaton & Cody 1974) and forest birds of Hawaii (Mountainspring & Scott 1985), the results of which indicated that interspecific competition could negatively affect territory size and density, respectively.

Several bird species introduced from Britain to New Zealand are now declining in their country of origin and are consequently listed as birds of conservation concern, including common starling (*Sturnus vulgaris*), dunnock (*Prunella modularis*), house sparrow (*Passer domesticus*) and song thrush (*Turdus philomelos*; Inger *et al*. 2014; Eaton *et al*. 2015). Studying the success of these and other similar species in places to which they have been introduced may provide increased understanding of their ecology and how they interact with their environment. Identification of the relative importance of factors that regulate density could in turn inform conservation action within their natural range.

In this study, measures of bird densities for a selection of focal species (native to Britain, introduced to New Zealand) were compared at recreational parks in 2 study areas: one in northern England and the other in Canterbury, New Zealand. Site characteristics (size and proportion of habitat cover) and species richness (indicating potential for interspecific competition) were also compared, with the aim of assessing these as potential explanatory factors for differences in species density between the 2 study areas. For the latter, the guild concept was applied (Krebs 1985; Simberloff & Dayan 1991).

MATERIALS AND METHODS

Twenty-four sites were selected in each of the 2 study areas (Fig. 1 & 2). Timing constraints and other

Table 1. Candidate model descriptions for GLM analysis. D = density; fg = foraging guild diversity; spp = site species richness, area = site area; trees = mean cover of trees and shrubs; grass = mean cover of grassland; built = mean cover of built.

Model	Formula	Description
M1	D ~ fg + spp + area + trees + grass + built	Species richness (foraging guild, site) & site characteristics
M2	D ~ fg	Foraging guild diversity only
M3	D ~ spp	Site species richness only
M4	D ~ fg + spp	Species richness (foraging guild, site)
M5	D ~ fg + spp + area	Species richness (foraging guild, site) & site characteristics (site area)
M6	D ~ area + trees + grass + built	Site characteristics
M7	D ~ trees + grass + built	Site characteristics (habitat types)
M8	D ~ fg + area	Species richness (foraging guild) & site characteristics (site area)
M9	D ~ fg + trees	Species richness (foraging guild) & site characteristics (trees & shrubs)
M10	D ~ fg + grass	Species richness (foraging guild) & site characteristics (grassland)
M11	D ~ fg + built	Species richness (foraging guild) & site characteristics (built)
M12	D ~ fg + trees + built	Species richness (foraging guild) & site characteristics (trees & shrubs, built)

practicalities precluded random or systematic site selection (which therefore limits inference beyond the sites studied). However, sites were chosen to represent a range of site characteristics (*e.g.*, size, proportion cover of different habitat types).

Differences in timing of the seasons between the northern and southern hemispheres necessitated a gap of ~6 months between field survey periods for the 2 study areas, to ensure surveys were conducted in the same season. The England sites were surveyed between 3 and 18 July 2014, whilst the New Zealand sites were surveyed between 15 December 2014 and 3 January 2015.

The area of each site was measured using an appropriate geographic information system tool: for northern England sites, the MAGIC website (DEFRA 2014); for Canterbury, New Zealand sites, MapInfo version 6.0 with 1:50,000 scale maps (LINZ 2014).

A 150 m grid was super-imposed onto a recent aerial photograph (Google Maps 2014) to determine bird count station locations. The stations were, therefore, ~150 m apart. At most sites, bird counts were completed at all grid intersections falling within the park boundary. However, for some of the larger sites, counts were completed at a random selection of grid intersections. The 'count area' was defined as the area within a circle of 150 m radius around a bird count station. Some stations were within 150 m of the park boundaries and therefore in these cases bird count areas included the immediately adjacent land.

For each count area, a habitat assessment was completed using aerial photographs (Google Maps 2014), assigning habitats to 4 categories: trees and shrubs (woodland, scattered trees, scrub, hedgerows); grassland (open areas with a continuous grass sward); built (buildings, hard-standing, roads); and other (any other habitat types). Each habitat type was given a score of 0-10, to indicate the approximate percentage cover within the count area (0 = 0%, 1 = 1-10%, 2 = 11-20%, 3 = 21-30%, 4 = 31-40%, 5 = 41-50%, 6 = 51-60%, 7 = 61-70%, 8 = 71-80%, 9 = 81-90%, 10 = 91-100%). There was no assessment of the surrounding landscape, however to ensure comparisons between study areas were valid, all sites selected were within an urban/sub-urban setting.

At each count station, a 5-minute bird count was carried out using a method adapted from Dawson & Bull (1975). Presence of each species detected (by sight or sound) was recorded at each station. All fieldwork was completed by a single observer, in suitable weather conditions (avoiding heavy rain and strong winds), starting at least one hour after sunrise and finishing before 1300 h. In total, 108 and 120 counts were completed at the England and New Zealand study areas, respectively. At the northern England sites an audio recording of each 5-minute period was made using a hand-held Sony ICD-PX312M digital recorder, with a microphone sensitivity range of 75 - 20,000 Hz. These recordings were later analysed by a second observer to confirm identification of any bird calls not identified during

Table 2. Site characteristics and number of bird counts completed for sites in the northern England study area. Habitat values are mean scores indicating proportion of count area covered (on a scale of 0-10), for all counts completed at that site.

Site name	Area (ha)	No. of counts	Habitat types			
			Trees & shrubs	Grass-land	Built	Other
Alexandra Park, Cramlington	9.6	6	2.8	6.2	1.7	0.2
Beacon Park, Pickering	6.2	3	2.3	7	2	0
Burradon Community Recreation Centre	2.9	3	2.7	5.3	3	0
Churchill Playing Field, Whitley Bay	12.2	6	2.2	6.5	2.2	0
Croft Park, Blythe	3	3	1	6.7	3.7	0
Duncombe Park, Helmsley	68.9	8	2.3	7.9	1	0.5
Filey Brigg	24.4	6	2.2	6.3	0.5	2.7
Highfield Road Recreation Ground, Malton	1.6	3	1	3.7	6.7	0
Hirst Park, Ashlington	9.9	6	3.5	4.7	1.8	0
Kirkbymoorside Sports Ground	2.8	2	1	7	4	0
Lockey Park, Wideopen	6.6	9	1.6	7.8	1.3	0.6
Malton Cemetery	3.2	3	3.7	4.3	2.3	0.3
Museum Gardens, York	3.9	3	2.3	2.7	4.7	1.3
Peasholme Park, Scarborough	13.6	3	3.3	1.3	4	2
Peoples Park, Ashington	8.4	6	2	7	2.2	0
Rillington Playing Field	1.2	3	1.7	4.7	3	2.7
Norton Road Riverbank, Norton	0.6	2	2	2	7	1
Snainton Recreation Ground	2.6	3	1	5.3	2.3	1.7
South Bay, Scarborough	24.1	6	2.8	3.7	2.7	1.7
South Park, Darlington	23.6	3	5	3.3	0.7	1.7
St Peters Cemetery, Norton	2.2	3	2	3	7	0
Valley Park, Cramlington	6.9	6	2.8	6.3	2	0
Valley Park, Scarborough	2.6	3	4.3	1.7	4.3	0
Westfield Park, Cramlington	6.2	6	2.7	6.8	1.5	0

the surveys. This was necessary due to the relative lack of familiarity of the author with calls of non-focal bird species found outside of New Zealand.

To allow densities to be estimated, additional information was recorded for the following 10 focal species: chaffinch (*Fringilla coelebs)*, common redpoll (*Carduelis flammea)*, common starling, dunnock, Eurasian blackbird (*Turdus merula)*, European goldfinch (*Carduelis flammea)*, European greenfinch (*Carduelis chloris)*, house sparrow, rock pigeon (*Columba livia)* and song thrush. For each bird (or cluster of birds), the number of individuals was recorded, then assigned to 1 of 3 distance categories (0-25 m, 26-75 m, and 76-150 m). Situations for which birds were recorded but not assigned to a distance category included those flying overhead or into the count area, those thought to have moved prior to detection, those that were outside of the count area (>150 m from the station) and any focal species identified from the audio recordings.

Densities of focal species were calculated using DISTANCE version 6.2 (Thomas *et al.* 2010). Observations not assigned to a distance category were excluded. A global detection function was fitted for each species, using pooled data from both study areas, then density estimates calculated separately for each study area. To ensure global detection functions were appropriate, study area-specific detection functions were calculated (for those species that had sufficient detections), and the resulting model AIC values compared to those with global detection functions. According to Buckland *et al*. (2001), a model with a global detection function can be used where the AIC value is smaller than the

Table 3. Site characteristics and number of bird counts completed for sites in the Canterbury New Zealand study area. Habitat values are mean scores indicating proportion of count area covered (on a scale of 0-10), for all counts completed at that site.

Site name	Area (ha)	No. of counts	Habitat types			
			Trees & shrubs	Grass-land	Built	Other
Amberley Domain	13.7	9	2.6	7.1	1.2	0.7
Argyle Park, Ashburton	12.2	6	2.2	7	1.8	0.7
Ashburton Recreational Reserve	36.5	9	5.2	3.6	2	0.1
Ashgrove Park, Rangiora	4	3	1	4	6	0
Barrington Park, Christchurch	4	3	1	4	6.7	0
Beckenham Park, Christchurch	3.8	3	1.7	2.7	6.7	0.7
Bradford Park, Christchurch	2.4	3	1	2.3	8	0
Brookside Park, Rollerston	9.8	6	1	7.3	2.5	1
Cheviot Domain	15.4	9	2.4	7.3	1	0.4
Darfield Domain	9.1	6	1.2	6.3	3.7	0.2
Dudley Park, Rangiora	3.9	3	1	4.3	5.7	0
Hagley Park South, Christchurch	68.9	12	2.9	5.8	2	0
Hansen Park, Christchurch	10.9	6	1.7	4.3	3.8	0.7
Hinemoa Park, Kaiapoi	2.3	3	1	3.7	6.7	0.7
Kaiapoi Domain	4.6	3	4	2	4.3	0
Kaiapoi Park	7	3	1.3	6.7	3.3	0
Matawai Nature Park, Rangiora	4.8	3	4	1.7	5	0
Murphy Park, Kaiapoi	2.8	3	2	5.3	1.3	1.7
Rakaia Domain	19.1	9	2.7	5.8	0.9	1.8
Somerfield Park, Christchurch	7.8	3	1	4	6	0
Sydenham Park, Christchurch	4.3	3	1	3.7	7	0
Tinwald Domain	28.7	6	3	5.5	1	1.3
Waltham Park, Christchurch	2.3	3	1	2.7	8	0.3
West Melton Domain	5.9	3	1.7	7.7	1.3	0

sum of the study area-specific model AIC values. Models were selected by comparison of detection function curve fit, delta AIC and coefficient of variation (%CV). To allow statistical comparison, density was also estimated for each site.

All other statistical analyses were performed using R version 3.1.2 (R Core Team 2014). Significant differences between the northern England sites and the New Zealand sites were tested for using Student's *t*-tests and Wilcoxon rank sum tests. To provide insight into possible interspecific competition, each species recorded was assigned to a single foraging guild (the main guild for that species), based on classifications defined by Gonzalez-Salazar *et al*. (2014), using information on species ecology from Mitch Waite Group (2013) and Miskelly (2013). For each site, focal species foraging guild diversities were calculated by summing the number of species present within the relevant guild.

For focal species with significantly different densities between the 2 study areas, generalised linear models (GLMs) were used to test for potential relationships between density (response variable), site characteristics (site area, proportion cover of trees and shrubs, grassland, built), site species richness and foraging guild diversity (explanatory variables). A negative binomial distribution was used, and densities were tested for over-dispersion. Model selection was carried out using an information theoretic approach, following Zuur *et al*. (2013). Twelve *a priori* candidate models were considered for each species (Table 1) and the top 3 models chosen for each species based upon their AIC weights. The percentage of variance explained

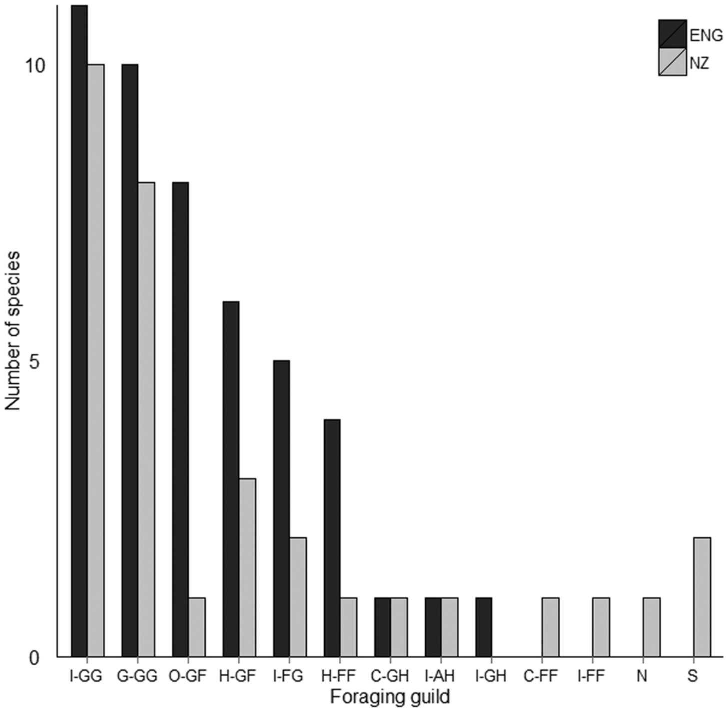

Fig. 3. Number of species per foraging guild recorded within the England (ENG) and New Zealand (NZ) study areas. For key to foraging guild abbreviations see Table 4.

by each model was calculated using the following formula: ((null deviance - residual deviance) / null deviance) x 100. Diagnostic plots were used to test the validity of each model, following Zuur *et al*. (2013).

RESULTS

Site characteristics

Site size was highly variable in both countries (Tables 2 & 3), with England sites ranging from 0.6 - 68.9 ha (mean 10.3 ha) and New Zealand sites ranging from 2.3 - 68.9 ha (mean 11.8 ha). There was, however, no significant difference between mean site sizes from the 2 study areas (W = 247.5, p = 0.409). Regarding proportion cover of broad habitat types (Tables 2 & 3), there was no significant difference between study areas for trees and shrubs (W = 382, p = 0.051), grassland (W = 303.5, p = 0.757), built (W = 236, p = 0.288) or other (W = 276, p = 0.801). This indicated that the sites were broadly similar in character in both study areas.

Species richness and foraging guild diversity

At the northern England sites, 49 taxa, including 2 identified to genus only, were recorded (Table 4), from 9 orders, 26 families and 40 genera. Frequency of occurrence (percentage of sites at which a species was recorded) varied considerably, from 4.2 - 95.8%, and the mean number of species per site was 14.2 (±0.810 SE_{mean}). Excluding the 2 taxa identified to genus only, the proportion of species recorded that were native to Britain was 93.6%.

A considerably shorter species list was obtained for the New Zealand sites, consisting of 34 taxa (including 2 identified to genus only; Table 4), representing 8 orders, 22 families and 29 genera. Frequency of occurrence ranged from 4.2 - 100%, and the mean number of species per site was 13.6 (±0.697 SE_{mean}). Excluding the 2 taxa identified to genus only, the proportion of species recorded that were native to New Zealand was 50.0%, whilst 40.6 % were native to Britain. Frequency of occurrence was generally higher for introduced species.

Despite the higher number of species recorded in the northern England study area, there was no significant difference in species richness between the 2 study areas (t = 1.179, df = 23, p = 0.251).

A wide range of foraging guilds was recorded (Table 4). Although fewer species were recorded at the New Zealand sites, a wider range of guilds (n = 12) was recorded there than in the northern England study area (n = 9; Fig. 3). In both study areas, insectivore-ground gleaner (I-GG) and granivore-ground gleaner (G-GG) guilds contained the highest numbers of species.

Focal species

For distance sampling analysis, the half-normal and hazard-rate models provided the closest fit to the detection function curves (Table 5). Rock pigeon was excluded from the focal species analysis as there

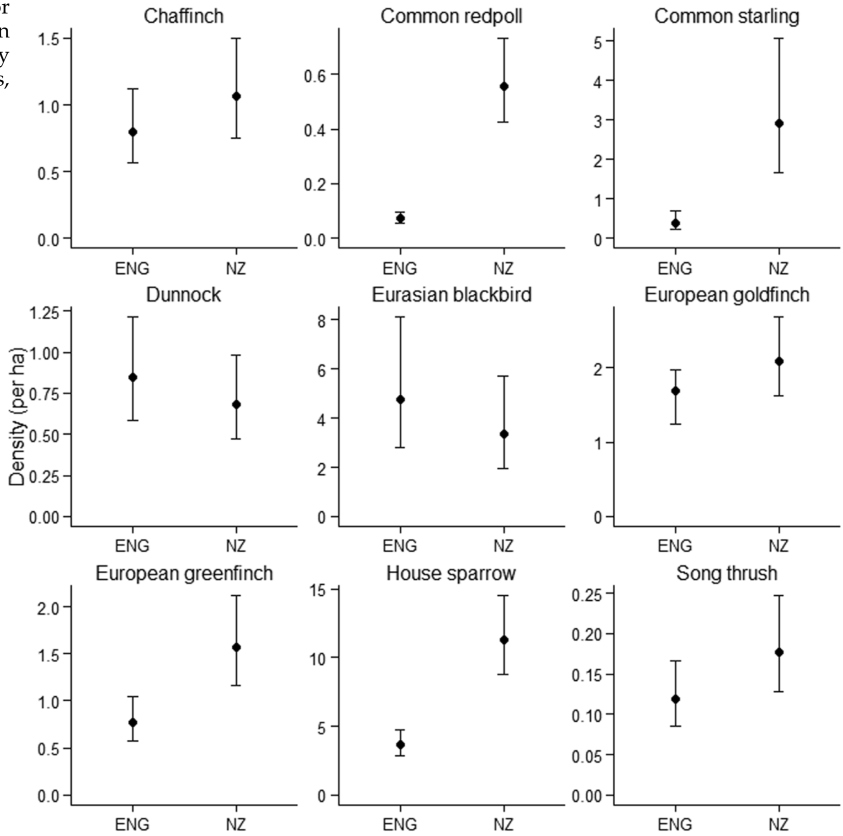

Fig. 4. Density estimates for each species at the northern England (ENG) and Canterbury New Zealand (NZ) study areas, with 95% confidence limits.

were only 40 detections, which was well below the recommended minimum of 60-80 (Buckland *et al.* 2001).

Four focal species had significantly higher densities at the New Zealand sites: common redpoll, common starling, European greenfinch and house sparrow (Fig. 4; Table 6). These 4 species belong to 2 foraging guilds: G-GG (common redpoll, European greenfinch and house sparrow) and I-GG (common starling). Each of these foraging guilds, when combined with O-GF (also potential competitors), contained significantly higher numbers of species at the England sites (G-GG & O-GF: t = 5.100, df = 23, p < 0.001; I-GG & O-GF: t = 3.391, df = 23, p = 0.003). This highlights a potential difference in composition of bird communities between the 2 study areas, which may affect these 4 focal species.

Analysis of common redpoll, common starling, European greenfinch and house sparrow densities, site characteristics and species richness revealed several potential relationships (Table 7). Common starling density was negatively related to proportion cover of trees and shrubs. There was evidence to suggest that as site species richness increased, so did common starling, European greenfinch and house sparrow densities. Conversely, common starling and house sparrow densities were negatively associated with their respective foraging guild diversities. No significant relationships were identified for common redpoll. The proportion of variation explained by the models was relatively low, the 'best' models achieving 2.9% (common redpoll), 43.8% (common starling), 10.0% (European greenfinch) and 26.4% (house sparrow). There was no evidence of over-dispersion and diagnostic plots did not reveal any potential problems with the models.

DISCUSSION

Site characteristics appeared broadly similar between the 2 study areas (northern England and Canterbury, New Zealand), with no significant differences in park size or proportion cover of habitat types. This is not surprising, since parks from both study areas perform the same functions (*e.g.*, organised sports and informal passive recreation). Furthermore, many parks in New Zealand's urban areas were established by European settlers, who created them to be reminiscent of home (Wilson 2004), and even planted many familiar tree and shrub species. The vegetation assessment for this study

Table 4. Species recorded at the northern England (ENG) and New Zealand (NZ) study sites, with provenance (N = native, I = introduced), frequency of occurrence (% of sites) and main foraging guild (C-GH = carnivore-ground hawker; C-FF = carnivore-freshwater forager; G-GG = granivore-ground gleaner; H-FF = herbivore-freshwater forager; H-GF = herbivore-ground forager; I-AH = insectivore-aerial hawker; I-GH = insectivore-ground hawker; I-FF = insectivore-freshwater forager; I-GG = insectivore-ground gleaner; I-FG = insectivore-foliage gleaner; N = nectarivore; S = scavenger; O-GF = omnivore-ground forager).

Common name	Scientific name	Foraging guild	Provenance		% of sites	
			ENG	NZ	ENG	NZ
Australian magpie	*Gymnorhina tibicen*	I-GG	-	I	-	62.5
Bellbird	*Anthornis melanura*	N	-	N	-	20.8
Black shag	*Phalacrocorax carbo*	C-FF	-	N	-	4.2
Black-billed gull	*Larus bulleri*	I-GG	-	N	-	8.3
Black-headed gull	*Larus ridibundus*	O-GF	N	-	20.8	-
Blue tit	*Parus caeruleus*	I-FG	N	-	16.7	-
Canada goose	*Branta canadensis*	H-GF	I	I	8.3	4.2
Carrion crow	*Corvus corone*	O-GF	N	-	83.3	-
Chaffinch	*Fringilla coelebs*	G-GG	N	I	83.3	87.5
Chiffchaff	*Phylloscopus collybita*	I-FG	N	-	37.5	-
Collared dove	*Streptopelia decaocto*	G-GG	N	I	12.5	-
Common redpoll	*Carduelis flammea*	G-GG	N	I	16.7	79.2
Common starling	*Sturnus vulgaris*	I-GG	N	I	58.3	95.8
Coot	*Fulica atra*	H-FF	N	-	4.2	-
Dunnock	*Prunella modularis*	I-GG	N	I	70.8	62.5
Eurasian blackbird	*Turdus merula*	I-GG	N	I	91.7	95.8
Eurasian skylark	*Alauda arvensis*	G-GG	N	I	8.3	8.3
European goldfinch	*Carduelis carduelis*	G-GG	N	I	83.3	87.5
European greenfinch	*Carduelis chloris*	G-GG	N	I	70.8	91.7
Goldcrest	*Regulus regulus*	I-FG	N	-	4.2	-
Great black-backed gull	*Larus marinus*	O-GF	N	-	4.2	-
Great tit	*Parus major*	I-GG	N	-	4.2	-
Grey warbler	*Gerygone igata*	I-FG	-	N	-	33.3
Greylag goose	*Anser anser*	H-GF	N	I	8.3	-
Herring gull	*Larus argentatus*	O-GF	N	-	58.3	-
House martin	*Delichon urbica*	I-AH	N	-	25.0	-
House sparrow	*Passer domesticus*	G-GG	N	I	87.5	100
Jackdaw	*Corvus monedula*	O-GF	N	-	37.5	-
Kestrel	*Falco tinnunculus*	C-GH	N	-	4.2	-
Lesser black-backed gull	*Larus fuscus*	O-GF	N	-	8.3	-
Little owl	*Athene noctua*	I-GH	I	I	4.2	-
Long-tailed tit	*Aegithalos caudatus*	I-FG	N	-	16.7	-
Magpie	*Pica pica*	O-GF	N	-	29.2	-
Mallard	*Anas platyrhynchos*	H-FF	N	I	4.2	29.2
Meadow pipit	*Anthus pratensis*	I-GG	N	-	8.3	-

Table 4. Continued.

Mistle thrush	*Turdus viscivorus*	I-GG	N	-	8.3	-
Moorhen	*Gallinula chloropus*	H-FF	N	-	4.2	-
Mute swan	*Cygnus olor*	H-FF	N	I	4.2	-
New Zealand fantail	*Rhipidura fuliginosa*	I-AH	-	N	-	20.8
New Zealand scaup	*Aythya novaeseelandiae*	I-FF	-	N	-	4.2
Oystercatcher	*Haematopus ostralegus*	I-GG	N	-	8.3	-
Paradise shelduck	*Tadorna variegata*	H-GF	-	N	-	12.5
Peafowl	*Pavo cristatus*	O-GF	I	I	-	8.3
Pied wagtail	*Motacilla alba*	I-GG	N	-	16.7	-
Red-billed gull	*Larus novaehollandiae*	S	-	N	-	4.2
Red-legged partridge	*Alectoris rufa*	H-GF	I	I	4.2	-
Robin	*Erithacus rubecula*	I-GG	N	-	16.7	-
Rock pigeon	*Columba livia*	G-GG	N	I	29.2	37.5
Rook	*Corvus frugilegus*	O-GF	N	I	29.2	-
Sand martin	*Riparia riparia*	H-GF	N	-	4.2	-
Silvereye	*Zosterops lateralis*	I-FG	-	N	-	83.3
Song thrush	*Turdus philomelos*	I-GG	N	I	50.0	54.2
South Island pied oystercatcher	*Haematopus finschi*	I-GG	-	N	-	8.3
Southern black-backed gull	*Larus dominicanus*	S	-	N	-	62.5
Spur-winged plover	*Vanellus miles*	I-GG	-	N	-	41.7
Swallow	*Hirundo rustica*	H-GF	N	-	33.3	-
Swamp harrier	*Circus approximans*	C-GH	-	N	-	4.2
Swift	*Apus apus*	H-GF	N	-	54.2	-
Variable oystercatcher	*Haematopus unicolor*	I-GG	-	N	-	8.3
Welcome swallow	*Hirundo neoxena*	H-GF	-	N	-	62.5
White-faced heron	*Egretta novaehollandiae*	I-GG	-	N	-	4.2
Whitethroat	*Sylvia communis*	I-FG	N	-	4.2	-
Woodpigeon	*Columba palumbus*	G-GG	N	-	95.8	-
Wren	*Troglodytes troglodytes*	I-GG	N	-	75.0	-
Yellowhammer	*Emberiza citrinella*	G-GG	N	I	12.5	8.3

was limited, however, to information gleaned from aerial photographs. A more detailed assessment, for example using Hurst & Allen (2007), could reveal important differences in vegetation structure and species composition. The latter will become increasingly more likely due to the recent trend towards planting native species in New Zealand (MacLeod *et al*. 2012). An assessment of factors affecting habitat quality, for example abundance of suitable food resources (Johnson 2007), could also provide possible explanatory variables which may account for differences in bird densities.

A higher number of species was recorded overall in the England study area, although there was no significant difference in site species richness between the England and New Zealand sites. Although England had more species, many of these were recorded at low frequencies. Most species at the England sites were native to that country. Conversely, at the New Zealand sites half the species recorded were introduced, with frequency of occurrence generally higher than that for the native species. These data support the findings from other studies in New Zealand: that urban bird

Table 5. Results of distance sampling analysis: number of detections; model key function and adjustment term (HazCos = Hazard + cosine, HNormCos = Half-normal + cosine, HNormHerm = Half-normal + hermite); density per hectare and coefficient of variation (%CV).

Species	Detections	Model	England		New Zealand	
			Density	%CV	Density	%CV
Chaffinch	224	HazCos	0.794	17.47	1.063	17.48
Common redpoll	82	HNormCos	0.073	13.44	0.558	13.58
Common starling	205	HazCos	0.393	29.53	2.898	28.81
Dunnock	84	HNormCos	0.844	18.38	0.680	18.49
Eurasian blackbird	320	HazCos	4.758	27.58	3.344	27.53
European goldfinch	183	HNormCos	1.697	11.84	2.087	12.8
European greenfinch	326	HazCos	0.776	15.23	1.568	15.39
House sparrow	581	HazCos	3.658	12.92	11.292	12.89
Song thrush	73	HNormHerm	0.119	16.74	0.177	16.74

Table 6. Results of Wilcoxon rank sum tests for each species, testing for differences in density between the northern England and New Zealand sites. An asterisk indicates a significant difference ($p < 0.05$).

Species	Test statistic (W)	p-value
Chaffinch	217	0.143
Common redpoll	84	<0.001*
Common starling	94.5	<0.001*
Dunnock	284	0.941
Eurasian blackbird	239.5	0.321
European goldfinch	236.5	0.290
European greenfinch	160.5	0.009*
House sparrow	21	<0.001*
Song thrush	248	0.379

communities were largely dominated by introduced species (Day 1995; van Heezik *et al*. 2008; Spurr 2012). In their study of an urban area in Ohio, USA, Beissinger & Osborne (1982) reported an abundance of ground feeding species, which is a pattern repeated here, in both study areas. Interestingly, the range of foraging guilds represented was wider at the New Zealand sites. This could indicate differences in habitat composition and/or resource use (Simberloff & Dayan 1991), or it could be an artefact of assigning each species to a single foraging guild (discussed below).

Common redpoll, common starling, European greenfinch and house sparrow were present at significantly higher densities at the New Zealand sites, whereas other focal species densities were not significantly different between the 2 study areas. This suggests the presence of beneficial factors for these 4 species in these park environments, allowing them to exist at higher densities at the New Zealand sites. Site characteristics and interspecific competition were explored as possible explanatory factors. The analysis identified a potential negative relationship between common starling density and proportion cover of trees and shrubs. Other studies have described a similar relationship, for example in a study of Buenos Aires urban parks, Ifran & Fiorini (2010) recorded a negative relationship between density of the introduced common starling and the number of trees. This can be explained by the common starling's preference for open-ground foraging (Williamson & Gray 1975; Heather & Robertson 2000). In addition, we would expect common starling and house sparrow to be positively associated with buildings, since they often nest in cavities provided by man-made structures (Melles *et al*. 2003; Higgins *et al*. 2006). Indeed, in their study of urban bird densities in a New Zealand city, van Heezik & Adams (2014) found that house sparrow density increased in areas of higher density housing. Although no relationship between common starling or house sparrow densities and the built habitat was identified in the current study, this may reflect the lack of detailed habitat information recorded and a more in-depth assessment may give different results. Habitats beyond the site boundaries could also influence density. In a study in Canada, Melles *et al*. (2003) concluded that both local and landscape-scale resources were important in determining the distribution of urban birds. An assessment of the surrounding landscape was not attempted as part of this study.

The analysis indicated a significant positive relationship between common starling, European greenfinch and house sparrow densities and site species richness. Although this may seem counter-intuitive from an interspecific competition

Table 7. Results of generalised linear models testing relationships between density, site characteristics and species richness. Habitat variables were mean scores indicating proportion of count area covered (on a scale of 0-10), for all counts completed per site. AICw = Akaike Information Criterion weight; fg = foraging guild diversity; spp = site species richness, area = site area; trees = mean cover of trees and shrubs; grass = mean cover of grassland; built = mean cover of built. An asterisk indicates a significant relationship ($p < 0.05$).

Species	Model	AICw	% variation explained	Variable	Estimate	SE_{mean}	p-value
Common redpoll	M2	0.164	2.9	fg	-0.119	0.110	0.279
	M9	0.148	7.2	fg	-0.077	0.110	0.484
				trees	-0.342	0.276	0.216
	M4	0.135	6.7	fg	-0.273	0.166	0.101
				spp	0.131	0.104	0.209
Common starling	M1	0.567	43.8	fg	-0.312	0.114	0.006*
				spp	0.218	0.074	0.003*
				area	-0.005	0.015	0.764
				trees	-0.409	0.322	0.203
				grass	0.060	0.213	0.779
				built	0.231	0.201	0.249
	M9	0.197	30.2	fg	-0.170	0.075	0.024*
				trees	-0.551	0.182	0.002*
	M12	0.112	31.5	fg	-0.121	0.092	0.189
				trees	-0.459	0.196	0.019*
				built	0.094	0.100	0.347
European greenfinch	M3	0.357	10.0	spp	0.093	0.042	0.028*
	M4	0.318	13.4	fg	-0.120	0.091	0.187
				spp	0.155	0.063	0.014*
	M5	0.123	13.6	fg	-0.127	0.094	0.175
				spp	0.163	0.067	0.015*
				area	-0.003	0.011	0.749
House sparrow	M5	0.315	26.4	fg	-0.290	0.067	<0.001*
				spp	0.114	0.045	0.011*
				area	-0.013	0.008	0.101
	M4	0.272	23.3	fg	-0.259	0.066	<0.001*
				spp	0.081	0.042	0.052
	M2	0.125	18.1	fg	-0.164	0.046	<0.001*

perspective, many species would belong to different foraging guilds to the focal species and would therefore probably not be competing for food. A possible explanation could be that density and species richness are both positively correlated to one or more variables that were not measured. For instance, sites providing abundant resources (*e.g.*, nesting sites or food) or comprising greater habitat diversity may be capable of sustaining more species at higher densities, which would indicate a relationship between density and species richness. Site species richness and certain site characteristics (*e.g.*, trees and shrubs) may account for some variation between sites, however they cannot explain differences between the 2 areas studied, as these variables were not significantly different between the England and New Zealand study areas.

Focal species foraging guild diversities were significantly different between the 2 study areas, and there was an apparent negative relationship between densities of common starling and house sparrow and their respective foraging guild diversities. This suggests that interspecific competition may influence densities of these species. There have been studies that have demonstrated a relationship between interspecific competition and density in some bird communities (*e.g.*, Mountainspring & Scott 1985), however other potential explanatory factors must also be investigated before conclusions can be drawn. This study did not measure, for example, predation pressure, parasites, climate, or disturbance from traffic or people, any combination of which could potentially affect bird populations. Furthermore, the relatively low percentages of variation explained by the GLMs could also be an indication of missing explanatory variables.

Classifying species according to foraging guild can be useful, however it can potentially be misleading. Generally, each species is assigned to a single foraging guild based on the dominant foraging strategy. In reality, foraging niches are usually wider (Lešo & Kropil 2007), and can vary from one season to another. For example, although European greenfinches feed predominantly on seeds, they will also eat invertebrates during the breeding season (Newton 1967). Determining which species actually compete with one another for food and to what extent can be extremely difficult and therefore the results presented here must be interpreted with caution.

Another important resource which may lead to interspecific competition is nesting sites, which was not assessed here. In a study of urban birds in the USA, Reale & Blair (2005) concluded that nesting site was a critical resource which regulated the distribution of birds in an urban environment. An assessment of nesting guild competition would, however, require knowledge of which species were nesting at each site, which was beyond the scope of this study.

A further limitation of the study was that it did not take into account the abundance of potential competitors. Comparison of species densities may highlight relationships between specific species, however since density was measured for focal species only, such comparisons were not possible.

In conclusion, the results suggested that the site characteristics measured (size and proportion habitat cover) could not explain the significant differences in common redpoll, common starling, European greenfinch and house sparrow densities between the England and New Zealand study areas. Analysis of foraging guilds provided evidence of a potential relationship between interspecific competition and common starling and house sparrow densities, however more detailed study is required, of a wider range of variables, before any conclusions can be made.

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