A comparison of the diets of the Black-shouldered Kite *Elanus axillaris* and Nankeen Kestrel *Falco cenchroides* in the Canberra region

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We compare for the first time the diets of sympatric populations of the Black-shouldered Kite *Elanus axillaris* and Nankeen Kestrel *Falco cenchroides* in the Australian Capital Territory (ACT). Diets of the two species were documented by collecting prey remains (pellets, orts and remains) from nest sites between December 2002 and July 2008. The kite's diet comprised mostly small mammals (93% by mass); the kestrel consumed mainly invertebrates (86.1% by number), as well as some mammals, birds and reptiles (collectively 94.8% by mass). We discuss the observed limited dietary overlap, and possible factors that enable the two species to coexist in the ACT.

INTRODUCTION

An important aspect of community ecology is the understanding of the factors that enable ecologically similar species to inhabit the same environment (Begon *et al.* 1990). Schoener (1974) identified three main mechanisms of niche segregation in birds of prey: by habitat, food, and diel time of activity. Where critical resources, such as nesting sites, food or preferred habitat, are limited, it is expected that ecologically similar, co-occurring species will evolve strategies enabling them to survive within particular, relatively distinct niches (May 1973).

The diets of the Black-shouldered Kite *Elanus axillaris* (hereafter "kite") and the Nankeen Kestrel *Falco cenchroides* (hereafter "kestrel") have been well studied (Genelly 1978; Olsen *et al.* 1979; Marchant and Higgins 1993; Debus *et al.* 2006; Olsen 2014 and references therein). The kite (*Accipitriformes)* is a small mammal specialist, often being a crepuscular hunter (Debus 2012) of the introduced House Mouse *Mus musculus* and other small rodents (Debus *et al.* 2006). The kestrel *(Falconiformes)* is a generalist, daytime hunter that also includes small mammals in its diet (Marchant and Higgins 1993; Baker-Gabb 1984a, Starr *et al*. 2004). The kite and the kestrel are both found commonly across the Australian mainland and co-occur in various habitats, including arid areas and shrubland (Aumann 2001) and open country and pastoral zones (Baker-Gabb 1984b). Morphologically, adult kites are larger in terms of weight, wingspan and body length: weight – kite 249 g (male) to 293 g (female), kestrel 165 g (male) to 185 g (female); wingspan – kite 82-94 cm and kestrel 62-84 cm; body length - kite 33-37 cm and kestrel 30-35 cm. The kite also has much thicker tarsi and toes than the kestrel (Debus 2012, Olsen 2014).

The sympatry of the kite and kestrel populations in the Canberra region creates a situation where there is likely to be competition for food resources and thus a potential for dietary overlap. This situation therefore presents a unique opportunity to quantify and assess any dietary overlap at a local scale, and explore plausible explanations for the coexistence of the two species.

METHODS

Study Area

Nesting and roosting sites of the kite and kestrel were located within a 40 km radius of the Canberra Central Business District, ACT, Australia (35º17'54"S, 149º8'4"E).

Collection and analysis of prey material

Collection of pellets and prey material occurred between December 2002 and July 2008. To identify prey species, material was compared with representative samples from a combination of private collections and specimens from the Australian Museum, Sydney. For ease of analysis, prey items were categorised into four main groups: mammals, birds, reptiles and invertebrates. The number of prey items in each sample was estimated using the minimum number of individuals (MNI) technique outlined by Olsen *et al.* (2010). Adults and young share prey, so it was not assumed that one pellet represented one prey item.

The techniques used herein follow those of Marti *et al.* (1993) and those employed elsewhere in raptor dietary studies in Australia (e.g. Olsen *et al.* 2010, 2013; McDonald *et al.* 2012). Pooled data were used for the first three calculations.

(1) Index of Relative Importance (IRI): only pellets and fully identified prey were included in the analysis, which allowed for standardised calculations (particularly frequency of occurrence). We calculated the IRI using the following formula:

$$IRI = (N + V) F$$

where N is the number of prey items, V is the volume of prey and F is the frequency of occurrence of a prey item, and each is calculated as a percentage. The IRI yields a single value, which then allows prey items to be ranked according to their proportional representation in the sample and thus reduces the bias that results from using single measurements (Pinkas *et al.* 1971). In the present study prey mass was substituted for volume. A chi-square test of goodness-of-fit was performed to determine whether the four prey groups were equally preferred by both raptors ($\alpha = 0.05$).

(2) Mean prey weights were taken from the literature (see Appendix 1 for dataset) and used to calculate Geometric Mean Prey Weight (GMPW) (Marti *et al.* 1993). Using this metric, rather than overall mean prey weight, avoids potential biases related to the typically non-normal distribution of prey weights in raptor diets.

(3) Diet diversity was calculated using the Shannon Diversity Index (Marti *et al.* 1993), where:

$$H' = -\Sigma p_i \log p_i$$

and p_i is the number of prey species in a group, with calculations made for all prey groups.

(4) We used the Pianka Index (Pianka 1973) to estimate dietary overlap between the two species:

$$O = \Sigma p_{ij} p_{ik} / \sqrt{(\Sigma p_{ij}2, \Sigma p_{ik}2)}$$

where p_{ij} and p_{ik} are the proportion of prey species in the diets of raptor *j* and raptor *k*, respectively. The proportion of overlap is expressed as a percentage of the measure of similarity between the diets.

RESULTS

Across the four prey groups, the kestrel had the broadest selection of prey species, taking 29 invertebrate and 35 bird species. The overall GMPW for kestrel prey across all items was 6.4 g (Table 1). As a group, invertebrates comprised the highest proportion of the diet (81.6% by number; Table 2). Invertebrates also had the highest IRI (89.7%), followed distantly by reptiles (9.4%). Shannon's Index indicated that the kestrel's diet was slightly more diverse than that of the kite (H' = 0.659 kestrel and 0.904 kite). The kestrel consumed 5.2% invertebrates by biomass and 94.8% vertebrate prey. The three vertebrate groups were much more evenly distributed within the kestrel (mammals 43.4%; birds 29.5%; reptiles 21.9% by number) than the kite diet.

Overall, GMPW was greater for the kite (16.8 g), with the kestrel taking prey that were, on average, almost two-thirds lighter (GMPW = 6.4 g). The House Mouse contributed 92 % by number of all prey items consumed by the kite and was ranked as the most important prey item overall in its diet (IRI 99.9%). The kite consumed ~98% vertebrates; of these, by biomass ~93% were mammals (Table 2). Invertebrate prey also ranked in the IRI top five prey items for the kite, although the values were low in comparison with that for the mice, and they were not of great importance in the kite's diet overall (IRI <1%). A crayfish *Cherax* sp. recorded among the prey consumed marks a previously unrecorded food item for the kite. Diet diversity of the kite was highly skewed toward mammals; consequently 92% of prey by number (n = 382) was composed of a single species (House Mouse).

Table 1

Geometric Mean Prey Weights (g) for the kite and kestrel. Values in brackets indicate the percentage of total prey by number.

	Black-shouldered Kite		Nankeen Kestrel	
Mammals	68	(93.2)	83.1	(3.1)
Birds	28.1	(1.9)	55.2	(4.5)
Reptiles	60	(0.5)	39.2	(10.7)
Invertebrates	2.2	(4.3)	1.1	(81.6)
Overall GMPW	16.8		6.4	

Neither raptor species consumed prey from the four main prey groups equally (kite $\chi^2_{(3)}$ = 1029.36, n = 414; kestrel $\chi^2_{(3)}$ = 1479.14, n = 859). The Pianka Index of 8.6% indicated that there was only limited dietary overlap between the two raptor species, but there were differences in the proportions of items consumed from the four main prey groups. Kites took mostly mammalian prey, whereas kestrels mainly targeted invertebrates and reptiles (Table 2).

DISCUSSION

Olsen (2014) pointed out that the feeding ecology of coexisting species is expected to differ (Gause's Rule), and he has found this to be the case for other sympatric raptors, such as falcons and eagles. We found that the kite's diet in the Canberra region was dominated by small mammals, particularly the House Mouse. In contrast, the kestrel's diet was far more generalist, including a variety of small invertebrate and vertebrate prey. The importance of insects in the kestrel's diet (IRI 89.7%) echoes the results of Leach *et al*. (2015), who also found that insects (orthopterans) were the most important prey for this species (IRI 96.8%). Interestingly, despite these clear differences in diet, there was some overlap in the IRI results for the two raptor species and the Pianka Index also suggested limited dietary overlap.

In his observational study of kestrels in northern New South Wales, Genelly (1978) found that kites were recorded in 52.4% of surveys. The two species were found in the same area frequently, and interacted with each other in both an aggressive and non-aggressive manner. Aumann (2001) found that the highest numbers of foraging observations for the kite and the kestrel were made within the same diurnal time window (08.00-09.59), but in contrast Baker-Gabb (1984b) found that kites had a marked crepuscular peak in hunting activity. Therefore further study is required to ascertain whether temporal partitioning of foraging times is also a mechanism that facilitates the coexistence observed in the present study.

Another factor potentially facilitating diet disparity (and consequently coexistence) could be differences in morphology. The kite has a more robust tarsi and toes than the kestrel, which could give it an advantage in tackling larger prey. That the kite ate only mice, whereas the kestrel had a varied diet mostly comprising much smaller, lighter invertebrate prey that are somewhat easier to grasp than small mammals, suggests that the two raptor species may coexist partly by consuming different-sized prey. Again, further investigation of the significance of this disparity is required.

Table 2

Overall prey consumption of the two raptors, showing percentage of total prey (by numbers, biomass (gram weights and overall percentage) and IRI (total and overall for each prey class)).

	Mammals					Birds					Reptiles					Invertebrates				
	%	Biomass		IRI		%	Biomass		IRI		%	Biomass		IRI		%	Biomass		IRI	
	Total Prey	(g)	%	Total	%	Total Prey	(g)	%	Total	%	Total Prey	(g)	%	Total	%	Total Prey	(g)	%	Total	%
Black-shouldered Kite	93.2	7360	92.0	19692	99.9	1.9	385	4.8	0.9	<1	0.5	120	1.5	0	0	4.3	136	1.7	7.1	<1
Nankeen Kestrel	3.1	5919	43.4	38.9	0.5	4.5	4020	29.5	23.2	<1	10.7	2985	21.9	706	9.4	81.6	706	5.2	6705	89.7

The discovery of a previously unrecorded dietary element, a crayfish, among the kite's prey is surprising. It is possible that it was caught opportunistically on land, as crayfish are semi-aquatic (Withnall 2000) and are also strong walkers that are known to traverse land in search of favourable water bodies (Wade *et al.* 2004). Crayfish remains were identified in 3 pellets, which suggest that a significant part of this prey was processed and ingested.

Feather, claw, bone and podothecal (sole) material from a Sulphur-crested Cockatoo *Cacatua galerita* were found in three kite castings, but not considered likely 'prey' and not included in analyses. This species has never been recorded in the diet of the kite as either prey or carrion (Marchant and Higgins 1993; Higgins 1999). The possibility of a kite taking this species as prey is unlikely, given the relatively much larger body size of the cockatoo in terms of both mass (mean adult weight: cockatoo females 764 g and males 815 g; kite females 293 g and males 249 g) and wing length (mean adult wing length: cockatoo females 334 mm and males 344 mm; kite females 301 mm and males 295 mm; Marchant and Higgins 1993, 1999). It is therefore considered unlikely that the smaller (and presumably weaker) kite could physically restrain and kill a much larger and also highly gregarious bird; it is more likely that the food was secured as carrion. However, kites have not previously been observed scavenging, so this could be the first record of such an activity.

CONCLUSION

The dietary analysis of coexisting kites and kestrels presented here demonstrated that these two raptor species were markedly different in the food that they consumed. However, despite this disparity, there was some dietary overlap, with the two species sharing a few types of prey item (e.g. small mammals). Possible 'drivers' of the observed dietary disparity that may facilitate coexistence on a local scale could include temporal differences in hunting activity and/or morphological differences that affect prey capture capabilities. Further investigations in these areas are required to test these propositions.

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APPENDIX 1

List of prey items[1] taken by the Black-shouldered Kite and Nankeen Kestrel.

Black-shouldered Kite

Common Name	Scientific Name	No. of Items	Weight (g)
Mammals			
House Mouse	*Mus musculus*	313	18
House Mouse juvenile		69	9
Black Rat	*Rattus rattus*	1	180
Bush Rat	*Rattus fuscipes*	1	125
European Rabbit	*Oryctolagus cuniculus*		
European rabbit (juv.)		2	400
Total Mammals		**386**	
Birds			
Crimson Rosella	*Platycercus elegans*	1	135
Superb Fairy-wren	*Malurus cyaneus*	1	10
Double-barred Finch	*Taeniopygia bichenovii*	1	10
Other birds undetermined		5	46
Total Birds		**8**	
Reptiles			
Small dragon lizard undet.	*Amphibolurus sp.*	2	60
Total Reptiles		**2**	
Invertebrates			
Crustaceans			
Crayfish	*Cherax sp.*	1	115
Insects			
Beetles undetermined	Order Coleoptera	6	1
Grasshopper	Fam. Acrididae	5	2
Mantid egg case	Order Mantodea	1	0.2
Weevil	Fam. Curculionidae	5	1
Total Invertibrates		**18**	
Detritus and plant material		1	

* Feathers from a Sulphur-crested Cockatoo were detected in three castings (see Results and Discussion sections for treatment of this finding)

Nankeen Kestrel

Common Name	Scientific Name	No. of Items	Weight (g)
Mammals			
Antechinus undetermined	*Antechinus sp.*	3	27.5
House Mouse	*Mus musculus*	12	18
European Rabbit	*Oryctolagus cuniculus*	2	1000
European Rabbit juvenile		9	400
Bats undetermined	Order Chiroptera	1	20
Total Mammals		**27**	
Birds			
Galah	*Eolophus roseicapillus*	1	335
Crimson Rosella	*Platycercus elegans*	7	135

Nankeen Kestrel *(continued)*

Common Name	Scientific Name	No. of Items	Weight (g)
Birds			
Eastern Rosella	*Platycercus eximius*	7	106
Red-rumped Parrot	*Psephotus haematonotus*	3	61
Superb Fairy-wren	*Malurus cyaneus*	1	10
White fronted Chat	*Epthianura albifrons*	1	13
Magpie-lark	*Grallina cyanoleuca*	2	90
Australian Magpie	*Cracticus tibicen*	2	329
Australasian Pipit	*Anthus novaeseelandiae*	1	23
Brown Songlark	*Cincloramphus cruralis*	1	54
House Sparrow	*Passer domesticus*	5	27
European Goldfinch	*Carduelis carduelis*	2	18
Common Starling	*Sturnus vulgaris*	5	75
Small passerine undet.	*Passeriformes*	1	46
Other birds undetermined		5	57
Total Birds		**44**	
Reptiles			
Jacky Lizard	*Amphibolurus muricatus*	14	60
Small dragon lizard undet.	*Amphibolurus sp.*	9	60
Bluetongue skink undet.	*Tiliqua sp.*	2	300
Boulenger's skink	*Morethia boulengeri*	1	15
Skink undetermined	Fam. Scincidae	63	15
Small snake undetermined	Suborder Serpentes	3	15
Total Reptiles		**92**	
Invertebrates			
Molluscs			
Garden snail	*Helix aspersa*	1	6
Arthropods			
Huntsman spider	Fam. Sparassidae	14	1
Wolf spider	Fam. Lycosidae	35	1
Other spiders undetermined	Order Araneae	29	1
Millipede sp.	Class Diplopoda	1	1
Scorpion undetermined	Order Scorpiones	1	1
Christmas beetle	*Anoplognathus olivieri*	1	1
Christmas beetle	*Anoplognathus porosus*	7	1
Christmas beetle undet.	*Anoplognathus sp.*	54	1
Carab beetle	Fam. Carabidae	1	1
Longicorn beetle	Fam. Cerambycidae	2	1
Weevil	Fam. Curculionidae	17	1
Diaphonia beetle	*Diaphonia dorsalis*	1	1
Click beetle	Fam. Elateridae	5	1
Black beetle	*Heteronychus arator*	22	1
Geotrupid beetle	*Heteronyx sp.*	20	1
Other scarab beetles undet.	Fam. Scarabaeidae	101	1
Dung beetle	*Ontophagus australis*	11	1
Repsimus beetle	*Repsimus aenus*	3	1
Jewel beetle	Buprestidae	1	1
Other beetles undetermined	Order Coleoptera	175	1
Cicada	*Psaltoda moerens*	46	1
Bugs undetermined	Order Hemiptera	4	1
Flying ants	Order Hymenoptera	21	1
Epicoma moth	*Epicoma contristis*	1	1
Butterfly/Moth undetermined	Order Lepidoptera	5	1
Grasshopper	Fam. Acrididae	2	1
Locust	Fam. Acrididae	1	1
Mole crickets	Order Orthoptera	49	1
Grasshoppers	Order Orthoptera	69	1
Stick insect	Phasmatidae	1	1
Total Invertebrates		**701**	
Detritus and plant material		1	

[1] Prey weights taken from Olsen *et al.* (2008), Olsen et al. (2010) and McDonald *et al.* (2012).