The trophic structure of the breeding raptor guild of the Canberra region and its relationship with other Australian guilds

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This study examines the trophic structure of the raptor guild near Canberra, Australia, and also provides the first comparison of the trophic structure, dietary diversity, and overlap of three breeding raptor guilds across the Australian subcontinent. The study guild was very diverse in its diet, as shown by its trophic structure, with only three clear sub-guilds identified and five species that did not fit any particular sub-guild. There was little overlap in the diet of the various species. The three sub-guilds identified were raptors eating: (i) mammals and large birds (Wedge-tailed Eagle *Aquila audax*, Little Eagle *Hieraaetus morphnoides*, Whistling Kite *Haliastur sphenurus*); (ii) small vertebrates and insects (Brown Goshawk *Accipiter fasciatus*, Brown Falcon *Falco berigora*); and (iii) insect dominated (Nankeen Kestrel *F. cenchroides*, Southern Boobook *Ninox boobook*). The other species and prey were the Black-shouldered Kite *Elanus axillaris* (rodent specialist); White-bellied Sea-eagle *Haliaeetus leucogaster* (animals of aquatic origin); Collared Sparrowhawk *Accipiter cirrocephalus* (small birds and insects); Australian Hobby *F. longipennis* (aerial prey specialist: small birds, insects and bats); and Peregrine Falcon *F. peregrinus* (bird specialist). The Canberra guild had a higher dietary diversity and less overlap than the other Australian guilds. The potential role of intraguild predation is discussed.

Keywords: Raptors, Guild, Trophic Structure, Dietary diversity, Apex predator, Intra-guild predation, Australia.

INTRODUCTION

One of the most important problems in current ecology is to unravel how communities are assembled and maintained. Unfortunately, most raptor studies analysing prey overlap and competition only deal with two or three species (Charter *et al.* 2018; Milchev 2016; Muñoz-Pedreros *et al.* 2016; Wiens *et al.* 2014), making it difficult to understand the community structure. Full guild studies provide a better insight into the topic, but they are scarce. In Australia, there are only two studies that describe the diet of full raptor breeding guilds and that sampled for multiple years: one by Baker-Gabb (1984a) at Mildura, Victoria; and one by Aumann (2001a,b) in the south-west of the Northern Territory, both arid areas, though; therefore, information on raptor guilds for non-arid areas, where the dynamics may be very different, is lacking.

Jaksic (1985) mentioned that diurnal and nocturnal raptor guilds provide an excellent vehicle for the study of community ecology, since raptors are large and conspicuous and the study of their feeding habits and habitat selection patterns is therefore relatively simple compared with studying other taxa. Subsequently, trophic studies on birds of prey have emphasized the guild structure at the regional level (Jaksic 1988; Marti *et al.* 1993a, 1993b; Aumann 2001b; Corbett *et al.* 2014; Pande *et al.* 2018). Root (1967) originally introduced the term 'guild', applying it to 'a group of species that exploit the same class of environmental resource in a similar way'. This term groups species without regard to taxonomic relationships, as long as they overlap significantly in their niche requirements. Since its introduction, the meaning of the term has been modified (Marti *et al* 1993b) and there is disagreement on how researchers should use it (Jaksic 1981; Jaksic and Delibes 1987); however, there seems to be some consensus that it should be used when the study is focused on the constituent species and their interactions (Blondel 2003).

The diet of the 12 raptor species breeding in the Australian highlands has been described (Fuentes *et al.* 2024) and the aim of this paper is to analyse the trophic structure of this raptor guild. A particular focus was food partitioning between species – patterns of competitive use of food resources and how raptors aggregate into different feeding sub-guilds (*sensu* Root 1967). In contextualising this study, we compared the trophic structure of this guild with the other guilds of breeding raptors previously studied in the Australian subcontinent (Aumann 2001b; Baker-Gabb 1984a).

METHODS

The observations took place while working on a long-term study of a raptor community on the Southern Tablelands of New South Wales (34°50'–35°47'S, 148°40'–149°50'E). Details on the study area, food collections, species identification, biomass, and GMPW calculations can be found elsewhere (Fuentes *et al*. 2007, 2024; Fuentes and Olsen 2015; Olsen 1992; Olsen *et al.* 2008, 2010, 2014).

We calculated dietary metrics such as the Shannon Diversity (Shannon and Weaver 1949), Evenness, and Pianka Indices to explore the dietary overlap as in previous papers of our study (Debus *et al.* 2021; Fuentes *et al.* 2007; Olsen *et al.* 2006a,b, 2013a,b). The Shannon Index (ranging upwards from 0 = lowest diversity) reflects dietary species richness; Evenness Index values (between 0 and 1) reflect little (0) to high (1) dietary evenness or spread across prey categories; and the Pianka Index values (between 0 and 1) reflect no overlap (0) to complete overlap (1). To avoid pseudo-replication problems in the calculation of these indices, some unidentified groups were eliminated if there were individuals present in another category that belonged to the same group; for example, if there were Australian Raven *Corvus coronoides* and unidentified raven remains in a sample, the latter was eliminated from the diversity and overlap calculations. The same indices were calculated for the two Australian dietary studies mentioned above (Aumann 2001b, Baker-Gabb 1984a) for comparative purposes. The diversity and overlap of the three studies were compared using GLM (general linear models) and, when there were significant differences, these were followed using multiple comparisons using the Tukey-Kramer method. To perform pair-wise comparisons in the dietary diversity of species shared by the three studies we used a series of Hutchenson T-Tests (Hutchenson 1970) specifically designed for pair-wise comparisons of the Shannon Index (see Data Analytics UK 2023), using the Bonferroni correction to adjust the experiment-wise error rate.

Evaluation of the Trophic Structure: Feeding Sub-guilds

The dietary items identified for the 12 different raptors produced a 12 × 222 matrix (raptors × dietary items = 2664) used for the analyses described below. The analysis uses the number of dietary items, and not their biomass contribution, since its purpose is to explore the dietary overlap between species to describe their relationship in terms of their use of resources. All the species data sets used contained a minimum of 50 prey individuals as recommended by Marti *et al.* (1993a). The only exception was the Whistling Kite *Haliastur sphenurus* with a data set very close to the recommended size ($n = 48$) so caution must be exercised when interpreting the results for this species.

To analyse the structure of the community and assign raptor species to feeding sub-guilds, we used a dissimilarity measure based on the Pianka Index (Pianka 1973), which is commonly used to estimate dietary or niche overlap in birds of prey (Charter *et al* 2018; Jaksic *et al.* 1981; Marti *et al.* 1993a, 2007) and has been used in previous papers of the same project (Debus *et al.* 2021; Olsen *et al.* 2006a,b, 2010, 2013a,b). The Index is given by:

$$O = 1 - (\sum p_{ij}\, p_{ik} / \sqrt{\sum p_{ij}^{\,2} \sum p_{ik}^{\,2}}),$$

where p_{ij} and p_{ik} are the proportions of prey species (or other taxa/group) in the diets of raptors *j* and *k* respectively. The values obtained this way are expressed as a symmetrical dissimilarity matrix, ranging from 0 (complete overlap) to 1 (no overlap). The process was applied to the highest resolution; that is, the most precise taxonomic level possible to which we identified prey species (most to species or genera – see Appendix 1 and 2 in Fuentes *et al.* 2024).

The dissimilarity matrix obtained was then used as a base for the clustering process. Our rationale for using this approach was twofold. First, for consistency and to facilitate comparison with the results of previous studies (Jaksic *et al.* 1981; Jaksic and Delibes 1987; Marti *et al.* 1993a,b; Olsen *et al* 2006a,b). Secondly, we used a UPGMA clustering technique to produce the feeding sub-guilds and assigned an overall value of 80% diet similarity as a cut-off to determine such groups and for the clustering process, the Chord Distance (Legendre and Legendre 2012) was selected as a similarity measure, since it is practically equivalent to the Pianka Index in its formulation: equivalence that was confirmed by a Mantel matrix correlation analysis ($r = 0.996$, $P < 0.0001$). We took this approach to ensure that our results will be comparable to those using the traditional method (Jaksic 2000; Jaksic *et al.* 1981; Jaksic and Delibes 1987; Marti *et al.* 1993a,b). The use of UPGMA clustering strategy has been recommended by several authors when analysing dietary patterns of predator assemblages (Jaksic and Delibes 1987; Marti *et al*. 2007; Marti *et al.* 1993a,b). Initial exploration showed evidence of one outlier, the Black-shouldered Kite *Elanus axillaris*. We decided not to remove this species, since this difference seems more an outcome of the pattern we wanted to explore, given that the diet of this kite has almost no overlap with that of any of the other resident raptors. (The Barn Owl *Tyto alba* was not included, reflecting the lack of breeding records near Canberra: Fuentes *et al.* 2024).

The data were then analysed using Multidimensional Scaling following the same parameters described above: to evaluate the discreteness and isolation of the feeding sub-guilds obtained and to correlate these findings with the original set of attributes (dietary item categories). We started the ordination analysis with six dimensions; the preliminary run produced no solution and indicated the possible effect of outliers and other deviations. Further exploration revealed the existence of one outlier and high positive skewness, a problem remedied using a double square transformation. Since the subsequent NMS suggested a 3-dimensional solution, the procedure was re-run using the recommended solutions and the produced seeds (centroids). All analyses were performed in SAS OnDemand and PC-Ord 6.0.

RESULTS

Trophic Structure: Feeding Sub-guilds and Dietary Metrics

The use of 80% as the minimum level of clustering by diet similarity enabled recognition of three main feeding sub-guilds – with three, two and two species in each – and five ‘solo’ predators or species that could not be ascribed to any sub-guild (Fig. 1). These groups were also evident on the NMS ordination plot (Fig. 2). A ‘mammal-large bird’ feeding sub-guild was composed of the two true eagles – Wedge-tailed Eagle *Aquila audax* and Little Eagle *Hieraaetus morphnoides* – and the Whistling Kite. They shared the consumption of medium-sized mammals, primarily European Rabbit *Oryctolagus cuniculus*, and, to a lesser extent, the consumption of European Hare *Lepus europaeus*, Sheep *Ovis aries* and several species of ground-feeding birds such as Galah *Eolophus roseicapilla*, Sulphur-crested Cockatoo *Cacatua galerita*, and Australian Magpie *Gymnorhina tibicen* among others. An ‘insect-small vertebrate’ feeding sub-guild was composed of the Brown Falcon *Falco berigora* and the Brown Goshawk *Accipiter fasciatus*. Approximately 50% of their total dietary items were insects, primarily cicadas, Christmas Beetles *Anoplognathus* sp. and grasshoppers. These two species also shared three main vertebrate food items: Rabbits, small skinks and three species of medium-sized parrots (Crimson Rosella *Platycercus elegans,* Eastern Rosellas *P. eximius*, and Red-rumped Parrots *Psephotus haematonotus*). The third sub-guild had an insect-dominated diet (around 80% of total items) and its members were the Southern Boobook *Ninox boobook* and Nankeen Kestrel *Falco cenchroides*. They

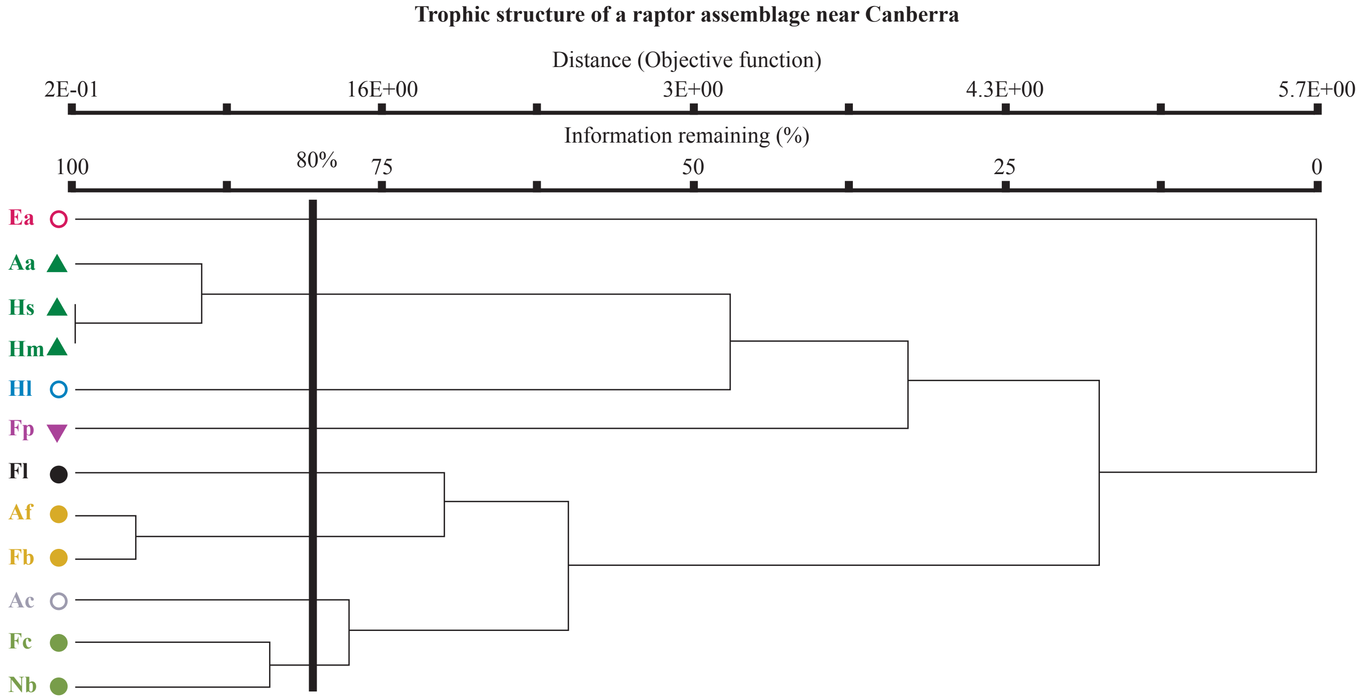

Figure 1. *Trophic structure of a raptor assemblage living near Canberra as given by the UPGMA clustering (Ea=* Elanus axillaris*, Aa=* Aquila audax*, Hs=* Haliastur sphenurus*, Hm=* Hieraaetus morphnoides*, Hl=* Haliaeetus leucogaster*, Fp=* Falco peregrinus*, Fl=* F. longipennis*, Af=* Accipiter fasciatus*, Fb=* F. berigora*, Ac= Accipiter cirrocephalus, Fc=* F. cenchroides*, Nb=* Ninox boobook*).*

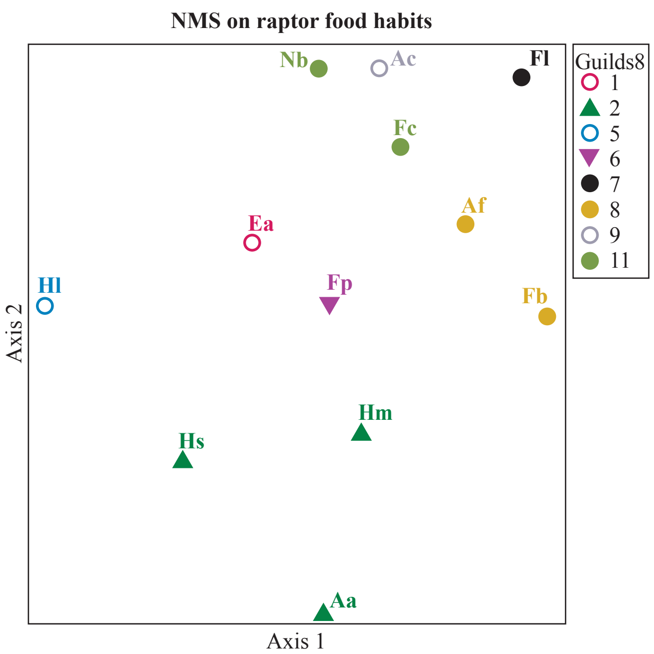

Figure 2. *NMS ordination of species in a raptor assemblage living near Canberra based on diet similarity. (Labels as in Figure 1).*

shared the consumption of several types of coleopterans, particularly species belonging to the family Scarabaeidae, including Christmas Beetles. They also overlapped in the use of House Mouse *Mus musculus* and Eastern Rosella. Among the solo hunters, there were three cases of specialised hunters whose diet was very different from all the other species (0, 27 and 46% similarity). The most extreme case was the Black-shouldered Kite whose diet was 96.1% House Mice – the highest degree of specialisation found. Another specialist was the Peregrine Falcon *Falco peregrinus*, the diet of which consisted of 96.5% birds. Finally, the White-bellied Sea-Eagle *Haliaeetus leucogaster* also showed a specialised diet that consisted of fish (23% of total items), ducks (36.7%) and freshwater turtles (8.3%). Thus, the Sea-Eagle was the only local species to fully exploit prey of aquatic origin. The other two solo hunters were more general in the taxa selected and had some level of overlap with the guilds. The Australian Hobby *Falco longipennis* was specialised in its hunting location, however, since its prey was almost completely aerial (birds, bats and flying insects – 98.8% of total items); this species had some overlap with the 'insect-small vertebrate' guild (71% similarity). Likewise, the Collared Sparrowhawk *Accipiter cirrocephalus* consumed mainly insects (62.1% of items) and birds (36.8%), the House Sparrow *Passer domesticus*, Common Starling *Sturnus vulgaris* and the two rosellas being the most important. The high number of insects and the species consumed by this raptor made its diet related to the insect-feeding guild (77% similarity).

Further exploration of the NMS ordination with the dietary items revealed that the trophic structure of the assemblage was mainly explained in terms of prey size. Prey size was inversely correlated with Axis 2 in Figure 4 ($r = 0.71$, $t = -0.636$). Raptors with large prey (large and medium mammal and large bird eaters) are located towards the lower end of the axis, with the Wedge-tailed Eagle the most extreme case, a finding that seemed to be linked with its high consumption of the largest prey species of any raptor in the assemblage: large macropods (see Fuentes *et al.* 2007 and Fuentes and Olsen 2015). Species

Table 1

Prey species of particular importance for the Raptor Guild near Canberra, as indicated by NMS axis correlation.

	Number of raptor species where the prey type was: Present	Important (>5% MNI)
Rabbit	9	6
Galah	7	1
Crimson Rosella	10	2
Eastern Rosella	9	1
Common Starling	8	2
Christmas Beetles	8	6
Cicada	10	5

with medium-sized prey (large birds and reptiles) were in the middle area of the plot, while species whose diet was dominated by small mammals, small birds and insects were localised in the plot's upper section.

Visual examination of the change in bubble size resulting from the correlation of the NMS ordination with each prey type revealed the categories that were particularly important for the diet of the whole assemblage. These are summarised in Table 1.

Dietary Diversity, Evenness and Overlap: Comparing Australian Guilds

Canberra's raptor guild exhibited high dietary diversity, with an average of 2.74 ± 0.700 SD in the Shannon Index (Table 2). Five species had Index values greater than 3, with the Wedge-tailed Eagle showing the greatest diversity with 3.28. The only species showing a value less than 2 was the Black-shouldered Kite (Index value = 0.695). The Evenness Index for the assemblage was high, with all but one species showing values exceeding 0.6 and up to 0.920 (Table 2), with an average of 0.761 (± 0.165 SD). Again, the Black-shouldered Kite was the exception with a very low Evenness Index of 0.290. Dietary diversity was significantly different between the three Australian guilds ($F = 11.07$; df = 2, 30; $P < 0.0005$: Table 2). Multiple comparisons based on the Tukey-Kramer procedure ($\alpha = 0.05$) revealed that the Canberra guild had a significantly more diverse diet than that of Mildura (Baker-Gabb 1984a) and the Northern Territory (Aumann 2001b), the guild of which itself had a significantly more diverse diet than that in Mildura. The three guilds shared six species: Brown Falcon, Nankeen Kestrel, Whistling Kite, Little Eagle, Wedge-tailed Eagle and Brown Goshawk. When only these species were considered, the diversity of the diet was even greater for Canberra (3.029 ± 0.180 compared to 1.560 ± 0.413 at Mildura and 2.546 ± 0.453 in the NT: $F = 24.72$; df = 2, 15; $P < 0.0001$). This significant result was followed by a series of Hutchenson T-Tests to compare each of the overlapping species of the three studies. The Canberra species were found to

Table 2

Comparative values of the Shannon Diversity Index and the Evenness Index between the three existing full breeding guild diet studies in Australia: Mildura, Victoria (Baker-Gabb 1984a), south-west Northern Territory (Aumann 2001b) and the Canberra Region (this study).

		Shannon Diversity Index			Evenness Index		
		Mildura, Vic.	South-west NT	Canberra Region	Mildura, Vic.	South-west NT	Canberra Region
Species shared by the 3 guilds	Whistling Kite	1.272	3.112	2.843	0.496	0.822	0.920
	Brown Goshawk	1.898	2.790	2.875	0.623	0.773	0.790
	Little Eagle	1.271	2.714	3.129	0.469	0.736	0.895
	Wedge-tailed Eagle	1.038	2.006	3.284	0.472	0.659	0.793
	Nankeen Kestrel	1.869	1.988	2.902	0.752	0.535	0.776
	Brown Falcon	2.012	2.668	3.140	0.683	0.685	0.825
Species present in 2 guilds	Spotted Harrier	1.544	1.511		0.602	0.776	
	Collared Sparrowhawk		2.369	2.587		0.696	0.768
	Australian Hobby		2.440	3.243		0.657	0.829
	Peregrine Falcon	1.903		3.150	0.721		0.693
Species present in 1 guild only	Black-shouldered Kite			0.695			0.290
	Black Kite	1.175			0.406		
	Black-breasted Buzzard		3.237			0.743	
	White-bellied Sea-Eagle			2.422			0.874
	Black Falcon	1.816			0.617		
	Grey Falcon		1.364			0.656	
	Southern Boobook			2.659			0.676
	Average	*1.580*	*2.382*	*2.744*	*0.584*	*0.703*	*0.761*
	St Dev	*0.362*	*0.610*	*0.700*	*0.118*	*0.079*	*0.165*

Table 3

Main and secondary dietary items (with emphasis on size) of the five solo predators and the three feeding sub-guilds in the Canberra Region.

#	Species	Feeding guild or solo predators	Main items	Secondary items
1	Black-shouldered-Kite	Solo (very specialised)	House Mice	
2	Wedge-tailed Eagle	Large-medium mammals and large birds sub-guild	Macropods and Lagomorphs	Large ground-feeding birds (ducks, galahs, and magpies, most 300–850 g)
2	Little Eagle		Rabbits	Medium and large birds (most 90–350 g)
2	Whistling Kite		Rabbits	Very diverse: medium-large mammals, birds, fish, crustaceans, insects
3	White-bellied Sea-eagle	Solo (specialised)	Aquatic prey: very large birds (GMPW 629.2 g – mainly ducks and egrets) and fish	Large reptiles (turtles and dragons)
4	Peregrine Falcon	Solo (specialised)	Medium and large birds (most 250–650 g)	
5	Australian Hobby	Solo (specialised)	Medium-small birds (GMPW 53.52 g)	Bats and flying insects
6	Brown Goshawk	Small vertebrates and insects (50% items) sub-guild	Small-juvenile rabbits	Medium-small birds (11–350 g) and insects
6	Brown Falcon		Small-juvenile rabbits and rodents	Medium skinks, medium-sized Psittaciformes (63–335 g) and invertebrates
7	Collared Sparrowhawk	Solo (generalist)	Insects and small forest-bush birds (Pigeons, rosellas and House Sparrow)	
8	Nankeen Kestrel	Insect dominated (>75% items) sub-guild	Insects (Main group coleopterans)	Small skinks (25 g), medium birds (62.43 g – big for its size), small ground mammals
8	Southern Boobook		Insects (Main group coleopterans)	Spiders, moths, small bats. Small birds.

have a significantly more diverse diet in 12 of the 15 potential comparisons; these being the seven species shared with Mildura and five of the eight shared with the Northern Territory. The three exceptions were the Collared Sparrowhawk, Whistling Kite, and Brown Goshawk, for which dietary diversity showed no significant difference. In accordance with the overall trend, it is also noteworthy that in the three cases of raptors shared by only two guilds, species from the Canberra region also had higher dietary diversity, two shared with the Northern Territory (Collared Sparrowhawk and Australian Hobby, Table 2), and the one shared with Mildura (Peregrine Falcon, Table 2). The same tendency was observed in the Evenness Index (Canberra: 0.833 ± 0.060; Mildura 0.583 ± 0.121; NT 0.702 ± 0.100 in the NT).

Regarding dietary overlap, the Pianka Index differed significantly among the three Australian studies (F = 25.32; df = 2, 163; P <0.001). Multiple comparisons showed that raptor species around Canberra had significantly smaller dietary overlap than the other two sites (25.9%, SD = 23.5%, n = 66); but also that the birds in the Northern Territory (43.8%, SD = 26.6%, n = 55: Aumann 2001b) had significantly smaller overlap than the ones at Mildura (61.5%, SD = 42.3%, n = 45: Baker-Gabb 1984a), with all indices calculated at the highest resolution possible (most dietary items identified to species level).

DISCUSSION

The raptor guild around Canberra was very diverse in terms of diet, as shown by its trophic structure, with only three clear sub-guilds identified and five species that did not fit a particular sub-guild, and with little overlap in the diet of the various species. Table 3 summarises the trophic structure of the guild, highlighting the primary and secondary prey of each predator, as well as the influence of prey size. The three sub-guilds identified were species feeding on (i) mammals and large birds (Wedge-tailed Eagle, Little Eagle, Whistling Kite). This sub-guild also includes the two species most likely to include carrion among their food items, the Whistling Kite and Wedge-tailed Eagle (Olsen *et al.* 2010, 2013a,b); (ii) small vertebrates and insects (Brown Goshawk, Brown Falcon); and (iii) mainly insects (Nankeen Kestrel, Southern Boobook). The other five raptors were single species variously specialising in rodents (Black-shouldered Kite); aquatic prey (White-bellied Sea-Eagle); small birds and insects (Collared Sparrowhawk); aerial small birds, insects and bats (Australian Hobby); and birds (Peregrine Falcon). Evidence suggests three main mechanisms behind the trophic structure of the guild (discussed below). There were three cases of intraguild predators, one of which, the Wedge-tailed Eagle, consumed a high proportion of other raptors when compared to the literature.

a) *Trophic Structure: Feeding Guilds*

Mechanisms behind the Trophic Structure

Evidence suggests there are at least three alternative, and perhaps complementary, mechanisms shaping the structure of the feeding guild in the Canberra region: 1) minor dietary overlap by distributing available prey by size; 2) opportunistic foraging behaviour by taking advantage of the local conditions: an ample prey base and diverse vegetation and land uses; and 3) Intraguild Predation (IGP) pressures. We discuss each in more detail.

The small dietary overlap in Canberra, particularly in comparison with other Australian guilds sharing many of the same species, suggests a resource partitioning strategy as one pathway of avoiding competition (see references in Charter *et al.* 2018), and the overlap matrix and cluster analysis based on the Pianka Index show evidence of this split. Axis 2 on the ordination plot (Fig. 2) is primarily influenced by prey size, a relationship that has been found before (Jaksic and Braker 1983) and is partially responsible for the resource partitioning. Table 3 shows a compilation of the twelve species divided on the three sub-guilds and the five solo hunters, indicating the main and secondary dietary items and emphasising the size differential. This trend is also observed in GMPW of each raptor (see Table 1 in Fuentes *et al.* 2024). The Australian Hobby and Brown Goshawk had similar-sized birds in their diet (around 140 g), but Hobbies focused on species abundant in open areas, while Goshawks focused on bush and forest or ecotone species, such as the Common Starling, Striated Pardalote *Pardalotus striatus,* and Superb Fairy-wren *Malurus cyaneus*. The Black-shouldered Kite and Southern Boobook ate similar-sized mammals (15–18 g), but the kite takes almost exclusively House Mice whereas the owl takes other rodents as well as small bats. The Nankeen Kestrel and the Southern Boobook show similar GMPW and both species ate many insects and similar-sized birds (40–60 g), but the Kestrel captures much larger mammals (93.1 g compared to 18.1 g for the owl) and some unusually large birds for its size (64.1 g), having the largest avian prey to predator ratio of the guild (0.36). There is a clear overlap in the food habits of these species, belonging to the same feeding sub-guild (adding to the fact that they are also the two main hollow-nesters of the guild). Although asynchronous in their habits, these similarities warrant a closer comparison of diet, foraging, and nesting habitats. In an unusual display of overlap within the guild, Peregrines, Brown Falcons and Little Eagles ate similar-sized birds (140–180 g). Although we only had three sufficiently large samples to calculate reptilian GMPW, it is noteworthy that the three species ate reptiles of very different sizes, with the Brown Falcon capturing the largest items (42.1 g), followed by the Nankeen Kestrel (25.0 g) and Brown Goshawk (17.6 g).

Secondly, overlap does not always indicate direct competition, since raptors are opportunistic predators and often exploit prey populations when they are abundant (Newton 1986; Charter *et al.* 2018), thus reducing the detrimental effects of competition. Charter *et al.* (2018) found that when the dietary overlap is high and raptors are more abundant, it was often an outcome of a local super abundant resource. There is some evidence of this last scenario at Canberra where the raptor guild seems to have an ample prey base available*,* which relates to the various vegetation types and/or land uses available. The Canberra study area includes a mixture of urban parks and reserves, farmland, river systems, dams and non-urban nature reserves (Namadgi National Park), and it has been described in previous papers as eucalypt-dominated open forest (in Canberra Nature Parks), woodland, open woodland and tree-dotted pasture, with River She-oak *Casuarina cunninghamiana* gallery forest on the Molonglo River (see Olsen *et al.* 2006a,b, 2010, 2013a; Fuentes *et al.* 2007). This myriad of habitat conditions produces many ecotones and buffer zones, which are among the top places for raptor abundance and richness (Piana and Mardsen 2012) and which give some raptor species opportunities to ambush-hunt from the edge of one vegetation type into another (Olsen *et al.* 2006b). Raptors in this mixture of suburban and wild habitats could benefit from the advantages of both, the wide prey base available to them in pristine habitats and the artificially increased abundance of some suburban/urban species (Korpimäki *et al.* 1990). There is evidence of some of the main prey species, such as the Eastern Grey Kangaroo *Macropus giganteus*, being abundant or superabundant in the Canberra region during the study period (Reardon 2003, Fletcher 2003). The same applies to many bird species, among which we have three cases. Firstly, some bird species have increased in abundance to historically high numbers at the time of the study (Veerman 2003), including the Crested Pigeon *Ocyphaps lophotes*, Crimson Rosella, Sulphur-crested Cockatoo, Magpie-lark *Grallina cyanoleuca*, Australian Magpie, Australian Raven, Little Raven *Corvus mellori* and Common Myna *Acridotheres tristis*. Secondly, we have species that have been locally abundant for a long time, including the Galah and Eastern Rosella. Finally, although the Common Starling has declined in numbers recently, its abundance is still high (Veerman 2003). These abundances are crucial since birds were principal prey items for eight of the 12 raptors and were, by taxon, the most important vertebrate group for the Canberra guild (34.2 %, n = 1359), and the taxa with the largest contribution to biomass (Fuentes *et al.* 2024). To make the best use of this ample prey base, the local raptors must be opportunistic and adapt to the available prey and fluctuations in its abundance (Charter *et al.* 2018). The Alternative Prey Hypothesis (APH) predicts that predators switch their diet from a main prey type to alternative prey following a decrease in abundance/availability of the former and go back to the main prey type as soon as its abundance/availability increases (Lack 1954). Evidence of APH is clear in Scandinavian communities, where owls adapt their foraging strategies to the cyclic population of voles (Rodentia, Korpimäki *et al.* 1990). In the Canberra region, however, between-season variation is much less – there is abundant water and vegetation year-round (even in drought) and prey is apparently plentiful all year with no marked abundance cycles. Thus, Canberra raptors (apart from the Black-shouldered Kite) have a diverse diet with no strong dependence on a single prey 'type'. Concerning APH, at least three Canberra raptor species have shown strong evidence of "prey-switching": The Wedge-tailed Eagle switched from a rabbit-based diet (43.8% of items in 1964 to 18% in 2002–04) to a more diverse diet based on rabbits, macropods (1.9 vs 19.4%) and birds (16.5 vs 42.4%; Leopold and Wolfe 1970, Fuentes *et al.* 2007), a pattern that has been relatively stable for the past 16 years (Debus *et al.* 2021). Although the Eastern Grey Kangaroo was the most abundant, there were five species of macropods in the diet of the eagles during this period (Appendix 2 in Fuentes *et al.* 2024). The Brown Goshawk shows a similar trend to the Wedge-tailed Eagle, decreasing the rabbit component of its diet since 1991–92 (18.2% to 7.9% of total items and 66.4% to 46.0% of biomass) and increasing the bird component (33.3% to 43.6% biomass), although samples sizes of the earlier exploration were small (Olsen *et al.* 2008, 2006b). The Peregrine Falcon and Australian Hobby both compensated for the decline of the European Starling between 1991–92 and 2002–03 by taking a greater variety of bird species, particularly small native ones, rather than taking more of one or two other major prey types (Olsen *et al.* 2008). Only long-term monitoring could indicate if some of these raptors return to their previous/historical prey or how they respond to fluctuations in the prey populations exploited in the present study.

Finally, the pressures exerted by predation, particularly from species within the guild (hence the term intraguild predation), are important in understanding the formation and functioning of raptor guilds (Sergio and Hiraldo 2008). IGP is the complex interaction between members of a guild that compete for resources and also kill each other. In this study we found five cases of IGP, with the Brown Falcon (*n* = 1) and Peregrine Falcon (*n* = 1) as two of them; but chief among IG predators in the area is the Wedge-tailed Eagle (*n* = 3), a trend still occurring today given that raptors have appeared recently in the diet of this species in Canberra, including the Little Eagle and Brown Falcon (Debus *et al.* 2021; Olsen *et al.* 2006b). We found raptors to account for 0.57% of Wedge-tailed Eagle food items, a very high level of IGP compared to the literature and that could have a great impact on the guild structure and nest selection. Hakkarainen and Korpimäki (1996) found strong nest displacement and reduced reproductive success in Tengmalm's Owls *Aegolius funereus*, even though they accounted for just 0.2% of Ural Owl *Strix uralensis* prey items. Thus, our findings suggest that, in the absence of other major predators (particularly mammalian predators such as the Dingo *Canis familiaris*), the Wedge-tailed Eagle is very likely the local apex predator. IGP affects the predated species in various ways, including decreased site-occupancy, breeding success and survival; nesting away from dominant species; and nesting on suboptimal territories (Hakkarainen and Korpimaki 1996, Sergio and Hiraldo 2008).

Preliminary evidence suggests that Wedge-tailed Eagles have such effects on the Little Eagle in the Canberra region. The number of Wedge-tailed Eagle breeding pairs has increased since the 1960s and has recently been very stable and with high reproductive success (Fuentes *et al.* 2007). As a scavenger, the Wedge-tailed Eagle may have been released from widespread poisoning during formerly intense persecution, thus facilitating its population increase. On the other hand, Little Eagle nesting territories have decreased in the region and this species is now considered vulnerable in several Australian jurisdictions including the study area (Olsen and Fuentes 2005, Debus *et al.* 2021, DELWP 2021). Wedge-tailed Eagles are approximately four times heavier than Little Eagles, equivalent to what the review of Sergio and Hiraldo (2008) found top intraguild predator killer species to be. The GMPW of birds captured by Wedge-tailed Eagles in the present study was 312.2 g (range 63–1300 g, discounting an unidentified thornbill, *n* =184). This range would include all the raptor species in the Canberra guild except the Sea-Eagle. There were size preferences however, with the Wedge-tailed Eagle mostly capturing avian prey of two size cohorts: birds between 300 and 350 g (with Galah, Magpie, and Rock Dove *Columba livia* as the main species) and birds between 640 and 850 g (mainly Sulphur-crested Cockatoo, Australian Wood Duck and Australian Raven). The former group accounted for 74 prey items (40.2% of birds taken and 30.0% of bird biomass) while the latter accounted for 20% of birds taken and 37.1% of bird biomass. Interestingly, the Peregrine Falcon and Little Eagle fall within this second group, and both have been found as Wedge-tailed Eagle food items in the area (Debus *et al.* 2021; Olsen *et al* 2006b and this study). Contrastingly, only seven birds were captured in the 350–650 g cohort (3.80% of total birds and 4.49% bird biomass), and four of them were juvenile Australian Ravens. These two avian prey size cohorts are probably related to differences in prey selection by male (prey 300–350 g) and female (prey 640–850 g) Wedge-tailed Eagles – an interesting pattern that merits exploration. Wedge-tailed Eagles would also benefit from preying on and excluding Little Eagles by removing a direct competitor (both belong to the same feeding sub-guild) of another main prey item, the European Rabbit, which is one of the main benefits derived from intraguild predators (Sergio and Hiraldo 2008). Wedge-tailed Eagles have been recorded chasing adult Little Eagles and destroying their nesting attempts, ultimately provoking the latter to abandon the territory (Rae *et al.* 2020). Eagle Owls *Bubo bubo* and Ural Owls have shown a similar predation-competitive interaction to Wedge-tailed Eagles and Little Eagles in the owl guild in Fennoscandia, where the three times bigger Eagle Owl has also shown more capacity to switch to larger prey, from small *Microtus* voles to the larger hare *Lepus* sp. and large galliform birds (Korpimäki *et al.* 1990) – similar to the observed switch of the Wedge-tailed Eagle from a rabbit-based diet to a diverse macropod-birds-lagomorphs based one in the study area (Fuentes *et al.* 2007). At the same time, the larger Eagle Owl preys on Ural Owls, excludes them from the best nesting sites and makes them use suboptimal nesting territories away from the intraguild predator and ultimately depressing their reproductive success (Hakkarainen and Korpimäki 1996).

Another effect of IGP occurs when the apex predator has a positive effect on the medium to smaller representatives of a raptor community by restricting intermediate mesopredators (Chakarov and Kruger 2010). In part this is an outcome of the minimum preferred size by IG predators: that is, at what size it becomes inefficient to hunt smaller guild members that the apex predator is insufficiently agile to kill regularly (Hakkarainen and Korpimäki 1996). Also, small raptors have been shown to coexist with large ones by having different ecological niches and resource choices (Hakkarainen *et al.* 2004). This way, they gain protection from other predators, even at the potential risk of being preyed upon by the protector (Rebollo *et al.* 2017). Understanding the extent and effect of this protection is crucial, since it is clear that the selective pressure caused by predation is direct and stronger than that caused by competition (Sergio and Hiraldo 2008 and references therein). Studies conducted in the European Alps also found that the diversity of diurnal raptors peaked at medium to high densities of a major intraguild predator (Sergio *et al.* 2003) and that diversity of a nocturnal raptor guild is positively related to the density of the apex predator (Sergio *et al.* 2007). This was the case in our study, since Wedge-tailed Eagles were nesting in suburban Canberra at high densities, with a nearest-neighbour distance of 1.93 km (± 0.90), and 2.72 (± 1.57) in riparian sites (Fuentes *et al.* 2003). Is the diversity of the Canberra raptor guild related to the high density of its main IG predator, the Wedge-tailed Eagle? IGP research on the Australian subcontinent is needed to better understand the impact of such predation on raptor guilds and communities more broadly, particularly in non-arid areas with temperate climates and stable prey bases. Most of the research of this kind comes from Europe and North America and within Australia from arid areas. The relationship between Wedge-tailed Eagles and the Peregrine Falcon is also worth exploring because a case of predation was found in the present study, and because the closely related Golden Eagle (*Aquila chrysaetos*) has shown Peregrines in its diet at various locations around the world (Sergio and Hiraldo 2008). The physical status (health) of the killed/consumed raptors is also an issue that requires further study, since there is evidence that raptors found as prey remains in other species' nests were in poor health or previously injured, or even might have been scavenged (Nick Mooney unpublished data).

b) Dietary Diversity

The assemblage explored here was very diverse in terms of diet, as shown by its trophic structure, with only three clear sub-guilds, five solo hunters and little overlap in the diet of the species. This contrasts with most raptor assemblages studied (see a compilation in Marti *et al.* 1993a) and indicates the diversity of the local prey base as well as opportunistic feeding. Even though the study took place in an extensive drought (Bureau of Meteorology 2023), the Canberra raptors seemed to have a wide variety of available prey from different taxa. Even a mainly coastal species like the Sea-Eagle was a breeding resident in the region, though its numbers were low.

As mentioned earlier, in the Australian subcontinent, the only two studies that include complete raptor guilds during the breeding season come from arid areas: Aumann (2001b) in the southwest Northern Territory and Baker-Gabb (1984a) at Mildura, Victoria. Other studies have dealt with non-breeding raptors (Baker-Gabb 1984b) or have sample sizes greatly biased towards one species (Corbett *et al.* 2014). The raptor guild around Canberra showed a very different pattern from the one in Mildura. Baker-Gabb (1984a) found that the diet of the local guild was dominated by one prey species, the Rabbit, being the most important food source (>40% of prey items) in eight of the ten species. There was no such dominance of any species in the Canberra guild. In fact, except for the Black-shouldered Kite, none of the Canberra raptors had a prey category contributing more than 30% to its diet. The raptor guild studied by Aumann (2001b) was strongly dependent on birds and reptiles, with the Budgerigar *Melopsittacus undulatus* as the main prey species, whereas the diet around Canberra included large contributions from insects, birds and mammals (38.2, 34.2 and 19.9 % respectively), reinforcing the fact that the raptors around Canberra do not have a dominant prey species and have a very diverse diet. The lack of diversity at Mildura was likely heavily influenced by the simplified habitat in the area. Contrasting with the diverse habitat in the Canberra region mentioned above, the habitat at Mildura consisted primarily of narrow (~20 m) laneways containing remanent old-growth mallee alongside largely cultivated (>1000 ha) wheat paddocks (Baker-Gabb 1984a and pers. comm.).

An interesting trend found is the importance of Psittaciformes (parrots) as a food source in all three studies. In Canberra, this taxon alone accounted for 18% of all food items by number (n = 443 MNI Psittaciformes) and 17.6 % of all biomass consumed by the raptor guild. This group was present in the diet of all species, and it was important in eight of them in terms of MNI (>5%: Table 4). Regarding biomass, eight of the twelve guild species derived more than 10% biomass contribution from this group, ranging from 11.2 to 44.3% (Table 4), with three species as main prey: Crimson and Eastern Rosellas and Galahs (75.8% of all psittaciform prey, n = 336 MNI); all of them also stand out in the NMS ordination plot of prey vs predator species (see Table 1). Among these species, it is interesting to note the importance of biomass supplementation of Psittaciformes to the diet of Nankeen Kestrels and Southern Boobooks (11.2 and 13.9% of total biomass), both members of the insect-dominated sub-guild. Parallel predation on this taxon was found in the Northern Territory, where the dependence of the raptors on Budgerigars was striking, accounting for 20.2–66.7% of all vertebrate prey items for six species (Aumann 2001b). Similarly, the Galah was a major prey item in Victoria, present in the diet of seven species and important in four of them. The role of Psittaciformes as major food for Australian raptors needs further study.

Table 4

Percentage contribution of Psittaciformes to the number of items (MNI) and total biomass to the raptor species of the Canberra Region.

Species	% MNI	% Biomass
Black-shouldered Kite	0.6	8.5
Whistling Kite	12.2	12.4
White-bellied Sea-Eagle	3.5	2.0
Brown Goshawk	9.6	12.8
Collared Sparrowhawk	6.4	28.0
Wedge-tailed Eagle	14.3	7.9
Little Eagle	20.0	11.3
Brown Falcon	7.5	8.5
Australian Hobby	19.4	32.6
Peregrine Falcon	39.0	44.3
Nankeen Kestrel	1.9	11.2
Southern Boobook	0.9	13.9

CONCLUSION

Canberra has a raptor community of 14 breeding species, the 12 reported in our study plus the Powerful Owl *Ninox strenua* and Swamp Harrier *Circus approximans*, both confirmed breeding in the area in low numbers (Olsen 1992; Olsen and Rehwinkel 1995). The Barn Owl is a common resident, but breeding pairs have not been confirmed. Except for the White-bellied Sea-Eagle, the 11 species all breed inside the city limits, in an urban or semi-urban context, a number unrivalled in any other major urban centre in the world (Bird *et al* 1996; Boal and Dykstra 2018; Olsen and Olsen 1990).

For a complete understanding of the status of the community, other factors such as species abundance, diversity, productivity and reproductive success need to be considered. “Cultural” sites, or raptors breeding near urban areas, have sometimes been reported to breed more often (i.e., in more years) and produce larger broods than their ‘wild’ counterparts (Korpimäki *et al.* 1990). Evidence suggests this to be the case for the Canberra guild, where six species (Black-shouldered Kite, Whistling Kite, White-bellied Sea-Eagle, Wedge-tailed Eagle, Little Eagle, and Nankeen Kestrel) had high reproductive success during the study period (Fuentes 2005), four had average success compared with literature records and previous time periods in the study area (Brown Goshawk, Brown Falcon, Peregrine Falcon and Southern Boobook: Fuentes 2005), and only the Collared Sparrowhawk had lower reproductive success and productivity than average.

Hence, the Canberra region has a diverse raptor guild, with almost all members breeding in an urban context and having above-average or average reproductive success. In areas with communities as remarkable as this, it becomes even more crucial to prioritize conservation efforts through a comprehensive community-based approach, including the local raptor guild and its prey base. This approach may produce complicated management decisions for species that have shown declines, such as the Little Eagle (Debus *et al.* 2021, DELWP 2021). It is likely to have extensive conservation implications beyond raptor guilds, since raptors in Australasia are often apex predators, particularly in the absence of mammalian predators. As such, they are excellent bioindicators of ecosystem balance (Jimenez *et al.* 2007), and outstanding ecological monitors.

Further analysis must include habitat and environmental factors related to nest and territory selection to understand the main factors behind the structure of raptor guilds. Future studies should emphasise understanding predator-prey dynamics and interspecific relationships (particularly IGP) among predators, in order to optimise management and conservation of the full community. The role of other predators in the area, such as introduced Cats *Felis catus* and Foxes *Vulpes vulpes*, should also be investigated.

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