Diet composition and prey choice of New Zealand falcons nesting in anthropogenic and natural habitats

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Abstract: In a biodiversity conservation exercise a native raptor has been reintroduced to Marlborough, a wine-growing area in New Zealand's South Island, on the assumption that the abundant passerines attracted to the grapes will provide a natural food resource for this predator. As part of a study to assess the value of vineyards as habitat for the threatened New Zealand falcon (*Falco novaeseelandiae*) we used remote videography and prey remains to compare the diet composition of falcons nesting in a vineyard-dominated landscape with that of falcons nesting in natural habitat in nearby hills. We also quantified the abundance and species composition of avian prey in the habitats surrounding each falcon nest. Generally there were more birds in the vineyards but the composition of available prey did not differ between vineyards and the nearby hills, nor did the composition of avian species in the breeding-season diet of falcons. Avian prey was the main food source for falcons during the breeding season, representing 97.9% of prey items by frequency and 83.3% of prey items by biomass. Mammals represented only 1.9% of prey items by frequency, but made up 16.7% of prey items by biomass. We also found that falcons preyed on introduced species more than would be expected, and on endemic species less than would be expected, based on their availability in the landscape. The absence of any significant differences in diet between native and vineyard habitats during the breeding season suggests that the latter may be a suitable alternative when natural habitats are unavailable, although further study must be conducted into the role of supplementary feeding on these effects. These findings pave the way for research in other production landscapes that could be used for conservation measures.

Keywords: agriculture; *Falco novaeseelandiae*; foraging; Marlborough; predator; remote videography; vineyard

Introduction

Primary production systems occupy over 35% of the ice-free land area of the world (Foley et al. 2007) and almost 60% of New Zealand (MacLeod et al. 2008). This prevalence, along with the global decline in natural areas, means that production systems are increasingly being viewed as areas in which biodiversity conservation should be carried out, in addition to that in conservation reserves (Edwards & Abivardi 1998; MacLeod et al. 2008). Reintroduction of extirpated species is one way in which primary production systems can increase local biodiversity. However, for reintroduction projects to be successful, the targeted area for release must contain the habitat and food resources needed to support natural behaviour and survival of the reintroduced individuals (IUCN 1998; Armstrong & Seddon 2008). Additionally, the threats that caused the decline of the target species in the region in the first place must be mitigated (IUCN 1998; Fischer & Lindenmayer 2000; Armstrong & Seddon 2008).

Falcons for Grapes (FFG), a recent project run by International Wildlife Consultants (UK) in New Zealand, focused on the reintroduction of the country's only remaining endemic bird of prey, the threatened New Zealand falcon (*Falco novaeseelandiae*) (Miskelly et al. 2008), into the country's largest wine-growing region, Marlborough (MAF 2009), in the South Island. The idea hinges on the notion that reintroduced falcons will have increased access to their primary prey, passerine birds (Fox 1977; Barea et al. 1999; Seaton et al. 2008), because vineyards represent an abundant food source for passerines in the autumn and winter (MAF 2009). Indirect

evidence suggests that this may be true. Falcons in vineyards have higher nest attendance, higher brooding rates, and higher feeding rates, and have also been found to feed their chicks larger prey items and a greater total biomass of prey compared with falcons in the 'hills', a term we use to describe the non-intensively farmed pastoral and timber plantation habitat in the hills of Marlborough (Kross et al. 2012a). However, studies of raptors overseas have sometimes shown that vineyards are poor foraging habitat for some birds of prey (e.g. Swolgaard et al. 2008). It is therefore important to determine whether the vineyard environment may be changing the foraging habits of reintroduced falcons.

Previous studies on the diet of the New Zealand falcon have focused on collections of prey remains and regurgitated pellets of undigested material (Fox 1977; Seaton et al. 2008), even though these methods are known to be biased (Redpath et al. 2001; Marchesi et al. 2002; Tornberg & Reif 2007). In one exception, Barea et al. (1999) used remote videography to study the diet of two pairs of nesting New Zealand falcons in a forested area of the North Island. In studies of overseas raptors, remote videography has been shown to be more accurate than the aforementioned indirect methods (Grønnesby & Nygård 2000; Lewis et al. 2004; Reif & Tornberg 2006), and more accurate than direct observations from hides (Delaney et al. 1998; Rogers et al. 2003). Remote videography also has the additional benefits of recording behaviours associated with prey handling or juvenile development, and of obtaining recordings of potential predators at nest sites (Delaney et al. 1998; Cutler & Swann 1999; Lewis et al. 2004; McDonald et al. 2005; Kross & Nelson 2011).

While there is plenty of evidence to suggest that predators are limited by the populations of their prey, the opposite can also be true, particularly in the case of generalist predators that take a range of prey species. For example, in Scotland, high densities of hen harriers (*Circus cyaneus*; a generalist species) can reduce populations of red grouse (*Lagopus lagopus scoticus*) (Thirgood et al. 2000). Recent studies have also shown that the roles of predators and prey can sometimes be changed in systems altered by invasive species. For example, in Indonesia, an endemic species of toad preys more on invasive ants than on endemic ants, leading to a positive effect on the endemic ants, which then limit the populations of insect pests in cacao plantations (Wanger et al. 2011). Finally, the food-web literature has emphasised for some time that, although single-predator – single-prey systems are unlikely to be top-down limited, generalist predators can have their populations subsidised by various prey species, and thereby exert significant top-down impacts on rare prey, even in adjacent habitats (Polis & Strong 1996; Rand et al. 2006).

Here, we compare the breeding-season diet of falcons nesting in hills, with that of nesting falcons that have been reintroduced into the intensively managed vineyards in Marlborough's river valleys. Our study provides essential information on the effect of habitat on the breeding-season diet of New Zealand falcons. We use remote videography as well as analysis of prey remains to assess the diet composition of falcons nesting in vineyards and of falcons nesting in the hills. We also compare these diet compositions with the availability of avian prey in the surrounding landscapes to determine whether falcons are selecting for or against specific prey species or guilds such as endemic and introduced birds.

Methods

Study area and species

Our study was based in the Wairau, Waihopai and Pelorous valleys of the Marlborough region and surrounding hill habitats.

We interviewed local farmers and forestry workers in order to locate falcon nests. Six non-vineyard falcon nests ('hill nests') were found either in steep-sided valleys dominated by a mix of native and introduced grasses and dense scrub (four nests), or in hillside forestry (*Pinus radiata*) plantations (two nests; Kross & Nelson 2011) (Fig. 1). In contrast, four falcon nests ('vineyard nests') were within the valley, either in a vineyard (two nests), or within forestry plantations adjacent to a vineyard (two nests) (Fig. 1). The key differences between the two nest types were that vineyard adults were provided daily with one-day-old poultry chicks as supplementary food on an ad hoc basis (though most of these were excluded from our analyses), and that falcons nesting in vineyards had their nests raised from the ground in order to reduce the chances of predation by invasive mammals. The falcons nesting in vineyards were all relocated as chicks by the FFG project from nests in habitat similar to the hill habitat that we sampled for this study. We asked volunteers and landowners from the FFG project to inform us if anything other than day-old chicks were provided to vineyard pairs and were able to identify and remove these items from our analysis on the two occasions that we were informed of this occurrence. However, after completing the study we were informed that vineyard falcons were fed, on an ad hoc basis, additional items including mist-netted song thrush and blackbirds, roadkill birds, and some mammals. No data were recorded on these feedings, but despite these there was close overlap in dietary preferences of falcons in the two habitats. Vineyard falcons had all been reintroduced as chicks as part of the reintroduction project, using a soft-release method known as hacking (Sherrod et al. 1982). The four vineyard nests were each a unique combination of male and female falcons, but the total number of females was two, and males three. Falcons were at least one year old at the time of nesting. Falcons found nesting in forestry plantations were always near the edge between the forestry blocks and either vineyards (in the case of vineyard falcons) or natural habitat (in the case of hill falcons).

The New Zealand falcon is a sexually dimorphic species, with males reaching a mean of 330 g and females reaching 531
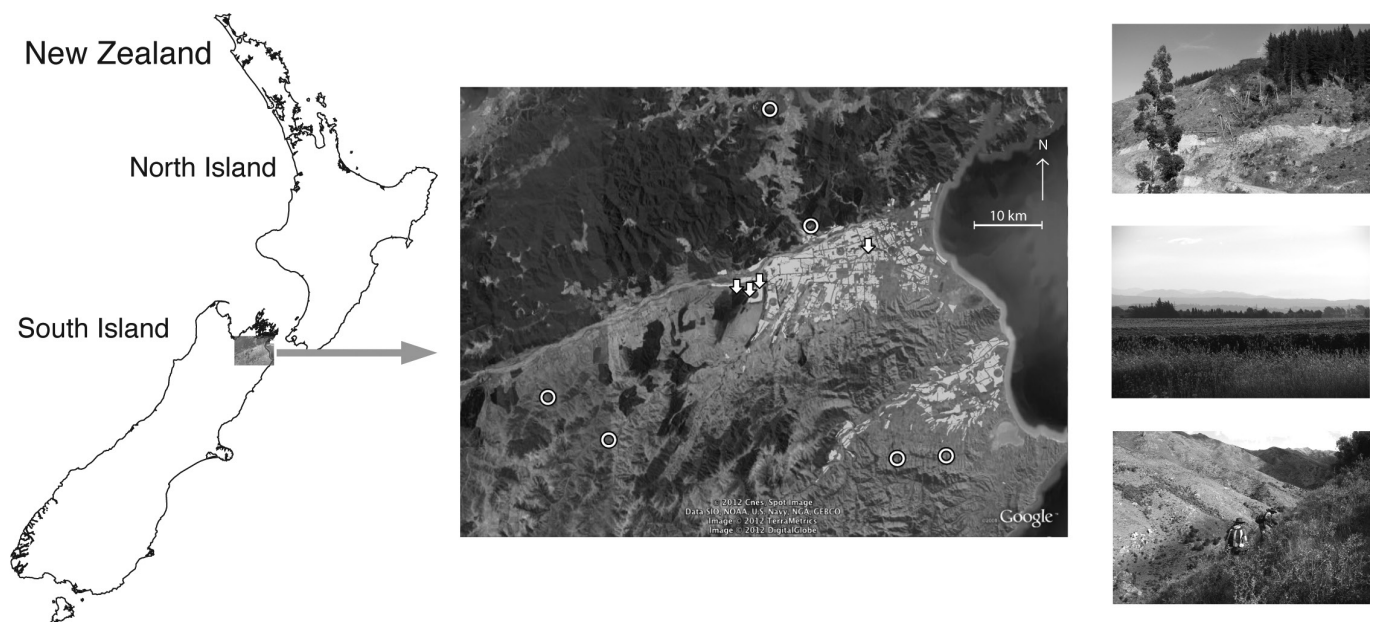
Figure 1. Map showing the locations of four vineyard falcon nests (white arrows) and six hill falcon nests (white circles) in Marlborough, New Zealand. Photos to the right of the map show, from top to bottom, typical habitat of falcon nests in plantation forestry (hill nests); typical habitat of falcon nests in vineyards; typical habitat of falcon nests in low-intensity grazing land (hill nests).

g within our study area (Fox 1977). Falcons in Marlborough have been shown to occupy territories of roughly 4 km² in which they remain resident throughout the year, and are generally found in the extensive grazing land that predominates in the subalpine region of Marlborough (Fox 1977).

Prey abundance

Five-minute bird counts (Bibby et al. 2000) were used at four locations representative of different habitat within 500 m of each falcon nest site. For example, for falcons nesting in forestry, at least one of the bird abundance counts always included the forestry habitat and the remaining counts included the nearby natural or vineyard habitat depending on the nest type. All birds that were seen or heard within 50 m of the centre of the count location were identified and counted to species level if possible, or were counted as unidentified birds. We took precautions to avoid counting the same individuals more than once in a single count: birds heard singing from the same location, seen after hearing the song of the same species from a similar area, or seen flying to multiple locations during the five-minute count were only counted once. Count locations were at least 150 m apart and were between 200 m and 500 m away from the nest. All four point-counts were made on at least three separate visits to each nest site, with data pooled across the representative habitats for each date that counts were conducted. Counts always took place within 3 h of sunrise and were not conducted in high winds, heavy rain, or extremely warm weather. Counts were also abandoned if the nesting falcons displayed any visible or audible nest-defence or hunting behaviour. Birds were categorised as either introduced, native, endemic, or unknown. Endemic species are those that are found naturally within New Zealand and breed only within New Zealand. Native species are found naturally within New Zealand, but also breed in other areas of the world. Introduced species are those that did not occur within New Zealand prior to human arrival and that were aided in their colonisation by human activities. We assume that endemic and introduced species are equally detectable in prey remains and bird counts.

New Zealand pipits (*Anthus novaeseelandiae*) were never observed in our prey abundance counts. New Zealand pipits display different behaviours, but are physically very similar to the introduced skylark (*Alauda arvensis*), so while we could be confident that pipits were not included in our prey abundance counts, they may have been included in the diets of falcons. As has been the case in previous studies (Fox 1977; Barea et al. 1999; Seaton et al. 2008), we have pooled the data between these two species and therefore assumed that any prey remains characteristic of the two species actually did belong to skylarks, which were common in both of our study habitats. We also pooled together the introduced cirl bunting (*Emberiza cirlus*) with the yellowhammer (*E. citrinella*) because of the close relatedness of these two species and because deciphering between the two species in prey remains is difficult.

Prey remains

Prey remains were collected opportunistically from nine of the 10 nests included in this study; the 10th nest was preyed on by a feral cat prior to our collecting prey remains and samples could not be taken. Remains were collected from within the nest scrape and the surrounding 50 m. Prey remains included any feathers, fur, beaks, feet, or bones that had not been consumed by falcons. Any of these items found within 50 m of a falcon nest were considered to have been falcon prey. When samples were collected from nests, all visible feathers and prey remains were removed, so that samples collected on different dates represented new prey items (Fox 1977). Samples were frozen, and then sorted by date and identified through comparison with reference collections at the University of Canterbury and at the Canterbury and Te Papa museums. Diagnostic features were used to determine the minimum number of individuals that could be present in each sample.

Remote videography

We used a portable remote videography system with a near-infrared camera placed at the edge of the nest or mounted to the side of nest barrels in the case of vineyard nests. The system uses motion-detection and was set to record at 30 frames per second (Kross & Nelson 2011). This recording system has been shown to lose only 16% of potential recording hours, primarily due to battery failure or camera dislodgement (Kross & Nelson 2011). We recorded for 101 days (1473 recording hours) at the six hill nests and for 88 days (1333 recording hours) at the four vineyard nests.

Video was reviewed using Quick-Time Player (version 7.6.4; Apple Inc., Cupertino, CA, USA) at a maximum speed of four times normal speed to a minimum speed of frame by frame, allowing quick review of non-important files and detailed review of important events. All feeding events were examined frame by frame to identify prey items to the most specific taxonomic level possible. Prey that could not be identified to species level were identified to family or order.

Statistical analyses

For each species identified, we counted the number of prey items as either the number observed in the video or the number counted from the prey remains, whichever was higher. This prevented any overestimation of prey by avoiding double-counting of individual prey items that were detected by both the video and prey remains. We compared the abundance of each prey species between vineyard and hill nests (with all nests pooled for each habitat type) using paired and unpaired *t*-tests and Wilcoxon rank sum tests. We used chi-square tests of independence to compare the selection of the different categories of avian prey between falcons in the two habitats, as well as to compare abundance of different prey types in the diet of falcons with the abundance of those prey types in the surrounding habitats. Prey biomass was taken as the mean adult biomass for each species given in Heather & Robertson (2000), except for 'duck species' and 'unidentified galliform', which were observed in falcon diet only as juvenile individuals and for which biomass was estimated by comparing individuals on film with previously positively identified prey items.

We used a generalised linear mixed model (GLMM) in the lme4 package (Bates et al. 2008) in R (v 2.7.2; R Development Core Team 2008) to determine whether falcons chose prey items based on prey availability or prey biomass. GLMMs allow for the inclusion of random effects, which are typically grouping factors within an experimental design, and therefore can account for the non-independence of replicates within groups (Bolker et al. 2009). We modelled the relative proportion of each species in the diet of falcons (each prey species in each nest being a replicate) with the relative proportion of each species in the surrounding habitat, the endemism of each species, the habitat type of the nest (vineyard or hill), and the average biomass of each species (Table 1) as predictors. The data for the relative proportion of each species in the falcon diet were transformed using an arcsin-square-root transformation and

Table 1. Prey species delivered to chicks at the nests of four pairs of New Zealand falcons breeding in vineyards and the nests of six pairs of falcons nesting in the hills, collected using a combination of video analysis of prey deliveries and prey remains.

Prey species	Mass* (g)	N	% frequency in diet	Percent total biomass
Birds				
Endemic				
Grey warbler (*Gerygone igata*)	6.5	13	0.62	0.13
Fantail (*Rhipidura fuliginosa*)	8	6	0.29	0.07
Bellbird (*Anthornis melanura*)	30	4	0.19	0.18
Brown creeper (*Mohoua novaeseelandiae*)	13.5	3	0.14	0.06
Long-tailed cuckoo (*Eudynamys taitensis*)	125	1	0.05	0.19
Tūī (*Prosthemadera novaeseelandiae*)	105	1	0.05	0.16
Banded dotterel (*Charadrius bicinctus*)	160	1	0.05	0.24
Tomtit (*Petroica macrocephala*)	11	1	0.05	0.02
Weka (*Gallirallus australis*)	850	1	0.05	1.23
Rifleman (*Acanthisitta chloris*)	7	1	0.05	0.01
Native				
Silvereye (*Zosterops lateralis*)	13	72	3.43	1.39
Introduced				
Greenfinch (*Carduelis chloris*)	28	141	6.71	5.85
Chaffinch (*Fringilla coelebs*)	22	107	5.09	3.49
Goldfinch (*Carduelis carduelis*)	16	88	4.19	2.08
Blackbird (*Turdus merula*)	90	46	2.19	6.13
Yellowhammer (*Emberiza citrinella*)	27	38	1.81	1.52
Song thrush (*Turdus philomelos*)	70	23	1.09	2.38
Skylark (*Alauda arvensis*)	38	23	1.09	1.29
House sparrow (*Passer domesticus*)	30	22	1.05	0.98
California quail (*Callipepla californica*)	180	24	1.14	6.40
Starling (*Sturnus vulgaris*)	85	20	0.95	2.52
Dunnock (*Prunella modularis*)	21	12	0.57	0.37
Redpoll (*Carduelis flammea*)	12	10	0.48	0.18
Feral pigeon (*Columba livia*)	400	1	0.05	0.59
Pheasant (*Phasianus colchicus*)	1300	2	0.10	3.85
Little owl (*Athene noctua*)	180	2	0.10	0.53
Duck species	40	1	0.05	0.06
Unidentified finch	20	156	7.43	4.62
Unidentified galliform	27.5	11	0.52	0.45
Unidentified passerine	20	1225	58.31	36.3
Total endemic birds			1.52	
Total native birds			3.43	
Total introduced birds			26.65	
Total birds		**2056**	**97.86**	**83.28**
Mammals				
European hare (*Lepus europaeus*)	1781	2	0.14	7.71
Stoat (*Mustela erminea*)	270	2	0.10	0.80
Rabbit (*Oryctolagus cuniculus*)	607	11	0.52	9.89
House mouse (*Mus musculus*)	17	14	0.67	0.35
Rat species	25	10	0.48	0.37
Total mammals		**39**	**1.90**	**16.68**
Insects				
Huhu beetle	2	1	0.05	0.003
Giant dragonfly	2	1	0.05	0.003
Total insects		**2**	**0.10**	**0.006**
Reptiles				
Skink species	5	2	0.10	0.02
Woodworthia spp.	12	1	0.05	0.02
Total reptiles		**3**	**0.14**	**0.04**

*Bird mass is the mean adult weight of each species in Heather & Robertson (2000). The mass for 'duck species' and 'unidentified galliform' is the mean estimated mass of juvenile individuals that were delivered to falcon nests as part of this study. These were estimated based on comparison with positively identified prey items of a similar size. Mass for mammals was taken as the mean weights of actual prey items taken by New Zealand falcons in our study area as recorded by Fox (1977). Gecko mass was taken from the Landcare Research New Zealand lizards database (http://nzlizards.landcareresearch.co.nz). Skink mass was estimated based on size on camera.

were modelled using Gaussian errors. Interaction terms were included between all fixed effects in the maximal model. We also included second- and third-order polynomial terms for the biomass of each species in order to account for any potential non-linear response of falcons to prey biomass (e.g. preference of prey over a threshold size). Nest site and prey species were included as crossed random effects to respectively account for the non-independence of prey items in a given nest and test for the effects of availability and biomass on attack rates of each separate species (rather than all species pooled together, in which case the effects of biomass and abundance could be confounded with other species traits).

We simplified models by first removing non-significant interaction terms, then polynomial terms, and then main effects until no further reduction in residual deviance (measured using Akaike's Information Criterion, AIC) was obtained. By adding a penalty for overparameterisation, AIC makes a trade-off between model fit and complexity, and is often used during stepwise model simplification to assess the validity of removing non-significant parameters from each nested model (Crawley 2007). We used a Markov chain Monte Carlo (MCMC) resampling method with 10 000 simulations to estimate P values and high posterior density (HPD) intervals for the fixed effects (carried out using the 'pvals.fnc' function in the LanguageR package (Baayen 2008) in R). We then compared the model estimates for relative proportion of each species in the diet of falcons with the actual observed relative proportions to determine whether falcons were taking individual species more or less than would be expected. Only individuals positively identified to species level were included in our analysis of falcon prey choice, with all unidentified birds excluded. All values are presented as the mean ± 1 standard error (SEM).

Results

Prey abundance

There was a non-significant tendency for vineyards to have more birds counted in total during five-minute bird counts compared with hill habitat ($t_{6.38} = 1.62$, $P = 0.15$). In vineyards, a mean of 76.0 ± 9.7 birds were counted per visit, whereas in the hills a mean of 56.0 ± 7.6 birds were counted. Vineyards had a higher abundance of introduced birds than did hill habitat (vineyards,

61.1 ± 8.3; hills, 36.3 ± 4.0; $t_{4.4} = 2.70$, $P = 0.049$), while hills had a higher abundance of native birds than did vineyards ($t_8 = 2.26$, $P = 0.051$; Fig. 2). There was no significant difference in the number of endemic birds ($t_8 = 1.16$, $P = 0.28$), or in the number of unidentified birds (W = 5, $P = 0.16$; Fig. 2).

### Prey identification and characteristics

Falcons primarily fed their chicks avian prey, which by number comprised 97.9% of prey and by biomass 83.3% of prey (Table 1). A total of 2056 individual avian prey items were identified using a combination of video ($n = 1990$) and prey remains ($n = 205$). Of the prey remains found in nests, 66 represented prey that were not identified using video. We counted an average of 205.6 ± 23.21 avian prey items at each nest using these two techniques together. On average, prey remains alone accounted for $3.8 \pm 1.4\%$ of the prey items included in our analysis, which only included unique individual prey items based on either video or prey remains.

Overall, 955 avian prey items were identified to the species level, including 291 supplementary food items (mostly day-old chickens) that were excluded from any further analyses. An additional 156 prey items were identified as unknown finches, 11 were identified as unknown Galliformes, and 1225 were identified as unknown Passeriformes.

Thirty-eight mammalian prey items were recorded using video, with one additional mammalian prey item identified using prey remains (Table 1). Of these, 30 were recorded at nests in the hills and 9 were recorded at nests in the vineyards. Mammals represented $2.4 \pm 0.8\%$ of the prey items delivered to hill nests and $0.9 \pm 0.5\%$ of the prey items delivered to vineyard nests, although this difference was not statistically significant ($t_{7.6} = 1.72$, $P = 0.12$). In both habitats combined, mammals represented only 1.9% of prey items delivered to nests by frequency, but made up 16.7% of prey items by biomass (Table 1). Two insect prey items were identified using prey remains, with one of those also identified on video. Three reptiles were identified on video but were not identified using prey remains, with two of these recorded at vineyard nests.

Prey selection

There was no difference between the proportion of introduced birds found in the diet of falcons nesting in hills and vineyards, when compared with the abundance of introduced birds in
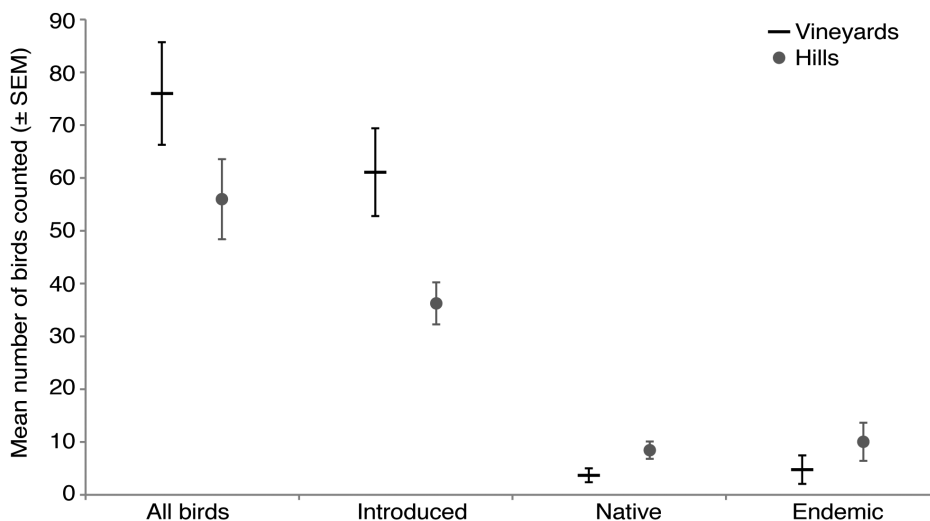
Figure 2. Mean (±SEM) abundance of birds counted and of the avian prey of the New Zealand falcon grouped according to endemism in representative habitats near nests in vineyard and hill habitats in Marlborough. The density of introduced birds ($t = 2.70$, $P = 0.049$) and native birds ($t = 2.26$, $P = 0.051$) differed significantly between the two habitats.

the respective surrounding habitats ($\chi^2 = 1.31$, $P = 0.25$). There was also no difference between the proportion of native ($\chi^2 = 1.01$, $P = 0.31$) or endemic ($\chi^2 = 0.01$, $P = 0.93$) birds found in the diet of falcons in either nest type, when compared with the abundance of those birds in the surrounding habitats. Similarly, nest site location (vineyard or hill) was removed from our generalised linear mixed model for proportion of prey species in the diet of falcons because AIC indicated a significant improvement in model fit after this term was removed. For this reason, we pooled data from both nest types when analysing prey selection.

In general, falcons in both habitats selected introduced birds more than would be expected from their abundance in the surrounding habitat (Fig. 3). Falcons selected introduced species more than they selected native species ($\chi^2 = 5.85$, $P = 0.02$) and more than they selected endemic species ($\chi^2 = 54.02$, $P < 0.0001$; Fig. 3). Falcons also selected the native species (silvereye *Zosterops lateralis*) over endemic species ($\chi^2 = 19.60$, $P < 0.0001$; Fig. 3).

The results of our generalised linear mixed model, which treated each species as a separate replicate, supported the results of the chi-square tests of independence. The best-fit model included only the main-effect terms for endemism, prey abundance, and prey biomass. The model predicted that, holding all other variables constant, the proportion of falcon diet consisting of endemic species did not differ significantly from zero (intercept $t = 1.41$, $P_{MCMC} = 0.12$), and that the proportion of falcon diet consisting of introduced species was significantly greater then endemic species ($t = 4.50$, $P_{MCMC} = 0.0001$). There was no significant difference between the proportion of falcon diet consisting of native vs endemic species ($t = 1.02$, $P_{MCMC} = 0.27$). The relative abundance of each species in the surrounding habitat had a very strong influence on the proportion of each species in the falcons' diet during the breeding season ($t = 11.89$, $P_{MCMC} = 0.0001$).

We found that some species were selected more than would be expected from our model estimates, and some were selected less (Fig. 3). All endemic species occurred below the fitted relationship between the proportion of each species in the diet of falcons and the relative abundance of those species in the surrounding habitat. Grey warbler (*Gerygone igata*) made up 3.7% of birds observed in abundance counts (expected proportion) but 2.0% of birds identified to species in diet of falcons (actual proportion). Similarly, fantail (*Rhipidura fuliginosa*) (expected; 4.7%, actual; 0.9%), bellbird (*Anthornis melanura*) (expected; 1.4%, actual; 0.6%) and tūī (*Prosthemadera novaeseelandiae*) (expected; 1.3%, actual; 0.2%) were all taken in falcon diet less often than expected based on their abundance. Redpoll (*Carduelis flammea*) (expected; 4.0%, actual; 1.5%) and goldfinch (*C. carduelis*) (expected; 16.0%, actual; 13.2%) also occurred in lower proportions in the falcons' diet than would be expected from their abundance. Greenfinch (*Carduelis chloris*) (expected; 11.6%, actual; 21.2%), blackbird (*Turdus merula*) (expected; 5.7%, actual; 6.9%), song thrush (*T. philomelos*) (expected; 2.0%, actual; 3.5%), starling (*Sturnus vulgaris*) (expected; 1.6%, actual; 3.0%), and house sparrow (*Passer domesticus*) (expected; 0.6%, actual; 3.3%) all occurred in higher proportions in the diet of falcons than would be expected based on their abundance.

Discussion

Although an increasingly common conservation method, reintroduction projects are financially costly and often do not achieve their goals or do not report on their outcomes
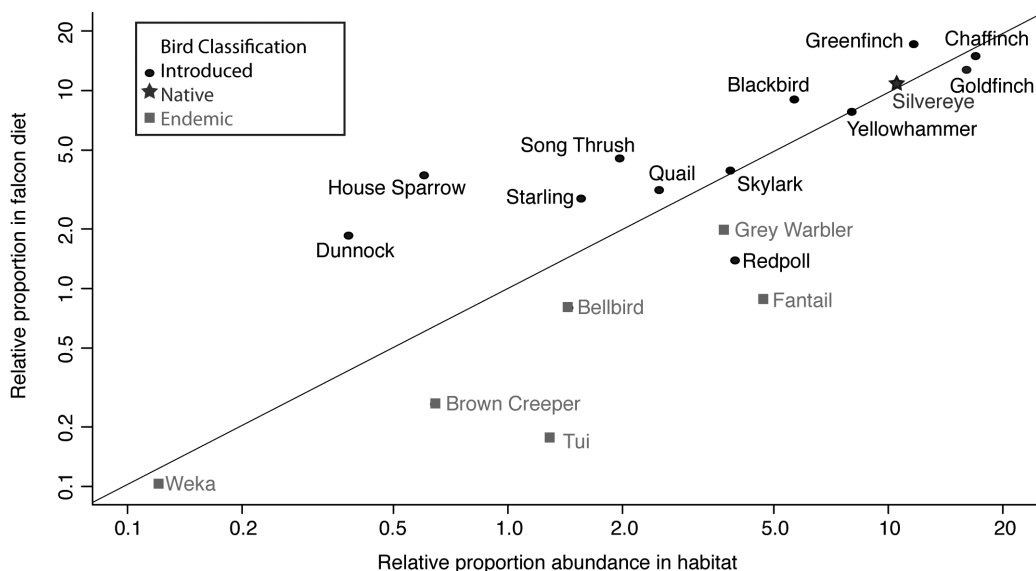
Figure 3. Prey selection of New Zealand falcons expressed as a relationship between the proportional relative abundance of each species in the diet of nesting falcons and that of each species in the surrounding habitat. The diagonal line represents the fitted slope of the relationship from a generalised linear mixed model, holding bird classification (i.e. endemism) and biomass constant ($y = 0 + 0.99*$ relative abundance of species in habitat). Only identified avian species were considered for this analysis. Species have been classified according to endemism to New Zealand. Species not shown were either found at 0% abundance in the habitat (introduced species: feral pigeon, pheasant, little owl, duck species; endemic species: long-tailed cuckoo, banded dotterel, tomtit, rifleman; See Table 1 for scientific names), or were found at 0% abundance in the diet (native species: welcome swallow *Hirundo neoxena*; endemic species: kingfisher *Todiramphus sanctus*, kererū *Hemiphaga novaeseelandiae*). Note that the data have been plotted against a non-linear (log) axis for ease of comparing species at both high and low abundances.

(Fischer & Lindenmayer 2000). For reintroduction projects to be successful, reintroduced individuals must be capable of displaying natural behaviours, and the target release sites must provide them with the food and shelter resources needed for survival (Fischer & Lindenmayer 2000; Armstrong & Seddon 2008). Higher prey abundance leads to higher breeding success and lower adult mortality rates (Daan et al. 1996), and is important for raptors residing in agricultural landscapes (Rodríguez et al. 2006). Feeding rates and prey availability, through their effect on nestling development, even have impacts on long-term behavioural characteristics such as foraging (Arnold et al. 2007). Here, we found no statistically significant difference between the abundance of prey in the two different habitats, and found that falcon diet in the two habitats was similar.

Falcons appear to select for introduced species and to select against endemic species. Similarly, falcon presence in vineyards has been shown to reduce the abundance of introduced pest birds, but not the abundance of native pest birds (Kross et al. 2012a). Our findings are congruent with those of Seaton et al. (2008), who found that many of the endemic species in their study area, a *Pinus radiata* plantation in the North Island, were selected against by foraging falcons, while an early observational study by Fitzgerald (1965) in the South Island also showed that, while endemic species were found in the nearby habitat, falcons were primarily feeding their juveniles with introduced species. Importantly, these findings suggest that, despite being an apex predator, the presence of falcons does not necessarily deplete the endemic avifauna of an area, particularly of species such as the tūī, that are being encouraged to recolonise Marlborough. However, it is important to note that our study had a relatively small sample size, and that only one species of native bird was recorded in the diet of falcons. Our results could therefore be influenced by the individual hunting preferences of the falcons that were sampled.

Many previous studies have assumed that predators such as falcons are opportunistic, and will choose prey based on their availability in an area (Fox 1977; Barea et al. 1999; Seaton et al. 2008). Clearly, falcons do take more abundant prey at greater frequencies, but our results also suggest that falcons are choosing, or are more effective at capturing, introduced avian prey over prey alongside which they evolved. This choice is most apparent for prey species that are of intermediate abundance.

Some of the similarity in the composition and abundance of bird populations in the two habitats may be explained by the use of forestry as nesting habitat by falcons in both the vineyards and the hills. However, our study area is characterised by arid hills used primarily for stock grazing or plantation forestry and river valleys used for intensive viticulture, all of which are dominated by introduced bird species, and this trend is more likely to explain the overlap in prey availability and falcon diet in both habitats. Therefore, we do not know what falcon diet preferences would be if introduced birds were not the dominant species in an ecosystem, such as in native forest, where endemic species would be relatively much more abundant. However, in a North Island study of two pairs of falcons nesting in native forest, endemic species were found to contribute a quarter of the birds fed to chicks, with introduced species making up half the avian prey (Barea et al. 1999). It is also important to note that falcons are capable of flying very long distances and, although unlikely, we cannot rule out the possibility that falcons nesting in the hills travel to the vineyards to hunt or vice versa.

We were able to remove all day-old chickens from our analysis of falcon diet preferences, but our results should be considered in light of the fact that wild birds were provided on an ad hoc basis to some falcons. Information from workers in the programme during the three years of data collection suggests that the frequency of this additional supplementary feeding was very low. Nevertheless, we prefer to be conservative in our conclusions and stress that some of the food items recorded here could have been provided by humans.

Previous studies have detected mammals at lower frequencies than we observed in falcon diets, but have still estimated that mammals make up a much larger proportion of the biomass fed to chicks (Fox 1977; Seaton et al. 2008). We found that mammals contributed a small proportion of the diet by both frequency and biomass when compared with previous studies of New Zealand falcon diet.

As has been shown in studies from other parts of the world (e.g. Mersmann et al. 1992; Grønnesby & Nygård 2000; Lewis et al. 2004; Margalida et al. 2005), video was a superior method for the detection of prey items and for the identification of prey delivered to the nest, although analysis of prey remains can be less costly and more time efficient than the use of video and therefore can allow for larger sample sizes. Our results suggest that the use of indirect methods is useful for the identification of prey species in the diet of falcons, but that these methods should not be used to calculate the total number of prey taken. For example, a previous study in Marlborough used only indirect methods to determine the diet of breeding New Zealand falcons and estimated that pairs caught a mean of 45.4 prey items per nest and recorded a maximum of 91 prey items at one nest (Fox 1977). Here, despite a much smaller sample size, we found evidence of a mean of 205.6 avian prey items per nest and a maximum of 331 prey items at one nest. Including both prey remains and remote videography for assessing the diet of New Zealand falcons provided us with estimates that were both robust and accurate.

We have shown previously that falcons nesting in vineyards have higher nest attendance rates and feed their chicks more food than falcons nesting in the hills (Kross et al. 2012b). Even with the recorded supplementary food (day-old chickens) removed from the data, falcons in vineyards still fed their chicks as often and with larger prey than falcons nesting in the hills (Kross et al. 2012b), and here we have shown that falcons in both habitats have similar prey availability and similar prey preferences. However, given the potentially confounding effects of the supplementary food provisioning, we strongly suggest that future falcon conservation work experimentally test the role of supplementary food in breeding behaviour and prey choice. We have also found previously that falcons living in vineyards provide ecosystem services in the form of reduced pest bird abundance and associated damage to grape crops, with associated economic benefits for viticulture (Kross et al. 2012a). Here, we have shown that, at least during the breeding season, the diet/prey-choice of falcons living in vineyards does not differ significantly from that of their counterparts nesting in non-intensively-farmed habitat in the hills of Marlborough. This lends support to the notion that reintroducing falcons into vineyards has a conservation benefit for the species, and indicates that production landscapes such as vineyards could act as suitable alternative habitat for some threatened species.

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