

DIETS OF WEDGE-TAILED EAGLES (*AQUILA AUDAX*) AND LITTLE EAGLES (*HIERAAETUS MORPHNOIDES*) BREEDING NEAR CANBERRA, AUSTRALIA

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ABSTRACT.—Recent concern about the decline of the Little Eagle (*Hieraaetus morphnoides*) in southeastern Australia has raised questions about whether Wedge-tailed Eagles (*Aquila audax*) might be implicated in this decline. The ecology, including the diet, of Little Eagles is rather poorly known. The diet of the Wedge-tailed Eagle is better documented, but the overlap in prey used by the two eagles has been little studied. Near Canberra between July 2002 and January 2008, we identified 1421 and 192 prey items from nests of Wedge-tailed Eagles and Little Eagles, respectively. Wedge-tailed Eagles' diet was similar to that reported elsewhere. In addition to European rabbits (*Oryctolagus cuniculus*), Little Eagles specialized on birds, but tended to avoid macropods, a main prey of Wedge-tailed Eagles, and there was little overlap in prey used by the two eagle species. Although Standardised Food Niche Breadth and Shannon Diversity Index were similar for the two eagles, Wedge-tailed Eagles captured significantly larger prey, as indicated by the difference in Geometric Mean Prey Weight, 1298 g for Wedge-tailed Eagles and 249 g for Little Eagles, which reflected the fivefold difference in mass between male Little Eagles and male Wedge-tailed Eagles. We suggest that direct competition for prey probably was not the cause of the Little Eagle decline.

KEY WORDS: *Wedge-tailed Eagle*; *Aquila audax*; *Little Eagle*; *Hieraaetus morphnoides*; *Australia*; *diet*; *pellet*.

DIETA DE INDIVIDUOS DE *AQUILA AUDAX* Y *HIERAAETUS MORPHNOIDES* ANIDANDO CERCA DE CANBERRA, AUSTRALIA

RESUMEN.—La reciente disminución de *Hieraaetus morphnoides* en el sudeste de Australia ha generado preocupación y generado dudas sobre si *Aquila audax* podría estar implicada en esta disminución. La ecología, incluyendo la dieta, de *H. morphnoides* es poco conocida. La dieta de *A. audax* ha sido mejor documentada, pero la superposición en las presas usadas por las dos águilas ha sido poco estudiada. Cerca de Canberra, entre julio de 2002 y enero de 2008, identificamos 1421 y 192 ítems de presas en los nidos de *A. audax* y *H. morphnoides*, respectivamente. La dieta de *A. audax* fue similar a la documentada en otros trabajos. Además del conejo europeo *Oryctolagus cuniculus*, *H. morphnoides* se especializó en aves, pero tendió a evitar los macrópodos, una de las principales presas de *A. audax*, y hubo poca superposición en las presas usadas por las dos especies de águilas. Aunque los índices de amplitud estandarizada de nicho alimenticio y de diversidad de Shannon fueron similares para las dos águilas, *A. audax* capturó presas significativamente más grandes, como lo indicó la diferencia en el peso promedio geométrico de la presa, de 1298 g para *A. audax* y de 249 g para *H. morphnoides*, lo que reflejó la diferencia en peso de cinco órdenes de magnitud entre el macho de *H. morphnoides* y el macho de *A. audax*. Sugerimos que la competencia directa por las presas no fue la causa de la disminución de *H. morphnoides*.

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The Wedge-tailed Eagle (*Aquila audax*) and Little Eagle (*Hieraaetus morphnoides*) are the two Australian representatives of the booted eagles. Recent DNA studies suggest that these two genera in the traditional sense are paraphyletic, with some *Hieraaetus* species more closely related to *Aquila* and vice versa (Wink and Sauer-Gürth 2004, Helbig et al. 2005, Lerner and Mindell 2005). The two genera may either be merged, or some species may be transferred between the two genera, with the Wedge-tailed Eagle in *Aquila* and the Little Eagle remaining in a more circumscribed *Hieraaetus* (Helbig et al. 2005, Debus et al. 2007a).

The Wedge-tailed Eagle occurs throughout mainland Australia, Tasmania, and southern New Guinea. The Little Eagle inhabits mainland Australia (though not Tasmania), with a closely related eagle in New Guinea classified as a separate species (*H. weiskei*; Debus 1998, Helbig et al. 2005, Lerner and Mindell 2005).

Little Eagles in Victoria had masses of about 623 g for males ($n = 3$) and 1113 g for females ($n = 16$; live-trapped birds; Marchant and Higgins 1993). Live-trapped Wedge-tailed Eagles in southern mainland Australia averaged 3132 g for males ($n = 23$) and 3800 g for females ($n = 23$; Brooker 1996). Thus, female Little Eagles (hereafter "LEs") average ca. 29% of the mass of female Wedge-tailed Eagles (hereafter "WTEs"), male LEs average ca. 20% of the mass of male WTEs, and male LEs ca. 16% of the mass of female WTEs.

The search for mechanisms that permit coexistence of similar species is a central issue of community ecology (Begon et al. 1990). Species that coexist are expected to develop mechanisms of niche differentiation, especially when faced with scarce resources (May 1973). Schoener (1974) argued that there are three main mechanisms of niche segregation in birds of prey: habitat, food, and time. Consequently, coexisting diurnal raptors are expected to select different prey species or different prey sizes, to segregate foraging areas, or to hunt at different times.

Compared with the WTE, the LE is less well known (reviewed by Marchant and Higgins 1993, Debus et al. 2007a, Debus and Ley 2009). The LE may be declining in parts of southeastern Australia, and WTEs may be implicated in this decline (Australian Capital Territory; Olsen and Fuentes 2005, Olsen and Osgood 2006). Olsen et al. (2008, 2009) showed a loss by 2007 of 10 of 11 original pairs that were present in 1992 in the Australian Capital Ter-

ritory. The LE is now classified as vulnerable in the Australian Capital Territory (Olsen et al. 2009). Barrett et al. (2007) reported a decrease of 38.7% for LEs in New South Wales, based on data from the first Atlas of Australian Birds (conducted between 1977 and 1981), and the New Atlas of Australian Birds (conducted between 1998 and 2001; Barrett et al. 2003).

In southern temperate Australia, LEs prey mainly on small mammals (especially juvenile and immature European rabbits [*Oryctolagus cuniculus*]), and some birds (mainly parrots and passerines <500 g), lizards and invertebrates, and rarely carrion, although in some parts of the New South Wales tablelands, they consume many small birds <100 g (Debus 1984, Bollen 1989, 1991, Olsen et al. 2006b, Debus et al. 2007a, Debus and Ley 2009). In southern semiarid and arid areas their diet is similar to that in the temperate zone (Baker-Gabb 1984, Falkenberg et al. 2000), but in more northerly (subtropical) arid areas, they take more lizards and invertebrates and far fewer rabbits. The little carrion eaten includes large mammals such as kangaroos (*Macropus* spp.; Marchant and Higgins 1993, Aumann 2001a, 2001b, 2001c).

The diet of WTEs is better studied (reviewed by Marchant and Higgins 1993, Debus et al. 2007b). In all parts of Australia, WTEs prey primarily on medium-sized and large mammals (especially adult rabbits, brown hares [*Lepus capensis*] and/or juvenile kangaroos), some large birds, and lizards; they also commonly eat large mammals (e.g., adult kangaroos, livestock) as carrion (Brooker and Ridpath 1980, Robertson 1987, Sharp et al. 2002a, Parker et al. 2007). However, in recent years, the ratio of rabbits to kangaroos in WTE diet in some areas decreased when the numbers of rabbits declined and the numbers of kangaroos increased (Fuentes et al. 2007).

WTEs and LEs coexist in the Canberra region, and they often breed within 5 km of each other. However, WTEs may displace LEs by nesting close to them (Olsen 1995, Olsen et al. 2006b). Given the published literature indicating that both eagles consume rabbits, we concluded that there was potential for interspecific competition. Sympatric, taxonomically close species in Europe such as the Bonelli's Eagle (*Hieraaetus* [now *Aquila*] *fasciatus*), Eastern Imperial Eagle (*A. heliaca*) and Golden Eagle (*A. chrysaetos*) compete directly with each other for lagomorphs (Ferguson-Lees and Christie 2001), but it is unknown whether WTEs compete with LEs for prey near Canberra.

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 1997, Garcia and Arroyo 2005, Olsen et al. 2006a). However, to clearly understand the effect of competition, studies should occur at a local scale, between neighboring 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 (Olsen et al. 2006a, 2006b), although Aumann (2001c) compared mean prey weight, dietary diversity (Shannon's Index) and dietary overlap (Pianka's Index) for a suite of diurnal raptors including WTE and LE. Thus, we examined the dietary relationships of LE and WTE pairs breeding within 5 km of each other near Canberra, and we calculated indices of dietary overlap as a means to assess potential competition between the species.

METHODS

Following Steenhof (1987), we defined an occupied nesting territory as an area containing one or more nest sites within the home range of a pair of eagles. Between July 2002 and January 2008 we searched the area inside a 40-km-radius of the Canberra Central Business District for occupied territories of both species and for nests containing eggs or young. We collected prey remains from each nest found. In 2002–03 we found 5 territories of LE and 32 territories of WTE. Because of the increasing difficulty of finding nests of the declining LEs, we used our limited time in subsequent years to search for LE nests and did no more collecting at some WTE nests previously studied.

Each territory included a mosaic of different vegetation types. The study area incorporated the Australian Capital Territory and bordering areas of New South Wales. The northern part of the Australian Capital Territory is primarily the city of Canberra, but the edges of the city and surrounding areas of New South Wales are mainly farmland and pastures. Most of the undeveloped hills and ridges in and around urban Canberra are protected nature reserves that, together, cover an area of 5720 ha. The major vegetation associations in these reserves are dry sclerophyll forest, open savannah, and woodland. Two protected corridors border the Upper Molonglo and Murrumbidgee rivers, up to 4 km wide and along the entire length of the Australian

Capital Territory (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. polyanthemus*) and Yellow Box (*E. melliodora*) in more open areas (NCDC 1988). The understory has abundant tussock grasses (*Poa* spp.), with the shrub (*Cassinia longifolia*) dominating more open areas. The Namadgi National Park (106 000 ha) covers much of the rest of the southern end of the study area. The habitat in the park is mainly wet sclerophyll forest, dry forest with open grassy valleys in the lower elevations, and alpine woodland in the higher areas. (A more complete description of the habitat and climatic parameters can be found in Taylor and COG 1992.) Adjacent land in New South Wales is dominated by grazing land and dry sclerophyll forest, scattered Yellow Box, Red Stringybark, and *Casuarina*.

Prey Collection and Analysis. Recommendations for collecting unbiased information on eagle diets are often contradictory. For example, Real (1996) concluded that pellets were more representative than prey remains for analyzing Bonelli's Eagle diet, whereas Sharp et al. (2002a) ignored pellets of WTEs in their analysis and relied solely on prey remains. In our study, we used no videos or hides for direct observation and thus relied on pellets, prey remains, and occasional observations of adults with prey. We combined these as in Seguin et al. (1998) and Marchesi et al. (2002).

Male WTEs and LEs had "plucking roosts" often in a dead tree, standing or fallen, 50 to 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 from under them, under nests, and inside nests at least once at the banding stage, and once after young had fledged. Five observations of prey deliveries or kills were also included, after we confirmed that these items did not appear in the following prey collection.

Pellets and prey remains were stored separately, and each pellet was placed in an individual sealed plastic bag. We identified and counted body parts to estimate the minimum number of prey items (MNI) in a pooled sample of pellets and prey remains and observations, in order to minimize 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.

Statistical Analyses. To estimate the minimum number of prey items (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, 2006b). 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 species was often found in each pellet. For example, in a sample containing rabbit fur in three pellets but only one rabbit tail and one rabbit mandible, we would tally one rabbit, the minimum number of individuals.

To estimate dietary biomass, we multiplied the MNI by the average mass for each prey species. The mean or median weights of most prey were taken from the literature (Appendix 1). For dietary biomass calculations on large mammalian prey >10 kg, such as kangaroos, we used an upper limit of consumed tissue for WTEs of 3800 g, based on the maximum usable biomass that WTEs can carry to the nest (Brooker and Ridpath 1980, Baker-Gabb 1984). For LE biomass calculations on large prey, we used an upper limit of tissue consumed at the nest of 740 g, based on estimates in Marchant and Higgins (1993) of what this species can bring to the nest, and estimates made for the similar-sized Whistling Kite (*Haliaeetus spheurnurus*) by Fuentes et al. (2005).

We applied prey wastage factors based on those used by Brooker and Ridpath (1980) and Baker-Gabb (1984): 33% for mammalian prey between 300 g and 10 kg and 17% for mammalian prey between 75 g and 300 g. For birds and reptiles, a 20% wastage factor was applied for species greater than 300 g, 12% for prey between 75 and 300 g, and 9% for prey <75 g.

To describe the overall diet of the two species, we calculated the Standardized Food Niche Breadth (SFNB; Colwell and Futuyama 1971) and the Geometric Mean Prey Weight (GMPW - Marti 1987) for the pooled data from all nests. We used the formula:

$$\text{SFNB}_{\text{sta}} = (\text{B}_{\text{obs}} - \text{B}_{\text{min}}) / (\text{B}_{\text{max}} - \text{B}_{\text{min}})$$

to calculate Standardized Food Niche Breadth (SFNB) where $\text{B}_{\text{obs}} = 1 / \sum p_i^2$ (p_i is the proportion of each prey type).

$$\begin{aligned} \text{B}_{\text{max}} &= \text{total number of prey species} \\ \text{B}_{\text{min}} &= 1 \text{ (minimum number of prey species)} \end{aligned}$$

Prey species that could not be identified were removed from the SFNB analyses. We included large macropods in the GMPW calculations because WTEs often hunted and killed large macropods in the Canberra region (Fuentes et al. 2007). However, we did not include adult sheep (*Ovis aries*) in these calculations because it is more likely that sheep were taken as carrion. We used a Wilcoxon Rank-Sum test to evaluate differences in prey mass, as the data did not conform to assumptions of parametric analysis.

We used the Pianka Index (Pianka 1973) to explore food overlap between LEs and WTEs:

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

where p_i and q_i represent the proportion of species i in the diet of the species p and q .

To contrast the differences in the proportion of prey items between LEs and WTEs we used a chi-square analysis on contingency tables. For differences between each prey class (mammals, birds, reptiles, and invertebrates), we subdivided the contingency tables as suggested by Zar (1999) and applied a chi-square test following the Haber method. The Shannon Diversity Index (Shannon and Weaver 1949) was used to estimate the dietary diversity:

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

where p_i represents the proportional contribution by number of each species in the sample.

All analysis and calculations were performed using SAS 8.0 (SAS Institute Inc. Cary, NC) and Excel 2000 (Microsoft Corporation).

RESULTS

We collected prey in 2004 from 17 WTE and 4 LE territories, in 2005 from 9 WTE and 5 LE territories, in 2006 from 11 WTE and 1 LE territory, and in 2007 from 11 WTE and 5 LE territories. LEs and WTEs had some overlap in prey, as reflected in the 192 LE and 1421 WTE prey items (Appendix 1). By frequency, LEs took 38.5% mammals and only 1.2% macropods. European rabbit was the most common food item for both raptor species, although it made up a higher proportion of LE diet by frequency (LE: 32.3%; WTE: 19.3%) and an even higher proportion by biomass (LE: 52.4%; WTE: 12.5%). WTEs took 55.2% mammals, particularly

eastern grey kangaroo (24.6% by frequency and 34.8% by adjusted biomass ($n = 196$). Both eagles consumed birds, but LEs ate more small species such as rosellas (*Platycercus* spp.), Magpie-larks (*Grallina cyanoleuca*) and European Starlings (*Sturnus vulgaris*) while WTEs took more large species such as ravens (*Corvus coronoides* and *C. mellori*; 5.1% of items), the grazing Australian Wood Duck (*Chenonetta jubata*; 3.6% of items) and Galahs (*Eolophus roseicapillus*; 4.8% of items; Appendix 1).

Food Niche Breadth was almost identical for the two eagles, with values of 0.16 and 0.14 for WTEs and LEs respectively. However, WTEs captured significantly larger prey, as indicated by the Geometric Mean Prey Weights, hereafter GMPW, (WTEs = 1298 g, LEs = 249 g; $Z = -9.72$, $P < 0.001$). The difference reflected the mass difference between the two eagle species: WTEs are about five times as heavy as LEs (Appendix 2).

The Pianka's Index indicated a 69.3% overlap in diet between the two eagle species. However, there was a significant difference in the proportion of prey classes (mammals, birds, reptiles, and invertebrates) between WTEs and LEs ($\chi^2 = 50.1$; $df = 3$; $P < 0.001$). WTE diet was slightly more diverse than LE diet (Shannon Diversity Index = 3.16 for WTEs and 2.94 for LEs), but this may have been partly due to the smaller sample size of LE pellets and prey remains.

DISCUSSION

Although our ability to draw conclusions from our study was somewhat limited by the disparity in sample sizes (Krebs 1998), we nonetheless believe this study makes a valuable contribution to our knowledge of the breeding ecology of Australian raptors. The diet of WTEs, as determined in this study, was similar to that of WTEs previously studied in southern Australia (Leopold and Wolfe 1970, Brooker and Ridpath 1980, Robertson 1987, Sharp et al. 2002a) with mammals dominating (primarily rabbits and macropods), and ground-feeding birds of secondary importance. The diet of the LEs is more difficult to compare with earlier studies because there are fewer accounts for southeastern Australia. The only detailed studies (Baker-Gabb 1984, Debus 1984, Bollen 1989, 1991, Debus et al. 2007a) indicated an overall similarity to this study in major taxa consumed, though LEs in this study ate more birds than did LEs in most previous studies: 45% by frequency in this study compared to 26.1% in Victoria (Baker-Gabb 1984), 13–26% in northern

New South Wales (Debus 1984, Debus et al. 2007a), and 10.6% in the Northern Territory (Aumann 2001a, 2001b, 2001c). However, the results of Bollen (1989, 1991) for LEs, in the same region as our study, were more similar: 38–69% birds. This tendency may place LEs into competition with Peregrine Falcons (*Falco peregrinus*) and Australian Hobbies (*F. longipennis*) nesting nearby (see Olsen et al. 2008).

The fivefold difference for GMPW between WTEs (1298 g) and LEs (249 g) in this study reflects the fivefold difference in mass between male LEs and male WTEs, which do much of the hunting during the breeding season (Debus 1998). Generally speaking, a raptor species' mass correlates with the GMPW of its prey, with Southern Boobook (*Ninox novaeseelandiae*), Grey Goshawk (*Accipiter novaehollandiae*) and Brown Goshawk (*A. fasciatus*) having the lowest prey/predator ratio measured and LE, White-bellied Sea-Eagle (*Haliaeetus leucogaster*) and WTE having the highest (Table 1). However, this ratio can differ from area to area. For example, Peregrine Falcons at higher elevations in Australia had a relatively larger GMPW because they took more prey such as ravens than did peregrines at lower elevations (Olsen et al. 2004, 2006b).

Studies that explore dietary overlap at the local scale are scarce among diurnal raptors. Both Nilsson (1984) and Korpimäki (1987) showed that the presence of competitor species at the local scale can affect reproductive success. In the present study, WTEs and LEs had some dietary overlap and interspecific interactions probably would have favored the larger WTE. However, WTEs consumed larger prey than did LEs, specifically macropods, rabbits, hares, and foxes. The LEs ate fewer mammals, especially hares and macropods, and no foxes. Unlike WTEs, LEs took many (mainly immature) rabbits. Both species may eat macropods as carrion (Marchant and Higgins 1993) so it is possible that the more numerous WTEs in the Australian Capital Territory region keep LEs from kangaroo carcasses, and that LEs would eat more kangaroo carrion if not constrained by WTEs. Rangers at Googong Dam, 17 km southeast of the Canberra Central Business District, observed that WTEs commonly fed on the carcasses of shot kangaroos, pigs, and goats, but White-bellied Sea-Eagles and LEs did not (M. Rodden, M. Gardner pers. comm.).

The number of LE territories in the Australian Capital Territory area has declined since 1992, from 11, some within 2 km of WTE territories, to one in an Australian Capital Territory survey (two of the 11

Table 1. Comparison of GMPW and relative prey size among various Australian raptor species.

SPECIES	REGION	RAPTOR MASS (g)	GMPW (g)	PROPORTION OF PREY SIZE	REFERENCE
Southern Boobook	Canberra region	283	7	0.02	Olsen et al. 2006b
Grey Goshawk	Queensland	545	25	0.05	Burton and Olsen 1997
Brown Goshawk	Queensland	440	22	0.05	Burton and Olsen 1997
Australian Hobby	Canberra region	250	22	0.09	Olsen et al. 2008
Brown Goshawk	Canberra region	440	45	0.10	Olsen et al. 2006b
Brown Falcon	Victoria	584	77	0.13	McDonald et al. 2003
Peregrine Falcon	Canberra region	745	132	0.18	Olsen et al. 2008
Whistling Kite	Canberra region	870	227	0.26	Fuentes et al. 2005
Peregrine	Canberra region	745	202	0.27	Olsen et al. 2004, 2006b
White-Bellied Sea- Eagle	Canberra region	2865	887	0.31	Olsen et al. 2006a
Little Eagle	Canberra region	868	249	0.29	This study
Little Eagle	Armidale, New South Wales	868	328	0.38	Debus et al. 2007a
Wedge-tailed Eagle	Canberra region	3466	1291	0.37	This study
Wedge-tailed Eagle	Canberra region	3466	1291	0.37	This study
Wedge-tailed Eagle	Armidale, New South Wales	3466	1309	0.38	Debus et al. 2007b
Wedge-tailed Eagle	Canberra region	3466	2131	0.61	Olsen et al. 2006a

nest sites contained WTEs), and from about 13 territories to 3 in another Australian Capital Territory survey (all three remaining LEs were 5 km away from WTE territories; Olsen and Fuentes 2005, Olsen and Osgood 2006, Olsen et al. 2008). This decline in LEs does not seem related to dietary overlap. WTEs may have been able to utilize the expanded macropod populations in and near Canberra (see Fuentes et al. 2007) and displace LEs simply because of their greater numbers and by nesting close to existing LE nests. Debus (2006) observed a WTE robbing a LE in this study area. It is noteworthy that rabbits have been increasing in the Australian Capital Territory during the course of this study, and by 2008 the territory government had initiated rabbit control measures, baiting, and shooting (N. Webb, M. Maconachie pers. comm.), so rabbit numbers do not appear to be implicated in the LE decline. Furthermore, there is no evidence that breeding populations of WTEs or LEs in Australia have increased or decreased in association with changes in rabbit numbers. In other studies, when rabbit populations decreased, territorial pairs of WTE either switched to other prey (Fuentes et al. 2007, Sharp et al. 2002b) or remained on territory but did not breed (Robertson 1987). In addition, Steele and Baker-Gabb (2009) monitored changes in raptor abundance before and after the introduction of Rabbit Calicivirus Disease (RCD) in 1995–96

as a pest control mechanism that caused severe declines in rabbit numbers, and found no detectable effect from the introduction of RCD on populations of rabbit-dependent species of raptors.

Seasonal or annual variation in prey availability (e.g., times of drought or good rains when certain prey may be sparse or abundant) may affect niche separation. Prey taken by each eagle species during these times may differ, and niches may be more or less separated. Our data could not reveal this, as they are specific to one region over a short period of time. In addition, our LE data are from a limited number of territories and it is possible that pairs had individual food preferences. Such preferences might bias our results and affect interpretations about dietary overlap. Future studies should compare equal numbers of breeding LEs and WTEs, something we could not do here because of local declines in LE numbers.

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Appendix 1. Frequency and biomass^a of prey items in the diets of Wedge-tailed Eagles (*A. audax*) and Little Eagles (*H. morphnoides*) breeding near Canberra, Australia.

CLASS	WEDGE-TAILED EAGLE			LITTLE EAGLE			
	PREY SPECIES	N	FREQUENCY (%)	BIOMASS (%)	N	FREQUENCY (%)	BIOMASS (%)
Mammals							
European rabbit (<i>Oryctolagus cuniculus</i>)	270	19.0	12.7	34	17.7	38.2	
Juvenile European rabbit	4	0.3	<0.1	28	14.6	14.2	
Brown hare (<i>Lepus capensis</i>)	91	6.4	11.4	2	1.0	2.3	
Eastern grey kangaroo (<i>Macropus giganteus</i>)	116	8.1	20.6	4	2.1	4.5	
Juvenile eastern grey kangaroo	80	5.6	14.2				
Swamp wallaby (<i>Wallabia bicolor</i>)	26	1.8	4.6				
Juvenile swamp wallaby	3	0.2	0.2				
Wallaroo (<i>Macropus robustus</i>)	20	1.5	3.55				
Tammar wallaby (<i>Macropus eugenii</i>)	2	0.6	1.6				
Red-necked wallaby (<i>Macropus rufogriseus</i>)	9	0.6	1.6				
Adult macropods (<i>Macropus</i> sp.)	3	0.2	0.5				
Juvenile macropods	4	0.3	0.4				
Sheep (<i>Ovis aries</i>)	42	2.9	7.5	2	1.0	2.3	
Lamb	12	0.8	2.1				
Common brushtail possum (<i>Trichosurus vulpecula</i>)	27	1.9	2.2	1	0.5	1.1	
Red fox (<i>Vulpes vulpes</i>)	19	1.3	3.4				
Red fox cub	16	1.1	1.5				
Echidna (<i>Tachyglossus aculeatus</i>)	6	0.4	0.8				
Black rat (<i>Rattus rattus</i>)	6	0.4	0.1	1	0.5	0.4	
Common Ringtail Possum (<i>Pseudocheirus peregrinus</i>)	5	0.4	0.1				
Southern brown bandicoot (<i>Isodon obesulus</i>)	4	0.3	0.1				
House mouse (<i>Mus musculus</i>)	4	0.3	<0.1	2	1.0	0.1	
Goat (<i>Capra hircus</i>)	4	0.3	0.7				
Mountain possum (<i>Trichosurus caninus</i>)	3	0.2	0.3				
Long-nosed bandicoot (<i>Perameles nasuta</i>)	2	0.1	0.1				
Cat (<i>Felis catus</i>)	2	0.1	0.3				
Juvenile cattle (<i>Bos taurus</i>)	2	0.1	0.4				
Horse (<i>Equus caballus</i>)	2	0.1	0.4				
Mammals subtotal	784	55.2	90.0	74	38.5	62.9	
Birds							
Domestic Fowl (<i>Gallus gallus</i>)	4	0.3	0.3				
Pied Cormorant (<i>Phalacrocorax varius</i>)	2	0.1	0.1				
Pacific Black Duck (<i>Anas superciliosa</i>)	5	0.4	0.2	1	0.5	1.1	
Maned Duck (<i>Chenonetta jubata</i>)	51	3.6	1.5	2	1.0	2.0	
Eurasian Coot (<i>Fulica atra</i>)				1	0.5	0.7	
Brown Goshawk (<i>Accipiter fasciatus</i>)				1	0.5	0.5	
Purple Swamphen (<i>Porphyrio porphyrio</i>)	2	0.1	0.1				
Great Egret (<i>Ardea alba</i>)	1	0.7	<0.1				
Little Egret (<i>Egretta garzetta</i>)	1	0.7	<0.1				
Straw-necked Ibis (<i>Threskiornis spinicollis</i>)	5	0.4	0.2				
Peregrine Falcon (<i>Falco peregrinus</i>)	2	0.1	0.1				
Australian Hobby (<i>Falco longipennis</i>)	2	0.1	<0.1				
Brown Falcon (<i>Falco berigora</i>)	2	0.1	<0.1				
Nankeen Kestrel (<i>Falco cenchroides</i>)	3	0.2	<0.1				
Rock Pigeon (<i>Columba livia</i>)	24	1.7	0.3	2	1.0	0.8	
Crested Pigeon (<i>Ocyphaps lophotes</i>)	2	0.1	<0.1				

Appendix 1. Continued.

CLASS	WEDGE-TAILED EAGLE			LITTLE EAGLE		
	PREY SPECIES	FREQUENCY (%)	BIOMASS (%)	FREQUENCY (%)	BIOMASS (%)	
Yellow-tailed Black Cockatoo (<i>Calyptorhynchus junereu</i>)	9	0.6	0.3			
Gang-gang Cockatoo (<i>Callocephalon fimbriatum</i>)	1	0.7	<0.1			
Galah (<i>Eolophus roseicapillus</i>)	68	4.8	0.8	6	3.1	2.4
Little Corella (<i>Cacatua sanguina</i>)	1	0.7	<0.1	2	1.0	1.2
Sulphur-crested Cockatoo (<i>Cacatua galerita</i>)	28	2.0	0.8	3	1.6	2.9
Musk Lorikeet (<i>Glossopsitta concinna</i>)	2	0.1	<0.1			
Swift Parrot (<i>Lathamus discolor</i>)				1	0.5	0.1
Australian King Parrot (<i>Alisterus scapularis</i>)	1	0.7	<0.1			
Crimson Rosella (<i>Platycercus elegans</i>)	41	2.9	0.2	10	5.2	1.8
Juvenile Crimson Rosella	3	0.2	<0.1	2	1.0	0.4
Eastern Rosella (<i>Platycercus eximius</i>)	20	1.5	0.1	5	2.6	0.7
Juvenile Eastern Rosella				1	0.5	0.1
Rosella undetermined (<i>Platycercus</i> sp.)	2	0.1	<0.1			
Red-rumped Parrot (<i>Psephotus haematonotus</i>)	3	0.2	<0.1			
Parrots undetermined (Order <i>Psittaciformes</i>)	2	0.1	<0.1			
Tawny Frogmouth (<i>Podargus strigoides</i>)	8	0.6	0.1			
Australian Owllet-nightjar (<i>Aegotheles cristatus</i>)	2	0.1	<0.1			
Laughing Kookaburra (<i>Dacelo novaeguineae</i>)	6	0.4	0.1			
Thornbill undetermined (<i>Acanthiza</i> sp.)	2	0.1	<0.1			
Red Wattlebird (<i>Anthochaera carunculata</i>)	4	0.3	<0.1	2	1.0	0.3
Spotted Quail-thrush (<i>Cincoloma punctatum</i>)				1	0.5	0.1
White-browed Babbler (<i>Pomatostomus superciliosus</i>)				1	0.5	0.1
Noisy Miner (<i>Manorina melanocephala</i>)	2	0.1	<0.1			
Magpie-lark (<i>Grallina cyanoleuca</i>)	12	0.8	<0.1	11	5.7	1.3
Black-faced Cuckoo-shrike (<i>Coracina novaehollandiae</i>)				2	1.0	0.3
Australian Magpie (<i>Gymnorhina tibicen</i>)	68	4.8	0.8	5	2.6	0.8
Juvenile Australian Magpie	11	0.8	0.1			
Pied Currawong (<i>Strepera graculina</i>)	6	0.4	0.1	2	1.0	
Grey Currawong (<i>Strepera versicolor</i>)	2	0.1	<0.1			
Currawong undetermined (<i>Strepera</i> sp.)	2	0.1	<0.1			
Australian Raven (<i>Corvus coronoides</i>)	32	2.2	0.8	1	0.5	
Little Raven (<i>Corvus mellori</i>)	5	0.4	0.1			
Juvenile Raven	14	1.0	0.3			
Raven undetermined (<i>Corvus</i> sp.)	21	1.5	0.5	3	1.6	2.2
White-winged Chough (<i>Corcorax melanorhamphos</i>)	9	0.6	0.1	2	1.0	0.8
Australasian Pipit (<i>Anthus australis</i>)				1	0.5	<0.1
Woodswallow undetermined (<i>Artamus</i> sp.)				1	0.5	0.4
Brown Songlark (<i>Cincloramphus cruralis</i>)	1	0.7	<0.1			
European Starling (<i>Sturnus vulgaris</i>)	24	1.7	0.1	7	3.7	0.7
Common Myna (<i>Acridotheres tristis</i>)				1	0.5	0.2
Undetermined birds	42	2.9	0.7	10	5.2	5.8
Bird subtotal	560	39.4	9.2	87	45.3	30.3
Reptiles						
Red-bellied black snake (<i>Pseudechis porphyriacus</i>)	2	0.1	<0.1			
Snake undetermined	1	0.7	<0.1			
Cunningham's skink (<i>Egernia cunninghami</i>)	7	0.5	0.1	4	2.1	2.0
Eastern water dragon (<i>Physignathus lesuevrii</i>)	2	0.1	<0.1			
Bearded dragon (<i>Pogona barbata</i>)	8	0.6	0.1	1	0.5	0.5

Appendix 1. Continued.

CLASS PREY SPECIES	WEDGE-TAILED EAGLE			LITTLE EAGLE		
	N	FREQUENCY (%)	BIOMASS (%)	N	FREQUENCY (%)	BIOMASS (%)
Dragon undetermined (Fam. <i>Agamidae</i>)	11	0.8	0.1			
Eastern blue-tongued skink (<i>Tiliqua scincoides</i>)	5	0.4	0.1	2	1.0	1.1
Blue-tongued skink undetermined (<i>Tiliqua</i> sp.)	5	0.4	0.1			
Shingleback skink (<i>Tilqua rugosa</i>)				1	0.5	1.1
Skink undetermined	7	0.5	0.1	1	0.5	0.4
Jacky lizard (<i>Amphibolurus muricatus</i>)				1	0.5	<0.1
Dragon lizard undetermined (<i>Amphiboluerus</i> sp.)				1	0.5	<0.1
Reptiles subtotal	48	3.4	0.7	11	5.7	5.3
Fish						
European carp (<i>Cyprinus carpio</i>)	1	0.7	<0.1	1.0	0.5	1.0
Invertebrates						
Cicada (<i>Psaltoda moerens</i>)	16	1.1	<0.1	4	2.1	<0.1
Black beetle (<i>Heteronychus arator</i>)	10	0.7	<0.1	1	0.5	<0.1
Crayfish (<i>Cherax</i> sp.)	2	0.1	<0.1	1	0.5	0.3
Christmas beetle undetermined (<i>Anoplognathus</i> sp.)				2	1.0	<0.1
Scarab beetle undetermined (Scarabaeidae)				1	0.5	<0.1
Longicorn beetle (<i>Phorocantha</i> sp.)				1	0.5	<0.1
Other beetles undetermined (Coleoptera)				7	3.7	<0.1
Grasshoppers (Orthoptera)				2	1.0	<0.1
Invertebrate subtotal	28	2.0	<0.1	19	9.9	0.3
Total prey items	1421			192		

^a Biomass Sources: (1) Higgins 1999; (2) McDonald et al. 2003; (3) Marchant and Higgins 1993, (4) Marchant and Higgins 1990; (5) Olsen et al. 2004; (6) Olsen and Tucker 2003; (7) Sharp et al. 2002a,b; (8) Strahan 2004; (9) Estimated based on remains located at nests; (10) Olsen et al. 2006a,b, (11) Ross Bennet unpublished data, (12) Robert Palmer unpublished data, (13) Sean Doody unpublished data.

Appendix 2. Indices of niche breadth in the diets of Wedge-tailed Eagles (*Aquila audax*) and Little Eagles (*H. morphnoides*) breeding near Canberra, Australia.

INDEX	WEDGE-TAILED EAGLE	LITTLE EAGLE
GMPW	1288	249
Shannon-Weaver	3.16	2.94
Standardized niche breadth	0.16	0.14