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Diets of breeding Brown Goshawks *Accipiter fasciatus* and Collared Sparrowhawks *A. cirrocephalus* near Canberra, Australia and comparisons with other regions and raptors

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We examined 80 Brown Goshawk *Accipiter fasciatus* and 27 Collared Sparrowhawk *A. cirrocephalus* collections of prey remains and pellets. They were obtained from 2002 to 2010 within 30 km of Canberra (ACT) from 36 Goshawk and nine Sparrowhawk breeding events in 24 and six territories, respectively. For Brown Goshawks, 412 prey individuals and six species not previously found in the species' diet were recorded; for Collared Sparrowhawks, 301 prey individuals and seven 'new' species were recorded. Dietary overlap was 43.5%, including 12 bird species taken by both hawks. In addition to European Rabbits *Oryctolagus cuniculus*, Brown Goshawks took birds (especially parrots, House Sparrows *Passer domesticus* and Common Starlings *Sturnus vulgaris*), reptiles and insects. Collared Sparrowhawks took mostly birds (especially House Sparrows, rosellas *Platycercus* spp., Crested Pigeons *Ocyhaps lophotes* and Common Starlings) and insects, but no mammals or reptiles. Sparrowhawks did not consume rabbits, a main prey item of Brown Goshawks and other raptor species in the Canberra area. Standardised Food Niche Breadth and the Shannon Diversity Index were similar for the diets of the two hawks, but Brown Goshawks captured larger prey, which was reflected in the 2.7 times difference in Geometric Mean Prey Weight between the species (Brown Goshawks 18.35 g; Collared Sparrowhawks 6.92 g), which resembled the 2.8 times disparity in mass between males of the two species (Collared Sparrowhawks 126 g; Brown Goshawks 350 g). Surprisingly, Sparrowhawks took seven Australian Magpies *Cracticus tibicen* (albeit probably juveniles), a species as large as the female Sparrowhawk. Both hawks take a much higher proportion of insect prey than do their ecological counterparts in North America, the Cooper's Hawk *Accipiter cooperii* and Sharp-shinned Hawk *A. striatus*, and the Eurasian counterpart of the Collared Sparrowhawk, the Northern Sparrowhawk *A. nisus*.

INTRODUCTION

Australia has four accipiter-type hawks, the Brown Goshawk *Accipiter fasciatus*, Collared Sparrowhawk *A. cirrocephalus*, Grey Goshawk *A. novaehollandiae* and Red Goshawk *Erythrotriorchis radiatus*. The first two are extensively sympatric throughout mainland Australia, Tasmania and the New Guinea region. The mean weights of Brown Goshawk males and females are ~350 g and 570 g, respectively; male Collared Sparrowhawks average ~126 g and females 240 g (Marchant and Higgins 1993; Olsen 2014). As female Collared Sparrowhawks average ~42% of the mass of female Brown Goshawks, male Collared Sparrowhawks average ~36% of the mass of male Brown Goshawks, and male Collared Sparrowhawks average ~22% of the mass of female Brown Goshawks, we would predict that there should be differences in the size of prey taken by the two species.

The diet of Brown Goshawks has been reasonably well studied in Australia, although there are few studies of the diet of urban individuals. In a small sample from Canberra, they took birds (60% by no.), insects (23%) and mammals (European Rabbits *Oryctolagus cuniculus* 18%), the last-named dominating by biomass (66%) (Olsen *et al*. 2006a). In a small sample from Darwin (Northern Territory), Brown Goshawks took birds (53%), reptiles (37%) and mammals (rodents, 10%) (Riddell 2015). In contrast, the ecology, including the diet, of the closely related Collared Sparrowhawk is poorly known.

The overlap in prey used by the two hawk species has been studied in detail only in arid central Australia (Aumann 2001), although other studies compared prey lists or records for the two species within a given region (Czechura *et al*. 1987; Debus *et al.* 1993). In south-eastern Australia broadly, Brown Goshawks take a wide variety of prey including birds, mammals, reptiles, insects and crustaceans, with birds often dominating numerically, but mammals (especially rabbits) often dominating by biomass (Baker-Gabb 1984a,b; Czechura *et al.* 1987; Aumann 1988). In the tropics, a similar variety of prey (including amphibians) is taken, with mammals or reptiles figuring strongly, as well as birds (Aumann 1990; Burton and Olsen 1997a,b; Aumann *et al.* 2016). By contrast, in south-eastern Australia Collared Sparrowhawks take predominantly small birds (80–90% by no., almost 100% by biomass; 80–90% of avian prey weighing <50 g) and some insects, but rarely mammals or reptiles (Czechura *et al.* 1987; Debus *et al.* 1993; Barnes and Debus 2014).

In breeding sympatry in central Australia, Brown Goshawks took mammals, birds, insects and reptiles, the last-named dominating numerically and especially by biomass (80%), whereas Collared Sparrowhawks took small birds (87% by no., mostly <50 g; >99% by biomass) and insects. Brown Goshawks

had much higher indices of dietary diversity and evenness, and dietary overlap between the two species was 46% (Aumann 2001).

Brown Goshawks and Collared Sparrowhawks coexist in the Canberra region, often breeding within 5 km of each other, although Brown Goshawks may take over Sparrowhawk territories and so displace them (Olsen 2014). As both hawks consume birds and insects, ecological theory on niche differentiation and segregation suggests that there is therefore potential for interspecific competition, especially in times of scarce resources (May 1973; Schoener 1974; Begon *et al.* 1990). According to such theory, coexisting diurnal raptors should, for example, select different prey species or sizes.

Studies of dietary relationships between raptor species are often performed at a regional as opposed to a local scale, and it is assumed that niche overlap indicates potential competition (Jaksić 1983; Jaksić and Delibes 1987; Marti *et al.* 1993; Burton and Olsen 1997a; Garcia and Arroyo 2005; Olsen *et al.* 2006a). However, to fully understand the effect of competition, studies should also occur at a local scale, between neighbouring pairs (Steenhof and Kochert 1985, 1988; Marti *et al.* 1993). Studies of this sort are less common (e.g., Nilsson 1984), and few have been undertaken for Australian raptors (Burton and Olsen 1987a,b; Aumann 2001; Olsen *et al*. 2006a,b, 2008, 2010, 2013a,b). Our main aim was therefore to examine the dietary relationships of Collared Sparrowhawk and Brown Goshawk pairs breeding in the same habitats in and near Canberra, and calculate indices of dietary overlap to assess potential competition between them.

Raptors elsewhere in the world are commonly used as models for the feeding ecology of Australian raptors (Olsen 2104), so our second aim is to draw dietary comparisons with ecological equivalents in other continents: (1) two sympatrically breeding hawks in North America – Cooper's Hawk *Accipiter cooperii* (male ~341 g, female ~528 g), approximating the Brown Goshawk, and the much smaller 'sparrowhawk'-type Sharp-shinned Hawk *A. striatus* (male ~101 g, female ~177 g) (Clark and Wheeler 1987), and (2) the Northern Sparrowhawk *A. nisus* (male ~150 g, female ~290 g), approximating the Collared Sparrowhawk (Newton 1986).

STUDY AREA AND METHODS

We searched an area within 30 km of central Canberra for occupied territories of both hawk species and for nests containing eggs or young. We defined an occupied nesting territory as an area containing one or more nest sites within the home range of a pair (Steenhof 1987). Male Brown Goshawks and Collared Sparrowhawks had 'plucking roosts', often in a live tree or on a dead fallen log 50–150 m uphill from the nest tree, and females had 'guard trees', often adjacent to, or uphill from, nest trees. We searched for these roosts and collected pellets and prey remains beneath them, under nests, and inside nests at least once during the nestling stage and once after young had fledged. Between 2002 and 2010, we found six Collared Sparrowhawk territories and 24 Brown Goshawk territories that were re-used annually and revisited by us during the study.

The edges of the city and surrounding areas are mainly farmland and grazing paddocks. Most of the undeveloped hills and ridges in and around urban Canberra are protected nature reserves that collectively cover an area of 5 720 ha. The major vegetation associations in these reserves are dry sclerophyll forest, open savannah and woodland. Two protected corridors bordering the Upper Molonglo River and Murrumbidgee River are up to 4 km wide and run along the entire length of the ACT (66 and 18 km, respectively). Riparian vegetation is dominated by River She-oaks *Casuarina cunninghamiana*, Scribbly Gum *Eucalyptus rossii*, Brittle Gum *E. mannifera*, Red Stringybark *E. macrorhyncha* and Blakely's Red Gum *E. blakelyi* woodland, with Red Box *E. polyanthemos* and Yellow Box *E. melliodora* in more open areas (NCDC 1988). The understorey has abundant tussock grasses *Poa* spp., with the shrub *Cassinia longifolia* dominating more open areas. A more complete description of the habitat and climatic parameters can be found in Taylor and COG (1992).

Prey collection and analysis

We combined pellet contents, prey remains and occasional observations of adults with prey to calculate a Minimum Number of Individuals (MNI) for the prey of both accipiter species (see Olsen *et al.* 2008 and Olsen 2014 for the rationale). Pellets and prey remains were stored separately, and each pellet was placed in an individual sealed plastic bag. We identified and counted prey body parts to estimate the MNI in a pooled sample of pellets, prey remains and observations to minimise biases in the food estimations (Collopy 1983; Seguin *et al.* 1998; Simmons *et al.* 1991). Feathers were identified through comparison with collections and museum specimens when necessary. Bones, hair and scales were identified by microscopy (following Brunner and Coman 1974 for mammalian hair) and by comparison with museum reference material. Herein, 'prey item' refers to *n* prey individuals (MNI), 'prey species' is self-evident, and 'prey [taxonomic] class' refers to the prey category of mammal, bird, reptile or invertebrate.

Dietary analyses

To estimate the MNI in the pooled sample of pellets and prey remains we counted teeth, skulls, bones, feet, tails, beaks, primaries and tail feathers, as in Olsen *et al*. (2006a,b). We did not assume that one pellet represented one prey bird, mammal or reptile, because adults and nestlings share prey items, take more than one meal from some large items, and more than one prey species was often found in each pellet. For example, in a Brown Goshawk sample containing rabbit fur in three pellets but only one rabbit tail and one rabbit mandible, we would tally one rabbit as the MNI. To estimate dietary biomass, we multiplied the MNI by the average mass of each prey species. The mean or median mass of most prey types were obtained from the literature (Appendix 1). We used several dietary metrics to describe the overall diet of the two species.

As the overall mean prey weight is sensitive to the presence of very large or very small prey, we used Geometric Mean Prey Weight (GMPW) (Jaksić and Braker 1983; Marti 1987) to compare prey sizes of the two hawks (see Olsen *et al.* 2008 and Olsen 2011 for a detailed explanation and rationale).

Diversity in a raptor's diet has two components: richness (the number of prey categories, species or other classification) and evenness (how uniformly represented the various kinds of

Table 1

Frequency and biomass of prey items in the diet of Brown Goshawks and Collared Sparrowhawks breeding near Canberra.

Prey class	Brown Goshawk			Collared Sparrowhawk		
	n	Frequency (%)	Biomass (%)	*n*	Frequency (%)	Biomass (%)
Mammals	64	15.57	61.4	0	0	0
Birds	164	39.66	36.7	140	46.2	98.7
Reptiles	26	6.33	1.5	0	0	0
Invertebrates	158	38.44	0.3	161	53.5	1.3

prey are). Thus, a raptor's diet has high diversity (i.e. represents a broader food niche) if many species are included in nearly equal numbers. Conversely, a diet comprising few species or with species represented in very different abundances has low diversity (i.e. represents a narrower food niche) (Marti *et al.* 2007).

We applied two diversity indices to the prey of each raptor species, Shannon's Diversity Index (Shannon and Weaver 1949) and the Standardised Food Niche Breadth (SFNB) (Colwell and Futuyma 1971). Although both indices measure richness and evenness, Shannon's index is weighted much more towards richness, whilst the SFNB index is more influenced by evenness (Marti, 1987).

The formula of the Shannon Diversity Index is:

$$H' = - \sum p_i \log p_i,$$

where p_i represents the proportional contribution by number of each species in the sample. These values range from one to N, with larger values representing a higher diversity.

The SFNB was calculated as follows:

$$SFNB_{sta} = (N_{obs} - 1) / (N_{tot} - 1)$$

and where N_{obs} is the reciprocal of the Simpson's Index ($N_{obs} = 1 / \sum p_i^2$) and N_{tot} is the total number of prey classes (see Marti 1987).

SFNB values range from 0 to 1, with a higher value demonstrating greater dietary evenness. Prey species that could not be identified were removed from the SFNB analyses.

To explore food overlap between Collared Sparrowhawks and Brown Goshawks we used the Pianka Index (Pianka 1973):

$$O = \sum p_i q_i / (\sum p_i^2 \sum q_i^2)^{1/2}$$

where p_i and q_i represent the proportion of species i in the diet of the species p and q. Pianka's index ranges from 0 (no overlap) to 1 (complete overlap).

Prey data were obtained from sources with enough dietary information to compare Brown Goshawk and Collared Sparrowhawk dietary metrics with those of other raptor species around the world. In addition, the weight of the predator (= average of male and female weights) was used to compare prey/predator ratios of these raptor species.

RESULTS

Brown Goshawks had a broader diet, obtaining species from each of the four identified prey classes. Birds and invertebrates were caught in similar frequencies and were almost 80% of the 412 prey items recorded (Table 1). Mammals, however, made up 61.4% of the total biomass and were almost exclusively rabbits (mostly juveniles). Brown Goshawks preyed on 29 identified bird species, although they tended to concentrate on parrots and Common Starlings *Sturnus vulgaris* (Appendix 1). Almost half of the insects caught were Red-eye Cicadas *Psaltoda moerens*, and skinks (Scincidae) made up most of the reptiles.

Collared Sparrowhawks preyed only on birds and invertebrates (Fig. 1). Although they took slightly more insects by frequency, birds made up 98.7% of the total biomass. Twenty-six identified bird species were taken, of which House Sparrows *Passer domesticus*, Common Mynas *Sturnis tristis* and Common Starlings were the most prevalent (Appendix 1).

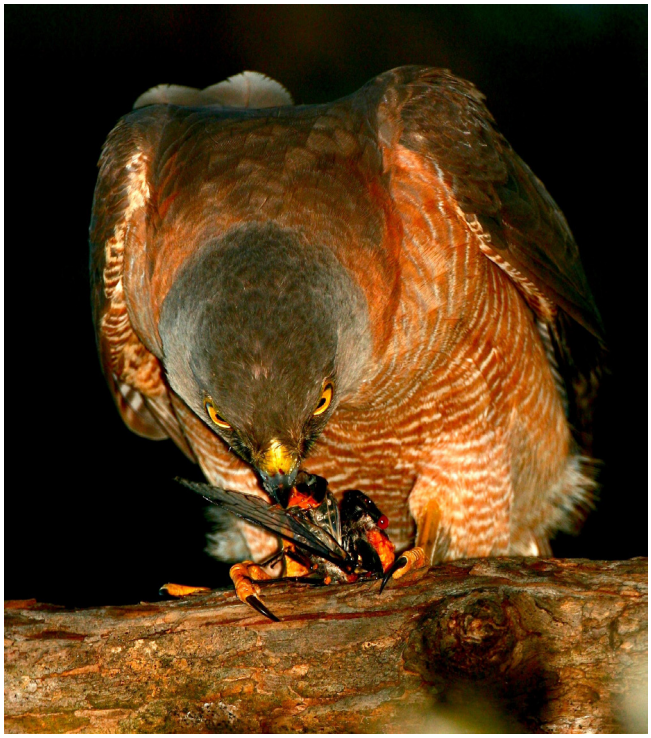

Figure 1. *Female Collared Sparrowhawk near its nest eating a Black Prince Cicada.*

Photo: S. Trost & J. Olsen

The food niche breadth of the two species was similar, with the Brown Goshawk (Shannon's Index 3.26) feeding on slightly more species than the Collared Sparrowhawk (3.08). Collared Sparrowhawks had a slightly higher SFNB (0.35) than Brown Goshawks (0.25), suggesting that they had a greater evenness in their prey. The Pianka index indicated a 43.5% overlap in diet between the two species, almost all of which was birds (Table 2). However, Brown Goshawks captured larger prey, as indicated by the Geometric Mean Prey Weights (Brown Goshawks = 18.4 g, Collared Sparrowhawks = 6.9 g). The difference reflects the mass difference between the two hawk species: Brown Goshawks are about 2.5 times as heavy as Collared Sparrowhawks.

Table 2

Geometric Mean Prey Weight (GMPW), Standardised Food Niche Breadth (SFNB), Shannon Diversity Index and Pianka Index (niche overlap) for Brown Goshawks and Collared Sparrowhawks in and near Canberra.

Species	GMPW	SFNB	Shannon Index
Goshawk	18.35	0.254	3.26
Sparrowhawk	6.92	0.351	3.08

Pianka Index = 0.435 (43.5% overlap in diet between the two species).

Goshawks that we observed hunting tended to ambush prey, such as Eastern Rosellas *Platycercus eximius*, Common Starlings and rabbits, from the edge of woodland, but they also flew through forest to surprise prey, and sometimes slammed into low foliage hunting Crimson Rosellas *Platycercus elegans* and Common Starlings. Quarry close to or in cover was not immune from attack; Goshawks pulled these prey from foliage with their long legs (J. Olsen pers. obs). Sparrowhawks hunted in a similar manner. Brown Goshawk prey included two nocturnal predators, the Southern Boobook *Ninox boobook* and Tawny Frogmouth *Podargus strigoides*.

We identified six prey species not previously recorded for Brown Goshawks: Australian King-Parrot *Alisterus scapularis*, Spotted Pardalote *Pardalotus punctatus*, Red Wattlebird *Anthochaera carunculata*, Noisy Friarbird *Philemon corniculatus*, Black-faced Cuckoo-shrike *Coracina novaehollandiae* and White-winged Chough *Corcorax melanorhamphos* (Appendix 1). We identified seven 'new' prey species for Collared Sparrowhawks: Crimson Rosella, Eastern Rosella, White-browed Babbler *Pomatostomus superciliosus* (a species said to be extinct in the ACT at the time of the collections), Eastern Spinebill *Acanthorhynchus tenuirostris*, Crested Shrike-tit *Falcunculus frontatus*, Australian Magpie *Gymnorhina tibicen* (probably juveniles) and Brown Songlark *Cincloramphus cruralis* (Appendix 1). Twelve bird species overlapped in the diets of the two hawks: Crested Pigeon *Ocyphaps lophotes*, Crimson and Eastern Rosellas, Red-rumped Parrot *Psephotus haematonotus*, Superb Fairy-wren *Malurus cyaneus*, Red Wattlebird, Noisy Friarbird, Magpie-lark *Grallina cyanoleuca*, Australian Magpie, House Sparrow, Common Starling and Common Myna. Woodswallows *Artamus* sp. were also recorded in the Sparrowhawk diet and Dusky Woodswallows *A. cyanopterus* in the Brown Goshawk diet.

DISCUSSION

Studies that explore dietary overlap at the local scale are scarce for diurnal raptors. Nilsson (1984) and Korpimäki (1987) showed that the presence of competitor species at the local scale can affect reproductive success. In the present study, Brown Goshawks and Collared Sparrowhawks had some dietary overlap and had interactions that probably would have favoured the larger Brown Goshawk. However, Brown Goshawks consumed larger prey than did Collared Sparrowhawks, specifically rabbits and medium-sized birds. Collared Sparrowhawks ate fewer medium-sized birds and no rabbits. Although both species took many insects, Sparrowhawks took proportionally more. Both hawks took Common Mynas, a species that is difficult for local Peregrine Falcons *Falco peregrinus* and Australian Hobbies *F. longipennis* to catch (Olsen *et al.* 2008).

Brown Goshawk diet

The diet of Brown Goshawks was similar to that recorded in other studies in south-eastern Australia (Baker-Gabb 1984a,b; Czechura *et al.* 1987; Aumann 1988), being predominantly birds and rabbits by both number and biomass. In the six studies in eastern and south-eastern Australia summarised by Marchant and Higgins (1993), mammals such as rabbits and rats, and birds such as parrots, pigeons and passerines, made up 72–92% of items. They accounted for 99% of biomass. The diet tended to vary across regions, with more rabbits in the diets of Victorian Brown Goshawks than elsewhere (Table 3). In tropical and arid areas, Brown Goshawks tend to eat more reptiles (Burton and Olsen 1997a,b; Aumann 1990, 2001; Riddell 2015; Aumann *et al.* 2016), so, in the future, goshawks near Canberra may take proportionally more reptiles if global warming makes reptiles more available in the goshawk breeding season.

Collared Sparrowhawk diet

Collared Sparrowhawks took more invertebrates than did those in previous studies, 53.5% by number, compared with 12–19% in Tasmania (Czechura *et al.* 1987), 5% in northern New South Wales (Debus *et al*. 1993), up to ~30% in south-east Queensland (inferred from Barnes and Debus 2014), and 13.5% in central Australia (Aumann 2001). This tendency may place Collared Sparrowhawks in competition with Australian Hobbies and Southern Boobooks nesting near them in the ACT (see Trost *et al.* 2008; Olsen *et al*. 2008).

Prey size and raptor body mass

Generally, raptor species' mean mass correlates with the mass of their prey (Jaksić and Delibes 1987; Poole and Bromley 1988; Marti *et al.* 1993), a relationship that is thought to be a mechanism that partitions available food resources (Marti *et al.* 1993). However, the precise relationship between these two metrics can vary intra-specifically among areas and sometimes only the female's mass is correlated with prey size (Reif *et al.* 2004). The two Australian raptor species that we analysed also tended to capture prey that related proportionally to their mass (Table 4). The almost three-fold difference in GMPW between Brown Goshawks (18.4 g) and Collared Sparrowhawks (6.9 g) in this study reflects the three-fold difference in mass between the males of the two species, which do much of the hunting

Table 3

The frequency (percentage by no.) of different prey classes in the diet of Brown Goshawks in different areas of their range (*n* prey items for each location in parentheses).

Prey class	Location							
	Canberra[1]	Melbourne[2]	Melbourne[3]	Mildura[4]	Tasmania[5]	Alice Springs[6]	Queensland[7]	SE Qld[8]
	(307)	(1769)	(126)	(246)	(318)	(272)	(363)	(69)
Mammals	15.5	26.2	60.3	48.7	16.7	4.8	11.8	8.7
Birds	39.8	63.4	37.3	34.5	54.7	25.4	33.1	75.4
Amphibians/reptiles	6.3	1.6	0.0	3.6	2.2	35.3	9.7	4.3
Invertebrates	38.3	8.6	2.4	8.9	26.4	34.6	45.4	11.6

Sources: (1): this study, (2) Aumann 1988, (3) Baker-Gabb 1984b, (4) Baker-Gabb 1984a, (5) Czechura *et al.* 1987 (Tas.), (6) Aumann 2001, (7) Burton and Olsen 1997a, (8) Czechura *et al.* 1987 (Qld)

Table 4

Relative prey size among accipiter species. Geometric mean prey weight (GMPW), mass of raptor (average of male and female) and prey/predator size ratio (GMPW/predator mass) of accipiters discussed in the text. Species ranked by prey/predator ratio. Raptor weights from Johnsgard (1990), Marti *et al.* (1993), Ferguson-Lees and Christie (2001), Debus (2012), Olsen (2014).

Species	Scientific name	Region	Raptor Mass (g)	GMPW (g)	Prey/ predator ratio	Reference
Collared Sparrowhawk	*Accipiter cirrocephalus*	Canberra	183	6.92	0.04	This study
Brown Goshawk	*Accipiter fasciatus*	Canberra	460	18.35	0.04	This study
Brown Goshawk	*Accipiter fasciatus*	Queensland	440	22.0	0.05	Burton and Olsen 1997a
Brown Goshawk	*Accipiter fasciatus*	Aust. tropics	376	21.7	0.06	Burton and Olsen 1997a
Northern Sparrowhawk	*Accipiter nisus*	Nordic countries	204	23.0	0.11	A. Lindén unpubl. data
Sharp-shinned Hawk	*Accipiter striatus*	North America	138	16.1	0.12	Marti *et al.* 1993
Northern Sparrowhawk	*Accipiter nisus*	Europe	204	31.4	0.15	Marti *et al.* 1993
Cooper's Hawk	*Accipiter cooperii*	North America	439	74.4	0.17	Marti *et al.* 1993

during the breeding season. However, there is regional variation in the proportion of invertebrates, birds, mammals and reptiles in the diets of Brown Goshawks (Table 3). Brown Goshawks in the ACT took proportionally more invertebrates than did Brown Goshawks studied in Melbourne or Mildura.

Comparison with hawks in other countries

Brown Goshawks and Collared Sparrowhawks in this study took more invertebrates than did their overseas counterparts. This does not mean that these two species are mainly insectivorous (see above), just that they are *more* insectivorous and less likely to take large vertebrate prey than are their overseas equivalents (Table 4).

Cooper's Hawk and the Brown Goshawk combine birds and mammals in their diet, breed near towns and forage by still-hunting from perches, short attack flights, and extended searching flights along woodland edges or other routes where prey can be surprised (Johnsgard 1990; Debus 2012; Olsen 2014). Both species take mostly small and medium-sized birds, but also small mammals, reptiles and invertebrates (Johnsgard 1990; Marchant and Higgins 1993). There is regional variation among Cooper's Hawks in the proportions of medium-sized birds and small mammals (50–130 g) that they take. These two prey types represent 14–37% and 8–22% of the mass of male and female Cooper's Hawks, respectively (Curtis *et al* 2006).

The Sharp-shinned Hawk is smaller than the Collared Sparrowhawk and less likely to breed in cities than Cooper's Hawk; it is also strongly migratory (Johnsgard 1990; Clark and Wheeler 1987). Sharp-shinned Hawks take mostly small birds, but occasional small mammals and insects too (Bildstein and Meyer 2000), whilst Collared Sparrowhawks in our study took 53.5% invertebrates by number. The Northern Sparrowhawk breeds across Eurasia, but is less migratory than the Sharp-shinned Hawk; it is similar in mass to the Collared Sparrowhawk, and like the latter it often lives in cities. Its diet consists almost entirely of birds averaging 5–120 g for males and 20–120 g for females, although females take some birds up to 500 g or more (Newton 1986). Thus, the Northern Sparrowhawk is a closer ecological equivalent to the Collared Sparrowhawk than the Brown Goshawk.

Among hawks from Australia and elsewhere considered in this study, those with large proportions of invertebrates in their diet took smaller prey relative to their body mass than those which consumed few invertebrates (Table 4). The Northern Hemisphere congeners of the Brown Goshawk and Collared Sparrowhawk, the Sharp-shinned Hawk, Cooper's Hawk and Northern Sparrowhawk, differed from the Australian hawks in having virtually no invertebrates in their diets (Table 5). In both the North American hawks, but particularly Cooper's Hawk, the proportion of reptiles in the diet increases with decreasing latitude i.e. towards warmer and drier regions (Table 5).

Table 5

Frequency (% by no.) of birds, mammals and reptiles in the diets of Sharp-shinned Hawk, Cooper's Hawk and Northern Sparrowhawk.

Species	Location	Birds	Mammals	Reptiles	Source
Sharp-shinned Hawk:	North America	97	3		Storer 1966
	E Oregon	98	2		Reynolds and Meslow 1984
	NW Oregon	97	3		Reynolds and Meslow 1984
	New Brunswick	100	0		Meyer 1987
	Colorado	91	9		Joy *et al.* 1994
	Arizona/New Mexico	97.1	0	2.9	Snyder and Wiley 1976
Cooper's Hawk:	California	26	5	69	Fitch *et al.* 1946
	Maryland	30	70		Janik and Mosher 1982
	New Mexico	60	37	3	Kennedy 1991
	Wisconsin	61	39		Bielefeldt *et al.* 1992
	North Dakota	70	30		Peterson and Murphy 1992
	Wisconsin	71	29		Errington 1933
	Michigan	84	16		Hamerstrom and Hamerstrom 1951
	Washington	90	10		Kennedy 1980
	Arizona/New Mexico	56.5	29.6	13.9	Snyder and Wiley 1976
Northern Sparrowhawk:	England/Scotland	97	3		Newton 1986
	Netherlands	98	2		Opdam 1979
	Norway	97	3		Selås 1993

Invertebrates in the diet

It is interesting that Brown Goshawks and Collared Sparrowhawks took proportionally more invertebrates than did their congeners in the Norther Hemisphere. The hooked beaks and curved talons of raptors are generally not well suited to insectivory and consequently raptors are energetically inefficient when capturing and transporting small invertebrate prey. If birds with straighter beaks find an abundant source of small insects, they can pick up several with their beak and carry them to the nest in one load. In contrast, raptors can only catch flying insects or glean them from leaves using their feet, not their beaks, and carry only one at a time to the nest. Compared with many Northern Hemisphere habitats, Australian vegetation, including eucalypts and *Acacia*, may have more abundant large invertebrates, such as spiders, cicadas, beetles and lepidopterans, in the foliage close to raptors' nests that conceivably facilitate more energetically efficient foraging for these invertebrates (Olsen 2014).

Concluding remarks

Conceivably the more numerous Brown Goshawks in the ACT displace smaller Collared Sparrowhawks. We have observed Collared Sparrowhawks apparently actively avoiding Brown Goshawks by carrying prey from where it was caught, high over a goshawk territory and then descending to their own nest. Brown Goshawks may have been able to utilise expanding rabbit populations in and near Canberra and displace Collared Sparrowhawks simply because of their greater numbers and by nesting close to existing Sparrowhawk nests. The rabbit population increased in the ACT during this study, but there is no evidence that breeding populations of Brown Goshawks in Australia have changed in density in association with changes in rabbit numbers. For example, Steele and Baker-Gabb (2009) monitored changes in raptor abundance before and after the introduction of Rabbit Calicivirus Disease (RCD) in 1995–1996 as a pest control mechanism. The disease caused severe declines in rabbit numbers, but this had no detectable effect on populations of rabbit-dependent species of raptors, including the Brown Goshawk. Nevertheless, Brown Goshawks are declining in south-eastern Australia, presumably for other reasons, whereas Collared Sparrowhawk numbers appear to be more stable (Cooper *et al.* 2014). Pindone and other measures used to control rabbits may poison raptors, including Brown Goshawks (Olsen *et al*. 2013c).

Seasonal or annual variation in prey availability (e.g. during drought or good rains when certain prey may be sparse or abundant) may affect niche differentiation among raptors. Dietary overlap among co-habiting hawk species may increase or decrease in parallel with such variation in resource abundance. However, our data could not examine this, as they were obtained from just one region over a short period of time. In addition, the Collared Sparrowhawk data were from a small number of territories and it is possible that pairs had marked individual food preferences which could bias interpretations of dietary overlap. Future studies should ideally compare equal numbers of breeding Collared Sparrowhawks and Brown Goshawks, something we could not achieve because there were relatively fewer Collared Sparrowhawk territories in the Canberra region.

Although our ability to draw conclusions from our study was somewhat limited by the disparity in sample sizes for the focal species (Krebs 1998), we nonetheless believe that this study makes a valuable contribution to our knowledge of the breeding ecology of Australian raptors. For instance, our local-scale dietary comparison between the Brown Goshawk and Collared Sparrowhawk confirms the dietary differences identified in previous broader-scale studies (Czechura *et al.* 1987; Aumann 2001).

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Appendix 1

Number of prey items and their contribution to the dietary mass of Brown Goshawks and Collared Sparrowhawks breeding near Canberra, 2002–2010.

Brown Goshawk:				
Common name	Scientific name	Prey weight (g)	Total no. items	Biomass (g)
MAMMALS				
Common Brushtail Possum	*Trichosurus vulpecula*	2625	1	2625
House Mouse	*Mus musculus*	18	3	54
European Rabbit	*Oryctolagus cuniculus*	1000	9	9000
European Rabbit juvenile		400	51	20400
BIRDS				
Rock Dove	*Columba livia*	308	2	616
Crested Pigeon	*Ocyphaps lophotes*	210	7	1470
+Australian King Parrot	*Alisterus scapularis*	211	1	211
Crimson Rosella	*Platycercus elegans*	135	16	2160
Crimson Rosella juvenile		131	13	1703
Eastern Rosella	*Platycercus eximius*	105	18	1890
Eastern Rosella juvenile		105	3	315
Red-rumped Parrot	*Psephotus haematonotus*	61	2	122
Southern Boobook	*Ninox boobook*	300	1	300
Tawny Frogmouth	*Podargus strigoides*	330	1	330
Dollarbird	*Eurystomus orientalis*	134	3	402
Superb Fairy-wren	*Malurus cynaeus*	10	7	70
+Spotted Pardalote	*Pardalotus punctatus*	9	1	9
Striated Pardalote	*Pardalotus striatus*	12	7	84
+Red Wattlebird	*Anthochaera carunculata*	108	1	108
+Noisy Friarbird	*Philemon corniculatus*	109	2	218
Noisy Miner	*Manorina melanocephala*	110	1	110
Robin sp.	Fam. Petroicidae	15	2	30
Magpie-lark	*Grallina cyanoleuca*	90	8	720
Magpie-lark juvenile		90	4	360
+Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	105	2	210
Dusky Woodswallow	*Artamus cyanopterus*	39	1	39
Dusky Woodswallow juv.		39	1	39
Grey Butcherbird	*Craticus torquatus*	100	2	200
Australian Magpie	*Gymnorhina tibicen*	329	1	329
Pied Currawong	*Strepera graculina*	270	2	540
Australian Raven	*Corvus coronoides*	650	1	650
Raven sp.	*Corvus* sp.	590	1	590
+White-winged chough	*Corcorax melanorhamphos*	330	2	660
House Sparrows	*Passer domesticus*	20	1	20
Red-browed Finch	*Neochmia ruficauda*	11	4	44
Silvereye	*Zosterops lateralis*	20	1	40
Common Starling	*Sturnus vulgaris*	75	23	1725
Common Starling juvenile		75	3	225
Common Myna	*Acridotheres tristis*	116	4	464
Unidentified birds		156	14	2184

Appendix 1 (continued)

Brown Goshawk: (continued)				
Common name	Scientific name	Prey weight (g)	Total no. items	Biomass (g)
REPTILES				
Jacky Lizard	*Amphibolurus muricatus*	60	2	120
Small dragon lizard	*Amphibolurus* sp.	60	7	420
Skink sp.	Scincidae	15	17	255
INSECTS				
Christmas Beetle	*Anoplognathus viriditarsus*	1	18	18
Christmas beetle	*Anoplognathus* sp.	1	16	16
Chrysomelid beetle	Chrysomelidae	1	4	4
Diaphonia beetle	*Diaphonia dorsalis*	1	3	3
Stag beetle Lucanidae	*Lamprisma latreille*	1	3	3
Other scarab beetles	*Scarabaeidae*	1	3	3
Other beetles	*Coleoptera*	1	20	20
Red-eye Cicada	*Psaltoda moerens*	1	73	73
Butterfly/moth	Lepidoptera	1	1	1
Cockroach	Blattoidea	1	2	2
Grasshopper	Acrididae	1	7	7
Grasshopper	Orthoptera	1	6	6
Unidentified insects	Insecta	1	2	2
Total			**412**	**52222**

+Novel bird species for Brown Goshawk

Collared Sparrowhawk:				
Common name	Scientific name	Prey weight (g)	Total no. items	Biomass (g)
BIRDS				
Crested Pigeon	*Ocyphaps lophotes*	205	9	1845
+Crimson Rosella	*Platycercus elegans*	135	6	810
Crimson Rosella juvenile		131	1	131
+Eastern Rosella	*Platycercus eximius*	106	9	954
Eastern Rosella juvenile		100	2	200
Red-rumped Parrot	*Psephotus haematonotus*	61	1	61
Superb Fairy-wren	*Malurus cynaeus*	10	2	20
Red Wattlebird	*Anthochaera carunculata*	108	2	216
Little Wattlebird	*Anthochaera chrysoptera*	60	1	60
Noisy Friarbird	*Philemon corniculatus*	109	1	109
Fuscous Honeyeater	*Lichenostomus fuscus*	18	1	18
+White-browed Babbler	*Pomatostomus superciliosus*	39	2	78
+Eastern Spinebill	*Acanthorhynchus tenuirostris*	11	1	11
Flame Robin	*Petroica phoenicea*	20	1	20
+Crested Shrike-tit juvenile	*Falcunculus frontatus*	22	1	22
Grey Shrike-thrush	*Colluricincla harmonica*	65	1	65
Grey Fantail	*Rhipidura fuliginosa*	9	2	18
Magpie-lark	*Grallina cyanoleuca*	90	1	90
Woodswallow	*Artamus* sp.	35	1	35
+Australian Magpie (juv.?)	*Gymnorhina tibicen*	329	7	2303
+Brown Songlark	*Cincloramphus cruralis*	54	1	54
House Sparrow	*Passer domesticus*	27	22	594
European Goldfinch	*Carduelis carduelis*	18	8	144
Sparrow	*Passer* sp.	20	1	20
Diamond Firetail	*Stagonopleura guttata*	17	4	68
Common Blackbird	*Turdus merula*	95	2	190
Common Starling	*Sturnus vulgaris*	75	19	1425
Common Myna	*Acridotheres tristis*	116	16	1856
Common Myna juvenile		100	2	200
Unidentified birds		57	11	627

Appendix 1 (continued)

Collared Sparrowhawk:				
Common name	Scientific name	Prey weight (g)	Total no. items	Biomass (g)
MOLLUSCS				
Garden Snail	*Helix aspersa*	6	1	6
ARACHNIDS				
Huntsman spider	Sparassidae	1	1	1
Unidentified spiders	Araneae	1	3	3
INSECTS				
Christmas Beetle	*Anoplognathus porosus*	1	4	4
Christmas Beetle	*Anoplognathus viriditarsus*	1	4	4
Christmas beetle	*Anoplognathus* sp.	1	41	41
Black Beetle	*Heteronychus arator*	1	7	7
Stag beetle Lucanidae	*Lamprisma latreille*	1	1	1
Other scarab beetles	Scarabaeidae	1	4	4
Other beetles	Coleoptera	1	44	44
Red-eye Cicada	*Psaltoda moerens*	1	14	14
Black Prince Cicada	*Psaltoda plaga*	1	28	28
Bug	Hemiptera (Heteroptera)	1	2	2
Unidentified insects	Insecta	1	7	7
Total			**299**	**12410**

+Novel bird species for Collared Sparrowhawk

Biomass Sources: Fuentes *et al.* (2005, 2007); Higgins (1999); McDonald *et al.* (2003); Marchant and Higgins (1990, 1993); Olsen and Tucker (2003); Olsen *et al.* (2004, 2006a,b, 2008); Sharp e*t al.* (2002a,b); Strahan (2004); R. Bennet, R. Palmer and S. Doody unpubl. data.