New Zealand falcon prey selection may not be driven by preference based on prey nutritional content

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Abstract: Little is known about how diurnal raptors, as apex predators, select their prey. It has been hypothesised that they are opportunistic, taking prey according to availability, and that they select prey based on prey size. The threatened New Zealand falcon or kārearea (*Falco novaeseelandiae*) is New Zealand's only remaining endemic bird of prey. A previous study on prey caught by kārearea during the breeding season suggested that introduced avian prey were taken more often than expected, and endemic avian prey taken less often than expected, based on their abundance. There is a growing interest in the role that nutrients play in prey selection by predators. We used the nutritional geometry framework in a field study to determine the role that nutritional composition plays in prey choice. We built on an existing dataset to assess whether prey selection by kārearea can be explained based on prey body-mass, abundance, or nutritional characteristics. We determined the protein-to-lipid ratio and ash content of individuals across 16 species of prey and potential prey, including both endemic and introduced species, and modelled these against known prey consumption based on our earlier work. We found limited evidence for selective predation based on nutrient balancing. Instead, the relative abundance of each species in the surrounding habitat and the endemicity of each species were the most important predictors, with species body-mass playing only a minor role in prey choice. To investigate the apparent selection for introduced over endemic prey, future research could compare the behavioural adaptations of endemic birds against their natural predator with behaviours of introduced birds.

Keywords: diet; *Falco novaeseelandiae*; foraging behaviour; nutritional geometry; prey choice

Introduction

Animals often do not forage solely in an opportunistic manner, but may take into account prey preference, likelihood of risk, or nutritional composition of the food source (Krause & Godin 1996; Nelson & Jackson 2006; Behmer 2009). Diurnal raptors are well-known apex predators, but little is known about how they select prey. Many previous studies have assumed that raptors are largely opportunistic predators, and choose prey based on their abundance in the environment (Fox 1977; Barea et al. 1999; Salamolard et al. 2000; Gliwicz 2008; Seaton et al. 2008), but some studies have indicated that raptors select prey based on total available prey biomass (Bozinovic & Medel 1988), or on individual prey body size (Steenhof & Kochert 1988).

Birds of prey that have more abundant food sources early in the breeding season have greater breeding output because they lay larger clutches (Newton & Marquiss 1981) and produce more fledglings (Wiehn & Korpomäki 1997; Palmer et al. 2001). *Falco novaeseelandiae*, the New Zealand falcon or kārearea, is New Zealand's only remaining endemic bird of prey and consists of two subspecies (*F. n. novaeseelandiae* and *F. n. ferox*; Trewick & Olley 2016) both of which are classified as 'At Risk-Recovering' by the New Zealand Department of Conservation (Robertson et al. 2017). The interaction between kārearea and potential prey is of considerable relevance to management of this species because of its potential effect on population increase.

Conservation-related research, especially on island ecosystems that have been invaded by introduced species (Courchamp et al. 2003), typically examines predation on native species by introduced species. In a New Zealand context, a well-supported idea is that native species (often birds, but also reptiles) have not coevolved with (typically) mammalian predators and are prone to falling prey to introduced predators because of a lack of evolved defences (Diamond & Veitch 1981; Towns et al. 2001; Wilson 2004; Massaro et al. 2012; Stanbury & Briskie 2015). Prior to human arrival c. 1280 AD, New Zealand did not have significant mammalian predators, so this niche was filled by avian predators – one of these being the kārearea. This study is a follow-up to a previous field study conducted over the summer reproductive season of the 'eastern' falcon (*F. n. novaeseelandiae*). In the previous study, we found that kārearea, in both intensive agriculture (vineyards in the Marlborough region of the South Island of New Zealand) and nearby hill-grazing landscapes (Marlborough's high country), appear to select introduced (but not endemic) bird species as prey more often than would be expected given the relative abundance of prey in the surrounding habitats (Kross et al. 2013). Those results showed that while kārearea took larger and more abundant prey at greater frequencies, they also chose, or were more effective at capturing, introduced avian prey relative to the endemic prey alongside which they evolved. This interesting 'flip-side' to the more famous examples of introduced species being predators of native species might suggest that introduced bird species are less able to avoid attack

(perhaps by being behaviourally less nimble) than species that coevolved with kārearea, yet before exploring this theory it is important to first examine other important factors involved in prey selection.

For optimal foraging, predators are expected to maximise the size of the prey that can be taken with minimal searching time, handling time (chasing and subduing prey), and risk to themselves (MacArthur & Pianka 1966; Charnov 1976). Consequently, all other things being equal (e.g. equally visible to the predator), larger animals requiring higher energy expenditure will choose larger prey. Allometric relationships between predator and prey may explain predator behaviour, assuming the metabolic rate of the predator is known. This approach has been used on birds of prey by Bozinovic and Medel (1988), based on the metabolic equation for birds given by Nagy (1987). In an analysis of eight species (including raptors and owls), Bozinovic and Medel (1988) found a positive relationship between predator size and consumed prey body mass in several (but not all) species.

There is a growing interest in the role that nutrients play in prey selection by predators (Mayntz et al. 2005; Kohl et al. 2015), catalysed by the development of the nutritional geometry framework (Raubenheimer & Simpson 1997; Raubenheimer 2011). This framework considers how mixtures of nutrients might affect food choice and consumption. Studies using this approach have shown that many species of herbivores and omnivores, both in the lab and the field, choose foods and regulate the amounts eaten based on macronutrient (protein, lipid and carbohydrate) balance rather than energy content *per se* (Simpson & Raubenheimer 2012). Recent evidence suggests that some predators, including insects, spiders, fish, mink and bears, likewise select prey (or selectively eat certain body parts of prey) based on a requirement for a specific balance of macronutrients (reviewed in Kohl et al. 2015). However, few studies have applied this framework to examine prey choice of predators in the field (Machovsky-Capuska et al. 2016). This is an important omission, because understanding the factors that govern prey choice may play a role in conservation management. For example, Coogan and Raubenheimer (2016) used the nutritional geometry framework to develop models suggesting that a shortage of food high in lipid or carbohydrate content for North American grizzly bears (*Ursus arctos*) may lead to human-wildlife conflict during nutrient-limited seasons.

Here we report a study in which we applied the nutritional geometry framework to examine whether prey nutritional composition played a role in food selection by kārearea, or whether prey abundance or body mass were the primary drivers.

Materials and methods

We used previously published field data (Kross et al. 2013) as the basis for our nutrient composition analysis. Briefly, nestling diet at ten kārearea nests was assessed using a combination of video and prey remains over the course of three breeding seasons from 2008–2010. The analysis of both prey remains and remote videography is a robust way to avoid biases inherent in each system and accurately assess prey taken (Kross et al. 2013). At each nest site, modified 5-minute bird counts (Bibby et al. 2000; Hartley 2012) were used to measure the abundance of prey species at four locations in representative habitats within 500 m of the nest. Counts were truncated to a 50-m radius around the observer to partly control for differences in detectability and conspicuousness among species. While

5-minute bird counts pose concerns for comparisons between habitats and years (Hartley 2012), our counts were all conducted in similarly open habitat types (e.g. vineyards, low-intensity grazing land, planted/felled forestry blocks), and our analyses directly compared prey availability with prey consumption in each nest site, therefore, controlling for potential differences between years. These prey availability data were used to quantify the available prey species for kārearea in the habitats around each nest. By frequency, 97.9% of prey delivered to kārearea nests was avian (Kross et al. 2013), and 664 wild birds were positively identified to species level using the combination of videos placed at nests (Kross & Nelson 2011) and prey remains found at and near nests (Kross et al. 2013). We assumed that all species were equally detectable in both prey remains and bird counts (Kross et al. 2013).

For the nutritional composition analysis, we used 16 bird species that represented over 89% of the positively identified avian prey items in our field study, including five endemic species. We obtained frozen samples of birds from collections stored by the Department of Conservation or the University of Canterbury. The likely cause of death of each bird was noted at the time of initial carcass collection. Most specimens had been collected after being struck by cars, flying into windows, or being killed by domestic cats. To avoid sampling birds that had died for reasons that might seriously affect nutrient composition, carcasses with signs of disease, malnutrition and/or decomposition were not used.

Up to four individuals of each species were chosen for analysis (Table 1). The flight and body feathers of each individual were plucked and the beaks and feet were removed from the weka (*Gallirallus australis australis*), quail (*Callipepla californica*) and kererū (*Hemiphaga novaeseelandiae*), since kārearea normally remove the feathers of their prey species and do not consume the feet or beaks from large species (Fox 1977). We chose to remove the feet from all birds over 100 g because while the feet of starlings and blackbirds have been observed being consumed by kārearea on video, the feet of quail were found in uneaten prey remains in the study area (SMK, pers. obs.). The contents of the prey birds' digestive tracts were also removed because video analysis and analysis of uneaten remains at kārearea nests revealed that adults often remove these from avian prey (SMK, pers. obs.).

Samples were chopped into c. 1 cm cubes, frozen at -80°C for a minimum of 48 h, and then freeze dried to c. 4% moisture levels. Samples were then ground using a ball-mill for 2 minutes (Retsch MM2000, Hahn, Germany), stored in sealed containers and frozen again. Immediately prior to analysis, samples were re-dried overnight in a convection oven (Contherm Scientific Ltd, Wellington, New Zealand) at 60°C and re-ground in a coffee grinder. Total nitrogen was measured by Kjeldahl analysis (AOAC 981.10, AOAC 1990) using a Tecator Digestion System and a Kjeltec 8100 Distillation Unit (FOSS, Hillerød, Denmark). Crude protein was estimated by multiplying nitrogen by a factor of 6.25. Total lipid (ether extract) was measured using the Mojonnier method (AOAC 954.02). Moisture was measured by drying the sample in a convection oven at 125°C (AOAC 950.46) and combining this moisture loss with initial loss from the overnight drying. Ash was measured by ignition in a furnace at 550°C (AOAC 920.153).

We created separate linear mixed-effects models of the relative proportion of each prey species in kārearea diet at ten nests, for each of two response variables: the relative importance (i.e. percentage) of a prey item in the diet (1)

Table 1. Characteristics of species used for nutritional composition analysis.

Species	Common name	Endemism	Primary foraging guild	N	Body mass (live weight, g)	% Ash	% Protein	% Lipid	Protein: lipid	Lipid (g)/ individual
Gallirallus australis australis	Weka	Endemic	Omnivore	2	850	8.80	56.90	33.84	1.68	287.64
Anthornis melanura	Bellbird	Endemic	Nectarivore	3	30	11.78	63.38	22.94	2.76	6.88
Hemiphaga novaeseelandiae	Kererū	Endemic	Frugivore	4	650	14.62	66.55	15.76	4.22	102.42
Petroica macrocephala	Tomtit	Endemic	Insectivore	1	11	14.63	69.99	13.25	5.28	1.46
Prosthemadera novaeseelandiae	Tūī	Endemic	Nectarivore	3	105	14.97	76.19	8.16	9.34	8.56
Callipepla californica	California quail	Introduced	Granivore	3	180	13.29	74.43	10.50	7.09	18.90
Emberiza citrinella	Yellowhammer	Introduced	Granivore	4	27	13.36	67.21	16.06	4.19	4.34
Sturnus vulgaris	Common starling	Introduced	Omnivore	4	85	13.47	66.42	16.30	4.07	13.86
Passer domesticus	House sparrow	Introduced	Granivore	4	30	13.96	65.37	16.69	3.92	5.01
Turdus philomelos	Song thrush	Introduced	Omnivore	4	70	13.96	72.39	10.77	6.72	7.54
Carduelis flammea	Common redpoll	Introduced	Granivore	4	12	14.21	68.40	12.67	5.40	1.52
Turdus merula	Eurasian blackbird	Introduced	Omnivore	4	90	14.59	68.70	13.74	5.00	12.37
Fringilla coelebs	Chaffinch	Introduced	Granivore	4	22	14.81	68.70	13.05	5.27	2.87
Carduelis chloris	European greenfinch	Introduced	Granivore	4	28	14.87	66.08	15.02	4.40	4.21
Carduelis carduelis	European goldfinch	Introduced	Granivore	4	16	14.91	64.47	16.27	3.96	2.60
Zosterops lateralis	Silvereye	Native	Omnivore	4	13	12.59	68.32	15.60	4.38	2.03

by number and (2) by biomass (each prey species at each nest being a replicate). Predictor variables were the relative abundance of each prey species in the environment surrounding a nest, the endemicity of each species (a categorical variable including endemic, native, and introduced species), and the individual body mass of each prey species (as in Kross et al. 2013). Our candidate model set included all combinations of these three predictors and a nutritional variable, which was either the protein to lipid ratio of each prey species or the result of a principal components analysis compiling all three macronutrients for each prey species. We included two random effects: nest site to group non-independent prey per nest site; and prey species to account for multiple measurements of each species' abundance and nutritional components. We only included the 16 avian prey species for which we had nutritional information, therefore the total proportion of species at each nest did not sum to one (range 0.80–0.96). We used the lme4 package (Bates et al. 2015) in R v 3.3.1 (R Development Core Team 2016), which calculates Satterthwaite approximations to degrees of freedom. Models were fitted with REML to obtain parameter estimates, and with ML to compare log-likelihood and Akaike's Information Criterion between models. We used arcsine-square-root transformations to linearise proportional data, and have back-transformed model predictions in our results.

Because the protein, lipid and ash content of each prey species were highly correlated, we used a principal components analysis to summarise these data into two orthogonal axes that explained over 99% of the variance among them. The first axis, PC1, was positively correlated with ash and protein and negatively correlated with lipid. The second axis, PC2, was positively correlated with ash, negatively correlated with protein, and not correlated with lipid. Therefore, we would expect that if kārearea prey selection was positively driven by PC1, species with lower lipid content would be selected. Our candidate prey species proportion models (above) included alternative nutritional predictor variables for each prey species, either one or both principal component axis values, or the protein to lipid ratio.

Results

Given the differences in body size and foraging strategies between prey species, it was not surprising to find that prey species had variable nutritional compositions. However, introduced species (irrespective of foraging strategy) were considerably more nutritionally similar to each other (range % protein: 64.5–74.4; range % lipid: 10.50–16.69) than native and endemic species (range % protein: 56.9–76.2; range % lipid: 8.2–33.8; Table 1; Fig. 1). While endemic species had both the highest and lowest protein to lipid ratios, two endemic species fell in the middle of the spread of introduced species (Fig. 1). Endemic species were found at low relative abundances in the habitats surrounding falcon nests (Fig. 2a), but also represented potential prey items with the lowest and highest individual body mass (Fig. 2b). Many of the species analysed for nutritional content showed high variability between individuals (Fig. 1). Although the body mass of introduced species was considerably more uniform than that of native species (Fig. 2b), all species in this study are known prey of kārearea, as are species much larger than those used in this study, such as rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) (Kross et al. 2013).

For the importance of each prey species in kārearea diet by frequency of individuals consumed, the most important predictors were endemicity and relative abundance (Table 2). This model predicts that, holding the relative abundance of prey static, falcons select endemic species 0.09% of the time, but that this selection does not differ significantly from zero (95% CI: 0.0%, 0.24%, $t_{12.2} = 0.43$, p = 0.67). Introduced species are selected 1.91% of the time (95% CI: 0.21%, 5.23%, $t_{14.4}$
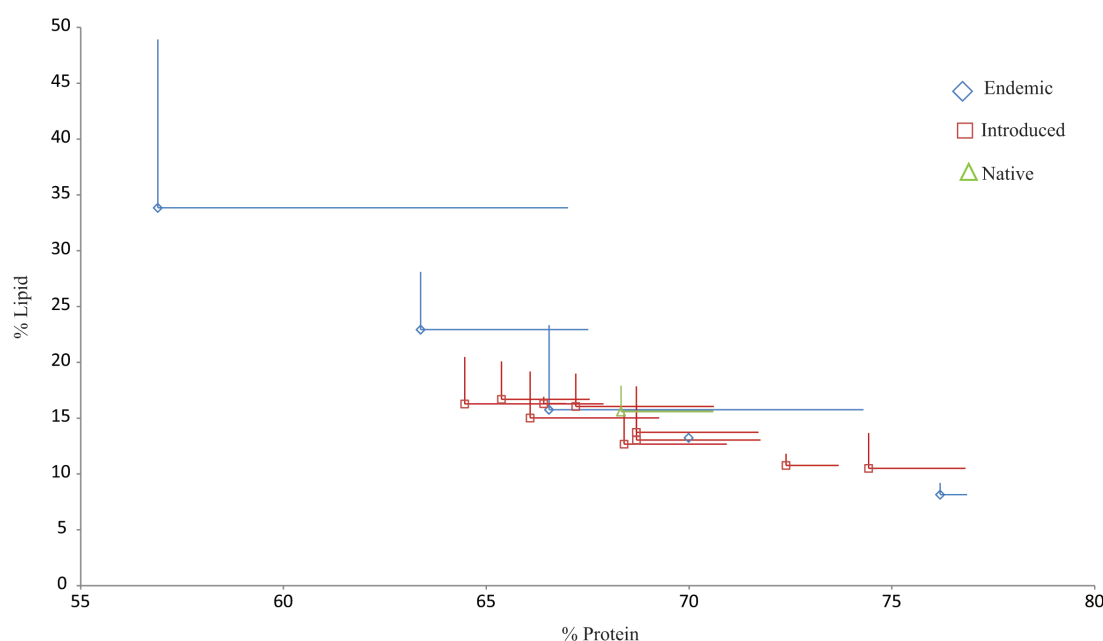
Figure 1. The relationship between protein and lipid content for each species in our study grouped by endemism to New Zealand, showing +1 standard error for both axes.
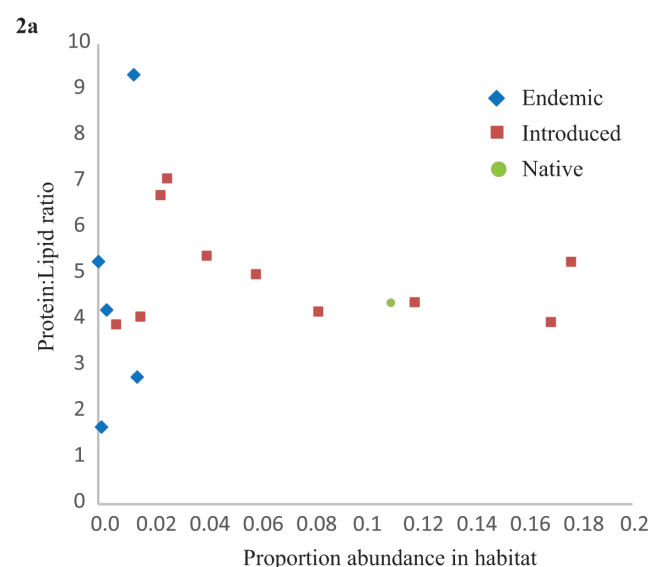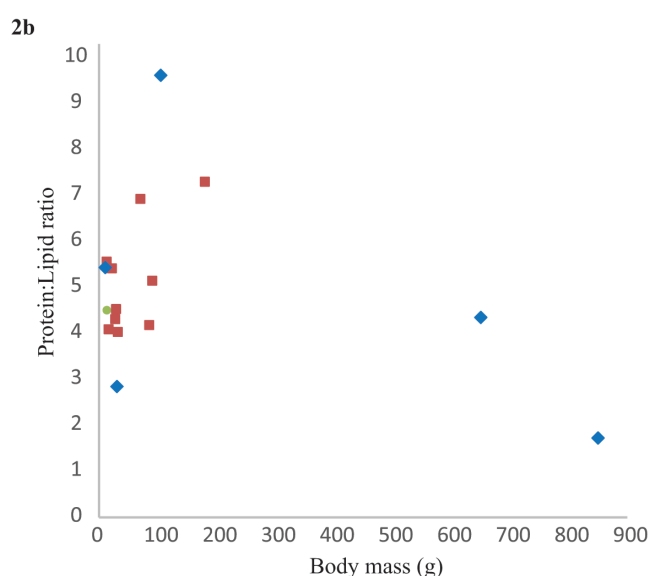

Figure 2. The relationship between the mean protein:lipid ratio in prey species compared to a) the relative proportion abundance of each prey species in the environment; and b) the mean body mass of each species.

= 4.57, p < 0.001), and native species are selected 1.98% of the time (95% CI: 0.0%, 9.41%, $t_{13.6}$ = 2.39, p = 0.03). For each 1% increase in the relative abundance of a prey species in the surrounding habitat, its likelihood of being selected as prey by kārearea increases by 94.79%, which indicates a nearly 1:1 ratio of increase (95% CI 72.70%, 98.62%, t_{77} = 8.80, p < 0.001). A model containing endemicity, relative abundance and the protein to lipid ratio of prey was the second-best-supported model, while a model containing endemicity, relative abundance, and body mass was the third-best-supported model (Table 2). These two models each had some support based on Akaike weight, but their weights were each less than half that of the best-supported model. Furthermore, both protein to lipid ratio (p = 0.53) and prey body mass (p = 0.76) were statistically nonsignificant variables in the models in which they were retained.

For the importance of each prey species in the diet by contribution to total dietary biomass, the best-supported model contained prey endemicity and relative abundance. This model predicts that, holding the relative abundance of prey static, falcons select endemic species 0.04% of the time, but that this selection does not differ significantly from zero (95% CI 0%, 0.79%, $t_{12.8}$ = 0.53, p = 0.60). Introduced species are selected 2.69% of the time (95% CI 0.005%, 10.03%, $t_{14.3}$ = 3.07, p < 0.01), and the native species is selected 0.48% of the time (95% CI 0%, 4.89%, $t_{13.7}$ = 0.53, p = 0.61). For each 1% increase in relative abundance of a prey species in the surrounding habitat, its likelihood of being selected as prey by kārearea increases by 61.95% (95% CI 18.64%, 94.73%, $t_{132.9}$ = 4.57, p < 0.001). The second- and third-best supported models each contained one additional parameter on the best-supported model: prey body mass and prey protein to lipid

Table 2. The eight simplest models for predicting the relative importance of prey species in the diet of kārearea by number (upper panel) and prey biomass (lower panel). The models tested the effects of the relative abundance of prey species in the habitat surrounding nests, the body mass of each prey species, the endemicity of each prey species to New Zealand (categorical: endemic, native or introduced), and the nutritional composition of each species (PC1, PC2 or protein:lipid (P:L)). Columns show the difference between each model and the best-supported model (ΔAIC), the number of parameters included in the model, and the Akaike weight (w_i) of the model.

	ΔAIC	log-likelihood	Model Parameters	w_i
Importance in diet by number				
~ Endemicity + abundance	0.00	127.04	7	0.46
~ Endemicity + abundance + P:L	1.44	127.32	8	0.22
~ Endemicity + abundance + body mass	1.88	127.11	8	0.18
~ Endemicity + abundance + body mass+ PC1	3.47	127.31	9	0.08
~ Endemicity + abundance + body mass + PC1 + PC2	4.05	128.02	10	0.06
~ Abundance	12.92	118.58	5	0.00
~ Endemicity	55.54	98.28	6	0.00
Null model	65.92	91.09	4	0.00
Importance in diet by biomass				
~ Endemicity + abundance	0.00	98.003	7	0.44
~ Endemicity + abundance + body mass	1.52	98.244	8	0.21
~ Endemicity + abundance + P:L	1.91	98.05	8	0.17
~ Endemicity + abundance + body mass + PC1	3.38	98.314	9	0.08
~ Endemicity + abundance + body mass+ PC1 + PC2	3.71	99.149	10	0.07
~ Abundance	5.11	93.447	5	0.03
~ Endemicity	17.90	88.054	6	0.00
Null model	28.20	80.905	4	0.00

ratio, respectively. These two models each had some support based on Akaike weight, but their weights were less than half that of the best-supported model (Table 2). Furthermore, both protein to lipid ratio (p = 0.79) and prey body mass (p = 0.56) were statistically nonsignificant variables in the models in which they were retained. Indeed, when plotted, there was no clear relationship between the relative proportion abundance of each prey species in the environment or mean body mass of prey species and their mean protein to lipid ratio (Fig. 2).

Discussion

Our results do not support the hypothesis that either body mass or nutritional content of the prey are primary drivers of kārearea prey choice, but rather suggest that both relative abundance of prey species and the endemicity of species are important (Seaton et al. 2008; Kross et al. 2013). We found that the nutritional composition of each species did not drive the prey choices of kārearea that we previously observed in the field (Kross et al. 2013). We were somewhat surprised to find so little variation in the nutritional content of introduced birds of different foraging guilds, since different diets can affect the balance of carbon to nitrogen, an index that is commonly used as a proxy for relative body protein content, even between members of the same species (Greer 2015; Greer et al. 2015; Novais et al. 2016). While we did find variation in prey composition, there was overlap between endemic and introduced species, which may explain why none of our models seeking to predict observed kārearea prey choices retained nutritional predictor variables. Although we found no evidence for selective predation based on nutrient balancing, these data are extremely hard to collect, and we had relatively small sample sizes for both the field work (Kross et

al. 2013) and the nutritional analyses. Thus, while these data do not support the hypothesis that kārearea select prey based on nutrient composition, it is possible that they might mix different types of prey to compose a nutritionally balanced diet. Given that for each response variable, one highly ranked model did retain protein-to-lipid ratio as a predictor variable, further research in this area is needed. However, our data also suggest alternative hypotheses for prey choice behaviour in kārearea, including that endemic species may have more effective anti-predator adaptations than introduced species for avian predators such as kārearea.

The 5-minute bird count method that we used may underestimate the relative abundance of less conspicuous species, including many endemic species (Hartley 2012). We believe that in our study, by truncating distance detections to within 50 m of the observer and doing counts in predominantly open habitats (e.g. grasslands, shrublands, vineyards, recently felled areas within forestry), we were unlikely to have significantly underestimated the relative abundance of endemic species, many of which are found more often in forested habitats (MacLeod et al. 2012). Furthermore, if the relative abundance of endemic species was higher than our results indicated, it would point to an even more pronounced preference by falcons to select introduced prey over endemic species. We encourage future researchers to incorporate distance sampling methodologies into their estimates of falcon prey abundance, or to use an even smaller sampling area to ensure equal detectability across prey species.

The pursuit strategies used by kārearea have evolved in the context of their flight capabilities, as well as their need to pursue rapid, erratically moving prey in three-dimensional aerial environments. As implied by Kane and Zamani (2014), prey evasive strategies are likely to create selection opportunities for specific hunting methods. It is possible that endemic birds

possess more specialised anti-predator behaviours in the face of native avian predators. New Zealand birds evolved with only avian predators prior to the introduction of mammals by human settlers. Many species of endemic New Zealand birds have been noted as displaying anti-predator behaviours not considered useful when facing mammalian predators (for example, freezing when threatened; Wilson 2004). These behaviours have been assumed to be a response to the visual hunting strategies of avian predators, which rely on detecting movement to track prey.

Another possible explanation for the apparent selection for introduced prey over endemic prey is that many introduced species typically spend more time in open habitats, and endemic species are found closer to dense cover. Kārearea are sparrowhawk-like in their morphology and are often considered to be a forest falcon because of their relatively short, wide wings and long tails (Fox 1977; Seaton 2007) that make them adept at hunting in forested environments. Kārearea do not typically dive or 'stoop' at prey from above, as is typical in other *Falco* species (Dekker 1980; Dekker & Lange 2001; Zoratto et al. 2010), but instead will glide or fly directly at prey from a perch, engage in tail chases, or use contour-hugging low flight to flush prey (Fox 1977). These hunting behaviours may be more successful against the generally open-habitat introduced bird species than against more forest-dwelling endemic species. Therefore, while our field surveys did quantify relative avian abundance in representative habitats around each nest, including both open and more forested habitats, kārearea may have been preferentially hunting in relatively open habitats, as kārearea were shown to do in North Island plantation forest (Seaton et al. 2008; Horikoshi et al. 2017). Our field-based findings (Kross et al. 2013) from South Island study sites agree with those of Seaton et al. (2008), in which many of the endemic species in their North Island study area were selected against by foraging kārearea. Likewise, in Marlborough, Fox (1977) observed 161 hunting attempts on avian prey, only three of which were on endemic species (two on fantail *Rhipidura fuliginosa*, one on New Zealand pipit *Anthus novaeseelandiae*; 0% success), compared with 151 observed attacks on introduced species (11 species; 28% success), and seven observed attacks on native species (four species; 28% success). We suggest that further research on the anti-predator adaptations of endemic New Zealand birds against native avian predators would be a fruitful avenue for future work. Given the difficulties of observing sporadic predation events, this research could be addressed in a citizen science project (Nelson & Fijn 2013). Citizens who see a falcon attack could film it; clips submitted to a single repository could then be analysed to assess differences in the evasive manoeuvres of native versus introduced prey birds. Such a study would be of considerable interest, as the existing literature is dominated by reports of endemic New Zealand birds lacking anti-predator adaptations against introduced predators.

Acknowledgements

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