

Diet of Southern Boobooks *Ninox boobook* and its relationship with breeding in Canberra, Australian Capital Territory, 1993–2019

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The breeding and non-breeding diets of the Southern Boobook *Ninox boobook* were studied in 16 breeding and 12 non-breeding territories in Canberra, ACT, from 1993–2019 by analysis of regurgitated pellets and prey remains under roosts and nests. The aim of the study was to investigate possible differences in diet composition over time (>20 years), in the breeding versus non-breeding season, across the phases of the breeding cycle and as a function of brood size. Breeding owls captured more insects than non-breeding owls, but dietary biomass of breeding owls was dominated by birds. Non-breeding owls captured more mammals than breeding owls by both number and biomass. Ground prey contributed 67.8% of dietary biomass for non-breeding owls, whereas bats, birds and flying insects constituted 77.8% of the diet of breeding owls. Non-breeding owls took fewer, but larger, mammals in 2006–2019 than in 1993–2005, specifically Black Rats *Rattus rattus* (12.8% of total biomass in 1993–2005 versus 54.5% in 2006–2019). Owls raising larger broods captured more arachnids, larger mammals (when feeding broods of 3), and birds (when provisioning broods of 4), together with a substantial component of invertebrate biomass. These patterns suggest that female Boobooks adjust their foraging to accommodate the demands of large broods. The temporal, seasonal, activity and brood size-related dietary variation observed variously may reflect (a) the abundance and activity of insects, (b) the contribution of agile males to food provisioning during the breeding cycle, (c) supplementation of the brood's diet with insect prey by female owls, (d) seasonal differences in foraging energetics (e.g. more perch-hunting in winter), (e) the female-bias in non-breeding samples (larger females taking larger, less agile, terrestrial prey), and (f) prey abundance in winter.

Keywords: Southern Boobook; owl; *Ninox boobook*; diet; seasonal; temporal; brood size; non-breeding

INTRODUCTION

The Southern Boobook *Ninox boobook* is a mottled, brown hawk-owl that inhabits the Australian continent and some islands to the north (Higgins 1999); it is a distinct species from the boobooks in New Zealand, Tasmania and Wallacea (Gwee *et al.* 2017). The diet of the Southern Boobook has been described at several sites in the breeding and non-breeding seasons of south-eastern Australia, although sample sizes during the breeding season have been limited (Higgins 1999; McNabb 2002; Penck and Queale 2002; Olsen *et al.* 2006; Fitzsimons and Rose 2007; Trost *et al.* 2008, Trost and Olsen 2016; Olsen 2011; McDonald and Pavey 2014). Notwithstanding that it is the smallest owl resident in mainland Australia (the Tasmanian Boobook *N. leucopsis* is smaller), the Southern Boobook is by global standards a medium-sized owl (i.e., >100 g). Its prey, at least by biomass, is mostly vertebrates, contrary to some prior reports (see Olsen 2011). Various factors can influence perceptions of the importance of invertebrates in its diet, such as analysis of the gut contents of dispersing juveniles that die in marginal habitat versus pellet collections from the active roosts of territorial adult owls (Olsen 2011).

Southern Boobooks tend to hunt in woodland and forest (Olsen *et al.* 2006). In the non-breeding season (autumn–winter), some Southern Boobooks that breed in Nature Parks in the Australian Capital Territory (ACT) move into suburban

areas to live and hunt (Olsen and Taylor 2001; Olsen *et al.* 2002). There are four phases of activity and foraging in Southern Boobooks in Canberra (Olsen *et al.* 2020). During the pre-breeding phase (15 August–30 September), pairs begin roosting together near potential nests and copulating. In the nesting phase (1 October–1 January), they lay and incubate eggs and tend nestlings; both male and female provide for their young. During the post-fledging phase (1 January–28 February), adults feed fledged young, but eventually they stop feeding them and the young become independent and disperse. Females desert the brood and leave juveniles in the care of the male; therefore, post-breeding dietary changes can begin in February or even January for females. Females then leave the breeding area, some to winter in Canberra suburbs (Olsen and Taylor 2001). During the non-breeding phase (1 March–14 August), the adults without dependent young winter together or apart.

Although Olsen *et al.* (2006), Trost and Olsen (2016) and Olsen (2011) described the breeding diet of a few pairs of Southern Boobooks in the ACT, and Trost *et al.* (2008) documented the winter diet, there is no published comparison of breeding versus non-breeding diets in a long-term (20+ years) study. Such a study may potentially reveal seasonal and long-term differences in diet composition, within-season (breeding-phase) disparities and the effects of brood size on diet, all of which prompted us to undertake the present investigation. Here we detail the breeding and non-breeding diets of Southern

Boobooks in multiple breeding and non-breeding territories in Canberra from 1993–2019, and compare the results with those of other studies on the non-breeding diet (Baker-Gabb 1984a; Campbell and Rose 1996; Rose 1996; McNabb 2002; Penck and Queale 2002; Fitzsimons and Rose 2007; Trost *et al.* 2008) and the breeding diet in the ACT and New South Wales (Rose 1996; Olsen *et al.* 2006; Olsen 2011; Trost and Olsen 2016). Southern Boobooks are sexually size-dimorphic (males ~270 g, females ~340 g; Olsen *et al.* 2010), which may have a bearing on their seasonal foraging ecology in terms of prey types consumed and hunting modes (e.g., sallying versus perch-pouncing) and locations. Brood size may also influence the foraging contribution of the female parent and the relative dietary proportions contributed by various prey types (Olsen 2011; Olsen *et al.* 2013).

STUDY AREA AND METHODS

The study was conducted within the Canberra city limits (35°79'S, 149°59'E). The owl breeding territories within which prey samples were collected are detailed elsewhere (Olsen *et al.* 2020). Aside from adjoining grazing land, habitat in the vicinity of Boobook roosts in Canberra Nature Parks is primarily eucalypt open forest and tall woodland, with a shrub layer notably of Native Cherry *Exocarpos cupressiformis*, within the foliage of which Boobooks commonly roost (see Olsen *et al.* 2002, Olsen and Trost 2007 and Olsen *et al.* 2013 for details). The nearby suburbs of Cook and Aranda retain remnant eucalypts and a native and non-native understorey in which the owls also roost. Suburban winter roosts were variously located in a backyard in Melba (one pair), a front yard in Weston (all females), a school playground in Kaleen and suburban Barton (comprising offices, school and houses) (see Olsen and Taylor 2001).

Adult and fledgling Boobooks were trapped, banded, colour-banded, sexed (adults) by measurement and presence of a brood patch and radio-tracked, as described in detail elsewhere (Olsen and Trost 1997; Olsen *et al.* 2008, 2010, 2011, 2013, 2020). Thirty minutes before dusk we located the owls by radio receiver or using previous knowledge of roosting sites and, provided we did not disturb them, we collected regurgitated pellets and prey remains from under the roost or nest site in daylight. If there was any danger of flushing the owls, we waited until they left the roost and then searched the ground by torchlight. Pellets from the Weston roost were collected by local householders.

A total of 1,170 regurgitated entire pellets, plus many fragments, and 55 prey remains (orts) were collected during the years from 1993 to 2010 in a total of 540 separate collection events spread across 16 breeding and 12 non-breeding territories. Pellets were measured (length and width, ± 1 mm) and analysed by A.B. Rose (the Australian Museum); in a few small, early samples he only provided a range of pellet sizes per sample. He identified prey from pellets and prey remains, counting body parts to estimate the minimum number of prey items (MNI) in a pooled sample of pellets and prey remains per site per collection date to minimise biases in the food estimations (after Collopy 1983; Marti 1987; Seguin *et al.* 1998; Simmons *et al.* 1991). Feathers were identified by comparison with feather collections and museum specimens when necessary. Bones, hair, invertebrate body parts and scales were identified by microscopy (following Brunner and

Coman 1974 for mammalian hair) and by comparison with museum reference material. We did not assume that one pellet represented one individual prey item. For analysis of the diet of successful breeding pairs and their dependent juveniles, almost all pellets were collected during the post-fledging period and hence dietary parameters for the breeding season are heavily biased towards that particular breeding phase. As per A.B. Rose's notes, random single, presumably moulted, feathers of large birds such as Galahs *Eolophus roseicapilla* and Australian Magpies *Gymnorhina tibicen* near Boobook roosts or nests were discounted as belonging to Boobook prey, these birds being too large and dangerous for a Boobook to handle. Rose specifically looked for gecko scales (Gekkonidae, three species in the Canberra region) in pellets, but found none. Later collections, from summer 2011–2012 to winter 2019, totalled 110 pellets and five orts from 55 collection events across two breeding territories and one winter site in one of these territories. These samples were analysed by Georgeanna Story of Scats About (www.scatsabout.com.au, last accessed 7 March 2023). The MNI in these samples were estimates based on the number of pellets collected on a given date at a given site and the intervals between collection dates at individual sites within a given season (breeding or non-breeding). We assumed, for instance, that two fresh pellets containing remains of a rat-sized mammal collected on one day might represent two meals from the same animal (MNI = 1), but similar evidence in two fresh pellets collected several days or more apart represent two prey animals.

We estimated the contribution of prey types to dietary mass by multiplying the MNI by the average weight in each prey category. The mean or median weights of most prey were taken from the literature (see Appendix 1). However, the weight of some species was estimated by A.B. Rose based on the actual prey remains found at the nests to make the estimates more accurate (e.g., using bone sizes of rodents) (Steenhof 1983; Marti 1987). In doing so we applied correction factors using the methods of Baker-Gabb (1984a) and Brooker and Ridpath (1980), and this also achieved consistency and allowed comparison with previous studies in this series of papers (Olsen *et al.* 2006, 2008, 2013; Trost *et al.* 2008). We assumed that the raptors wasted or discarded 33%, 17% and 9% of the biomass of large (>300 g), medium (75–300 g) and small (<75 g) mammals, respectively, 20%, 12% and 5% of large, medium and small birds, respectively, and 5% of reptiles. We also included invertebrates in the last category. On top of correction factors mentioned above and following Baker-Gabb (1984b), as well as to maintain consistency with previous studies (Fuentes *et al.* 2007; Olsen *et al.* 2006, 2008, 2013), we used an upper limit of 300 g of maximum total biomass consumed by this species. As in other papers in our long-term study of the raptors in the Canberra region (Fuentes *et al.* 2007, Olsen *et al.* 2006; Olsen 2011), we calculated overall geometric mean prey weights (GMPW) using the method of Marti (1987) and the GMPW for some particular prey groups (mammals and birds) when sample sizes allowed.

The data were subdivided to explore four main dietary trends:

- (a) Breeding versus non-breeding sites
- (b) Long-term patterns, by dividing the data into two time periods (1993–2005 and 2006–2020) which yielded reasonable sample sizes, giving us 2,045 versus 1,774 prey items in breeding territories and 621 versus 647 in non-

breeding territories. The year 2005 was also a threshold year for an apparent change in local insect abundance (Debus *et al.* 2020).

- (c) The effect of brood size, by dividing the breeding attempts into failed broods and broods of one, two, three and four young fledged (B1, B2, B3 and B4). As prey sample sizes were too small for the failed and B1 categories (see Table 1 for sample sizes of nest-years in each category), we eliminated them from the MNI and biomass calculations.
- (d) Seasonal variation, by dividing all the samples according to the season (pooled across years) in which they were collected and assigning them to the following categories: (i) Breeding 1 October–1 January, (ii) Post-breeding 1 January–28 February and (iii) Non-breeding 1 March–14 August.

We calculated the numerical frequency and biomass estimates of prey items and compared the proportional contribution of prey to the total MNI for the four trends mentioned above using Chi-square tests of association (Zar 1984). A subsample for the years 2004–2009 that had the largest sample sizes in both breeding and non-breeding seasons was also separately analysed using this procedure to investigate any sample-size effects and validate the overall analytical approach. Also, in this period we had an even sampling effort between breeding and non-breeding territories; there was no potential bias in prey analysis methodology (since it all was performed by A.B. Rose); and there is full time overlap in the sample. (i.e., we have breeding and non-breeding samples for multiple territories every year). For this latter analysis, prey was assigned to four categories (mammals, birds, insects and arachnids). There were only three items that were not in these categories ($n = 2$ reptiles and $n = 1$ millipede, out of $n = 5,087$ total prey items) and they were excluded from the analysis. Prey weights were analysed using general linear models (GLM). All post-hoc contrasts were subjected to a Bonferroni correction. All analyses were performed in SAS OnDemand, R-Studio 4.1.1 and Excel 365.

A caveat with respect to this entire analysis is that territories were sampled unevenly (e.g., some only or mainly early in the study period, others only or mainly later in the study period) and non-breeding samples (including those from post-breeding females that had deserted their broods before juvenile independence) were biased towards adult female owls. Furthermore, for post-2010 data, breeding samples were collected in 2011–2014 and non-breeding samples in 2017–19, so they do not overlap temporally. Before 2010 we collected data for both breeding and non-breeding seasons in every year.

RESULTS

A total of 488 intact regurgitated pellets (of the 1,170 in total) measured 10–55 × 8–33 mm (mean 27 × 18 mm). Two further, early subsamples (of the 1,170) measured by A.B. Rose (although the dimensions per individual pellet were not provided), measured 24–43 × 17–23 mm ($n = 10$) and 20–35 × 13–16 mm ($n = 3$), respectively i.e., they were well within the range of the larger sample of 488.

Breeding versus non-breeding diet

The breeding and non-breeding diets were significantly different ($\chi^2 = 660.9$, d.f. = 3, $P < 0.001$). Breeding owls

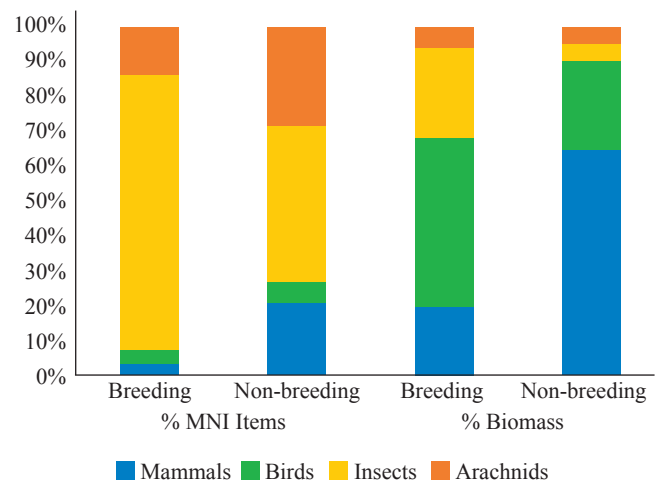


Figure 1. Breeding and non-breeding diet of Southern Boobooks in the ACT, expressed as percentage MNI and percentage biomass.

consumed proportionately more insects by number (79.0% versus 45.1% non-breeding, Fig. 1), whereas non-breeding owls captured more mammals (28.8% versus 3.3% breeding) and arachnids (28.2% versus 13.8% breeding). By biomass, birds formed the main prey group in the breeding season (48.5%), whereas mammals (64.6%) were the main item in the non-breeding season. The overall GMPW was significantly greater for non-breeding than breeding owls (3.1 versus 1.8 g) ($F = 220.7$; d.f. = 1; $P < 0.0001$). The bird GMPW did not differ with breeding status (Bonferroni correction, $P = 0.826$), whereas mammals were estimated to be slightly heavier during the non-breeding period (Breeding = 20.1 g versus Non-breeding = 26.1 g; Bonferroni correction, $P = 0.0003 < 0.013$).

The 2004–2009 subsample exhibited very similar patterns. Breeding and non-breeding diets were significantly different ($\chi^2 = 485.7$, d.f. = 3, $P < 0.001$), with mammals being a more prominent prey item during the non-breeding season (19.5% versus 2.5% breeding), as were arachnids (30.9% versus 15.3% breeding). Birds showed an opposite trend as in the overall sample, with the Boobooks consuming more avian prey during the breeding season (2.0% versus 1.8% non-breeding MNI; 33.3% versus 10.1% non-breeding biomass). Lastly, insects were captured more in the breeding season (79.9% versus 47.8% non-breeding).

The owls captured more ground-dwelling prey (mice, rats, spiders) during the non-breeding than the breeding period ($\chi^2 = 562.2$, d.f. = 1, $P < 0.0001$; 67.8% of total biomass comprised these three prey items) and more aerial prey in the breeding season ($\chi^2 = 465.3$, d.f. = 1, $P < 0.0001$; bats, birds and flying insects comprised 77.8% of total biomass). There was a significant seasonal difference in bat consumption ($\chi^2 = 5.96$, d.f. = 1, $P < 0.01$): they formed 32% of mammalian prey for breeding owls ($n = 40$, 1.0% of total prey), but only 1.5% for non-breeding owls ($n = 4$, 0.3% of total prey).

Long-term trends: 1993–2005 versus 2006–2019

Breeding diet by number of items (Fig. 2) was slightly different between the two time periods ($\chi^2 = 26.8$, d.f. = 3, $P < 0.001$): the consumption of birds (3.8% in 1993–2005 vs 3.9%

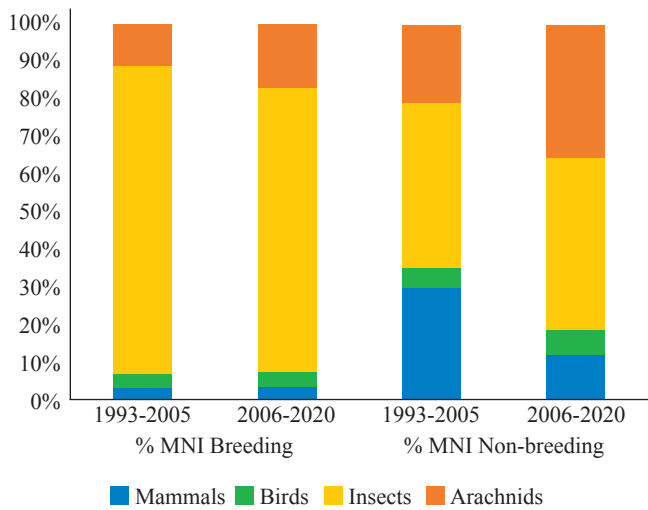


Figure 2. Long-term patterns in the diet of Southern Boobooks in the ACT, expressed as percentage MNI.

in 2006–2019) and mammals (3.1% vs 3.4%) was very similar in both periods, but there was a decrease in insects (81.9% vs 75.7%) and an increase in arachnids (11.1% vs 16.8%) in the second time period. Breeding biomass data showed similar trends (Fig. 3). The non-breeding diet differed significantly between the two time periods ($\chi^2 = 84.9$, d.f. = 3, $P < 0.001$). By number of items, fewer mammals (29.9% vs 12.1%) and more arachnids (20.6% vs 35.4%) were consumed in the non-breeding period in 2006–2019 than in 1993–2005.

There is an unusual contrast in the non-breeding data: although there was a 17.8% decrease in total number of mammals consumed between the two periods (Fig. 2), there was actually a 4.4% increase in mammal biomass in the more recent time period (62.0% vs 66.4%) because of a significant ($\chi^2 = 12.6$, d.f. = 1, $P < 0.01$) increase in the consumption of larger mammals, particularly Black Rats *Rattus rattus* ($n = 13$, 2.1% MNI, 12.8% biomass in 1993–2005; $n = 39$, 6.3% MNI, 54.5% biomass in 2006–2019). Also, on the basis of Rose’s analysis of skeletal material throughout the project, owls in the 1993–2005 period captured mainly juvenile Black Rats (11 of 13 or 84.6%), whereas in the 2006–2019 period they captured mostly adults (28 of 39 or 71.8%) ($\chi^2 = 22.2$, d.f. = 1, $P < 0.0001$). In contrast, the owls seldom consumed Black Rats in the 1993–2005 period during the breeding season, eating only three individuals in 13 years in the 16 territories studied.

The overall temporal pattern is also reflected in the GMPW. There were significant differences in prey mass consumed between time periods ($F = 18.2$; d.f. = 1; $P < 0.0001$) and with breeding status ($F = 227.4$; d.f. = 1; $P < 0.0001$). *Post-hoc* comparisons showed where these differences lay. Total GMPW was similar in both time periods for breeding owls (1.7 versus 1.7 g; Bonferroni correction $P = 0.947 > 0.016$), but higher for non-breeding owls in the 1993–2005 period (3.6 versus 2.6 g; Bonferroni correction $P < 0.001 < 0.016$). When the analysis was partitioned by prey taxonomic group, GMPW was similar for bird prey between the time periods and for owl breeding status (Bonferroni correction; $P > 0.212 > 0.006$). However, Mammalian GMPW was significantly higher for non-breeding

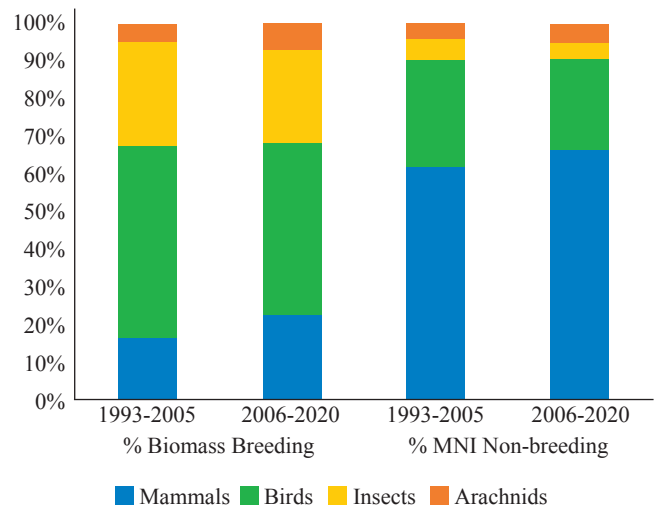


Figure 3. Long-term patterns in the diet of Southern Boobooks in the ACT, expressed as percentage biomass.

owls in the 2006–2019 period (50.2 g – Bonferroni correction; $P < 0.001 < 0.006$), when compared to the rest of the time periods and breeding statuses. There was no significant difference in GMPW for breeding owls between the 1993–2005 and 2006–2019 time periods (Bonferroni correction; $P = 0.549 > 0.006$); and also, for the non-breeding ones in 2006–2019 (20.0 g; Bonferroni correction; $P > 0.495 > 0.006$).

Effect of brood size on diet

Brood size had a significant effect on owl diet ($\chi^2 = 20.7$, d.f. = 6, $P < 0.005$). The MNI contribution to the diet of owls raising B4 was significantly different from that of owls raising B2 ($\chi^2 = 20.1$, d.f. = 3, $P < 0.001$) and B3 ($\chi^2 = 13.4$, d.f. = 3, $P < 0.005$), but there was no significant difference between the diets of owls raising these latter two brood sizes ($\chi^2 = 2.7$, d.f. = 3, $P > 0.05$). Owls with larger broods consumed fewer birds (MNI 4.2% for B2, 3.3% for B3, and 2.2% for B4; Fig. 4) and mammals (4.2% for B2, 3.3% B3 and 1.3% B4) than owls with smaller broods. In contrast, owls preyed more on arachnids (12.9% for B2, 13.4% B3, and 16.6% B4) and slightly more on insects (78.7% for B2, 79.8% B3 and 79.9% B4) when feeding larger broods. The diet of owls feeding B4 had a higher arachnid and insect biomass than that of owls raising smaller broods. Thus, owls raising B2 and B3 had a very similar prey biomass for arachnids (5.4 and 5.8%, respectively) and insects (26.4% for both), whereas parents raising B4 had a biomass contribution of 10.2% for arachnids and 38.3% for insects. Birds, insects and mammals all seem to be important contributors in total biomass for owls raising B2 and B3 (around 45% birds, 20% mammals and 26% insects: 94% of total biomass for both brood sizes), but for owls raising B4 the biomass of birds plus insects/arachnids was the main food source (44.8 + 48.5 = 93.3% of total biomass).

Although mammal MNI decreased with brood size (Fig. 4), a higher mammal biomass was consumed by owls feeding B3 than other brood sizes (Fig. 5). This was a result of owls with this brood size preying on particular types of large mammals, notably Sugar (Kreff’s) Gliders *Petaurus notatus*, Common

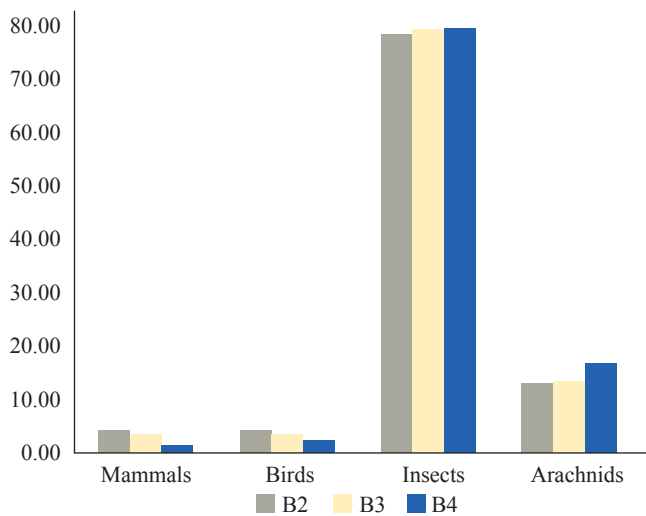


Figure 4. Percentage MNI contribution to diet brought to the nest for different brood sizes in Southern Boobooks in the ACT.

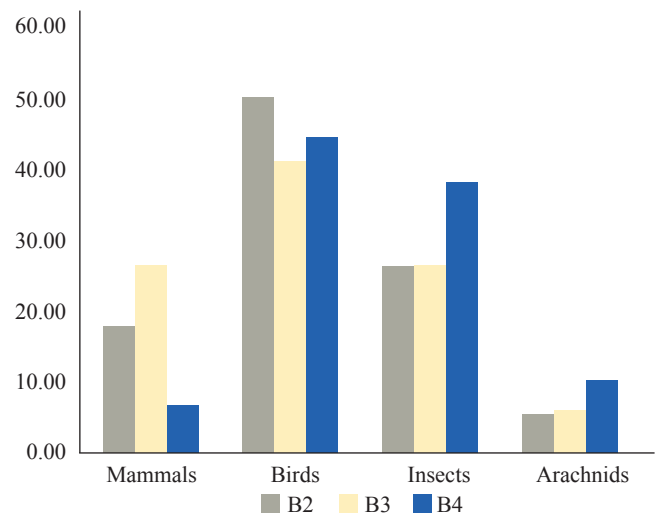


Figure 5. Percentage biomass contribution to diet brought to the nest for different brood sizes in Southern Boobooks in the ACT.

Table 1

GMPW of diet of adults rearing different brood sizes and in three within-year seasons for Southern Boobooks in the ACT during 1993–2019.

Brood Size	GMPW			Sample	
	All prey	Mammalian	Avian	Nest-years	MNI
Failed	4.71	N/A	N/A	5	31
B1	3.2	18.6	34.7	3	83
B2	1.87	17.26	38.92	19	1106
B3	1.68	24.18	39.44	31	1914
B4	1.59	17.14	44.1	7	685
Season					
Non-breeding	4.36	26.49	33.87	24	685
Breeding	1.86	19.89	52.2	11	553
Post-breeding	1.64	18.14	31.5	47	3153

Ringtail Possums *Pseudocheirus peregrinus*, European Rabbits *Oryctolagus cuniculus* and rats, all in small numbers. These species were taken exclusively by owls having B3, except for one Black Rat consumed by an owl raising B2. These species have a GMPW of 149.3 g, considerably larger than the average GMPW for mammals (Table 1). At the same time, owls raising B3 preyed heavily on House Mice *Mus musculus* ($n = 36$, 56% of mammalian prey), adding to the increase in mammalian biomass.

The GMPW showed a tendency to decrease as brood size being raised increased (Table 1). Although this decrease *per se* was not significant ($F = 1.1$; d.f. = 2; $P > 0.05$), there was a significant interaction between brood size and prey taxonomic group ($F = 2.6$; df = 6; $P < 0.05$), indicating that the relative consumption of some of the prey groups (birds and mammals) was different among owls raising different brood sizes. *Post-hoc* comparisons of each prey taxonomic category as a function of brood size being reared indicated the nature of this pattern. Mammalian GMPW was significantly higher for owls raising

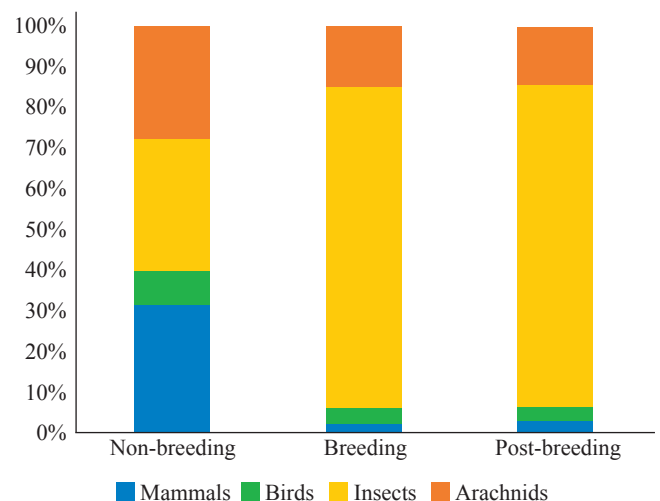


Figure 6. Seasonal variation in the diet of the Southern Boobook in the ACT, expressed as percentage MNI. Non-breeding = 1 March to 14 August; Breeding = 1 October to 31 December; Post-breeding = 1 January to 28 February.

B3 (24.2 g) than for those rearing B2 and B4 (17.3 and 17.1 g; Bonferroni correction; $P < 0.0001 < 0.008$). Generally, owls with larger broods took fewer birds, although avian biomass increased in owls raising B4, with birds being the main taxon contributing to dietary mass for this brood size (44.8%). However, bird GMPW was not significantly different between owls raising differently-sized broods (Bonferroni correction; $P > 0.05$).

Seasonal variation within the year

Breeding and post-breeding season diets were similar in terms of the number of prey items consumed ($\chi^2 = 2.7$, d.f. = 3, $P > 0.05$), but they differed from that in the non-breeding season ($\chi^2 = 298.0$ and 834.2, d.f. = 3 and 3, $P < 0.001$; Fig. 6 and 7). Owls captured more mammals (MNI 31.4% for non-breeding versus 2.3% for breeding and 3.0% for post-breeding) and spiders (27.6% for non-breeding versus 14.8% for breeding

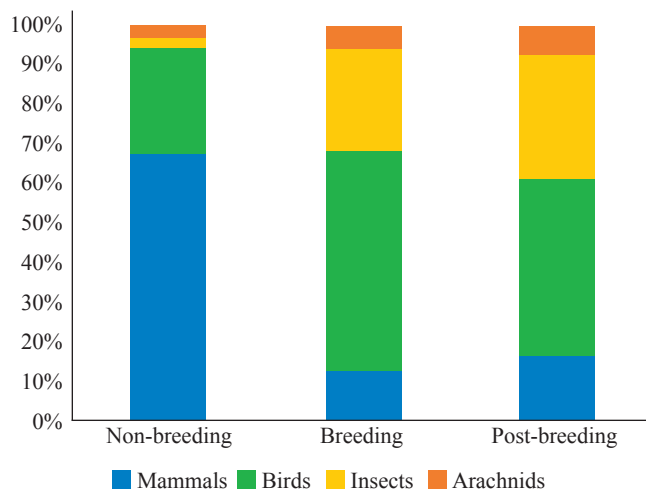


Figure 7. Seasonal variation in the diet of the Southern Boobook in the ACT, expressed as percentage biomass.

and 14.0% for post-breeding) but fewer insects (32.4% versus 78.8% and 79.6%) in the non-breeding than the breeding and post-breeding periods.

During the breeding and post-breeding seasons, biomass in the diet was dominated by birds (56.0 and 44.9%, respectively, Fig. 7) and insects (25.7 and 31.6%, respectively), whereas in the non-breeding period biomass was dominated by mammals (67.5%). Five species comprised 77.0% of the total dietary mass during the non-breeding season, namely House Mice, Black Rats, Common Starlings *Sturnus vulgaris*, Common Mynas *Acridotheres tristis* and House Sparrows *Passer domesticus*.

The non-breeding season diet had a higher GMPW than the breeding and post-breeding diets (Table 1; $F = 5.4$; $df = 2$; $P < 0.001$). Avian GMPW was significantly higher in the breeding than the post-breeding and non-breeding periods (52.1 versus 31.5 post-breeding and 33.9 g non-breeding; Bonferroni correction; $P < 0.001 < 0.008$), which was largely an outcome of the owls preying on medium-sized birds, namely Eastern and Crimson Rosellas *Platycercus eximius* and *P. elegans*, Crested Pigeons *Ocyphaps lophotes*, Bar-shouldered Doves *Geopelia humeralis* and Common Mynas, all weighing 100–200 g. Contrastingly, in the post-breeding and non-breeding seasons the owls preyed mainly on Passeriformes (Common Blackbirds *Turdus merula*, House Sparrows, finches Estrildidae, a few starlings, mynas and rosellas, but no doves). Mammalian GMPW was significantly higher during the non-breeding than the breeding and post-breeding seasons (Bonferroni correction; $P < 0.001 < 0.008$).

DISCUSSION

An important conclusion is that regardless of the way in which the samples were grouped by season, time period or brood size, Boobook diet was constantly dominated by biomass by vertebrates, the only exception being in owls rearing B4, where invertebrate biomass comprised 48.6% of the diet, an even higher percentage than birds (44.3%). Invertebrates dominated numerically in the breeding and post-breeding diets.



Figure 8. Southern Boobook with a captured bat in Canberra.

Photo: Jerry Olsen and Susan Trost.

Breeding versus non-breeding diet

The breeding diet was dominated numerically by flying insects, birds and micro-bats (Fig. 8) whereas the non-breeding diet was dominated by rodents and spiders (i.e., terrestrial prey), which is reflected in the higher overall GMPW of the non-breeding diet (although vertebrate GMPW was similar). This difference may reflect the following factors: (1) seasonal abundance and activity (e.g. nuptial and other flights in summer) of insects, (2) the major contribution of the smaller and more agile male Boobooks to food provisioning during the breeding cycle, (3) supplementation of the brood's diet with insect prey by female Boobooks (females hunt insects close to the nest while awaiting vertebrate prey deliveries by the male: Olsen 2011; Olsen *et al.* 2013), (4) differences in Boobook seasonal foraging energetics (e.g. more energy-saving perch-hunting in winter), and (5) the female-biased non-breeding samples (larger and heavier female Boobooks taking larger, less agile, terrestrial prey). Also, this disparity could be an outcome of relative prey abundances in winter. Winter in Canberra is cold (mean winter low temperature 0.7 °C; mean lowest winter temperature -1.5 °C; Bureau of Meteorology 2023) and there are fewer invertebrates available than during the rest of the year. Also, some birds migrate, making them unavailable in winter (e.g., pardalotes, some honeyeaters, orioles) and leaving local mammals as the main prey available in this season, particularly ground mammals as some bats go into torpor. Also, Boobooks seem more oriented to terrestrial prey in winter (J. Olsen pers. obs.). The differences regarding laboratories in charge of the analysis in post-2010 samples, relating to breeding data for 2011–13 and non-breeding data for 2017–19, probably affected

the seasonal comparison minimally if at all, because the few territories sampled were among those for pre-2010, and the post-2010 samples were much smaller. Also, the 2004–2009 subsample showed the same overall patterns and it was not affected by such bias.

Long-term dietary patterns

Overall, the owls' breeding diets were fairly similar in the two time periods investigated, including in GMPW. An increase in arachnids in the second period was the main difference recorded, a pattern also observable in the non-breeding diet. A major apparent long-term dietary trend was the decline in the numerical contribution of insects and rodents, as well as the increase in the contribution of spiders. There was also an increase in the size of rodents taken (more adult and fewer juvenile Black Rats than previously). This pattern is reflected in the lower overall GMPW but higher mammal GMPW than earlier on in the study. This trend may reflect a decline in insect abundance in recent years (e.g., Debus *et al.* 2020), the location of the sites of later non-breeding samples (i.e., mostly urban) and post-2005 non-breeding samples being from female owls. We are unaware of any rodent population data that would shed light on this issue, but it is possible that, for instance, increasing use of second-generation anticoagulant rodenticides (cf. Mooney 2017) might have been reducing rodent numbers in recent years.

Brood size and diet

It is difficult to separate cause and effect and any confounding effect of territory location (e.g., bushland versus urban/perurban) on the available prey profile. However, it appears likely that three dietary factors facilitated the raising of large broods: (1) a diverse and abundant mammalian prey resource, (2) a high invertebrate abundance and females supplementing the brood with invertebrate prey, and (3) that for the largest broods, female parents also contributed to hunting by capturing relatively large birds. Sample sizes for failed broods and B1 were small (Table 1), but there is a possibility that parents in such breeding attempts were not catching sufficient large vertebrate prey (mammals and birds) (as reflected in the low overall GMPW) to enable a viable breeding attempt or even raising a brood of only one, particularly when the vertebrate GMPW of broods >1 is considered (Table 1). Further study is needed to evaluate how nesting failure is influenced by the availability and capture of larger prey. Other factors could also be involved, such as nest predation, territorial conflicts, and climate. Some of these factors were observed in some territories during the study.

Seasonal dietary variation

Not surprisingly, the breeding diet and post-breeding diet (the latter comprising the post-fledging and independence stages of the breeding cycle) were similar in terms of dominant prey types (birds and insects) and GMPW. The similarity reflects the fact that these periods were in the season of high insect abundance (summer) when female parents supplemented the diet of nestlings, especially in larger broods, with insects and birds. The slight differences between breeding and post-breeding diets (slightly higher mammal and insect biomass,

and slightly lower avian biomass and GMPW in the latter period) may variously reflect the fact that juveniles foraged for some insects while still being fed by male parents and females deserted the brood and consequently did not capture bird prey for the young, instead foraging for themselves on prey more typical of their non-breeding diets.

The difference between the non-breeding and breeding/post-breeding diets was similar to that already noted in the breeding/non-breeding comparison. That is, birds and insects dominated numerically and by biomass in the breeding and post-breeding phases, and mammals and spiders dominated and GMPW was higher in the non-breeding season (although avian GMPW was highest in the breeding season).

Comparison with other studies

The present study encompasses the small samples of the Boobook's breeding diet in the ACT described by Olsen *et al.* (2006, 2013), Olsen (2011) and Trost and Olsen (2016). Otherwise, there would be little with which to compare the Boobook's breeding diet. Certainly, some of the stomach and pellet samples analysed by Rose (1996) date from the breeding season, but there he provides no information on the age or breeding status of the owls involved. These samples variously contained insects, spiders and a bird (starling) (stomachs from September to January) or insects, birds and mammals (pellets from October to January) from the same general prey spectrum as in the present study.

The findings of the present study on the Boobook's non-breeding diet, together with those of Trost *et al.* (2008), are similar to those of other accounts that were based on pellets collected over the autumn–winter period (Baker-Gabb 1984a; Campbell and Rose 1996; Rose 1996; McNabb 2002; Fitzsimons and Rose 2007; McDonald and Pavey 2014). The latter studies documented a diet composed of invertebrates, birds and mammals, with invertebrates (insects and spiders) dominating numerically but mammals dominating strongly (>70%) in terms of biomass. Of note in the non-breeding diet is the high number of spiders, similar to what was found in the south-eastern inland (Fitzsimons and Rose 2007) and in the arid zone, Boobooks exploiting a rodent outbreak (McDonald and Pavey 2014). As previously noted (Rose 1996; Trost *et al.* 2008; Olsen 2011), Boobook stomachs containing only insects in winter (Rose 1996; Penck and Queale 2002) reflects a sampling bias towards road and window collision-killed immature owls foraging in marginal habitats, whereas the few stomachs of adult owls in autumn–winter contrastingly contained mammals as well as insects (Rose 1996).

The absence of geckos (Gekkonidae) in the pellets and prey remains of owls in 26 years of study is noteworthy. Owls were seen to carry geckos to the nest often (Fig. 9), but the lizards never appeared in prey samples, possibly because they were swallowed whole, completely digested and left no bones or scales in pellets. The paucity of Krefft's Gliders in the diet is also noteworthy, as they are the same size as Black Rats. However, the gliders are aggressive, "bluff" the owls, cannot be caught from above (J. Olsen pers. obs.), and are also treated as nest predators or competitors and driven off rather than preyed upon by the owls (Olsen *et al.* 2020).



Figure 9. Southern Boobook taking a Marbled Gecko *Christinus marmoratus* to its nest in Canberra, an item that never appeared in pellets or prey remains in 26 years of study.

Photo: Jerry Olsen and Susan Trost.

Future research

It would be useful to study the same Boobook territories in the future, analysing comparable dietary sample sizes to achieve replication over time and hence a better understanding of the patterns identified in the present study. It would also be valuable to obtain more gender-balanced and habitat-balanced (e.g., non-urban as well as urban) non-breeding diet samples to elucidate the extent to which such biases in the present investigation may distort the picture of the non-breeding owl diet. The reason for the absence of geckos in the diet and potential means to avoid their underestimation as a food source needs further examination.

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APPENDIX 1

Prey species and number of prey individuals in the diet of the Southern Boobook in Canberra (ACT) from territories sampled in the breeding (total 16 territories) and non-breeding seasons (total 12) during 1993–2005 and 2006–2019 (two and one territories, respectively), as a basis for the biomass calculations outlined in Methods i.e. $n \times (\text{prey weight minus appropriate wastage factor})$, for the four analysis categories (seasons, time period and brood size). Prey weights taken from previous related studies and relevant literature. Individual invertebrates assumed to average between 0.5 and 2 g.

Species	Weight (g)	1993–2005		2006–2019	
		Br	Non-br	Br	Non-br
Kreff's Glider <i>Petaurus notatus</i>	128	2			
Kreff's Glider subadult	128	1			
Common Ringtail Possum <i>Pseudocheirus peregrinus</i> juv	200			1	1
White-striped Freetail-Bat <i>Tadarida australis</i>	36	1			
Gould's Wattle Bat <i>Chalinolobus gouldii</i>	14	10	1		
Common Bent-wing Bat <i>Miniopterus schreibersii</i>	15	3			
Long-eared bat <i>Nyctophilus</i> sp.	10			2	
Eastern Broad-nosed Bat <i>Scotorepens orion</i>	11	1			
Large Forest Bat <i>Vespadelus darlingtoni</i>	5		1		
Bat sp. (Microchiroptera)	20	24	2	1	
House Mouse <i>Mus musculus</i>	18	62	201	5	2
House Mouse juv	9	13	1		
Bush Rat <i>Rattus fuscipes</i>	125	1	1		
Black Rat <i>Rattus rattus</i>	180	1	11	1	19
Black Rat juv	50	1	22		
Rat <i>Rattus</i> sp.	180			3	2
Rodent sp. (Muridae)	50			1	
Rabbit <i>Oryctolagus cuniculus</i> juv	250		2	1	
Small mammal	20	2			
Crested Pigeon <i>Ocyphaps lophotes</i>	205	2	1		
Bar-shouldered Dove <i>Geopelia humeralis</i>	129	1			
Australian Owllet-nightjar <i>Aegotheles cristatus</i>	44	2			
Red-rumped Parrot <i>Psephotus haematonotus</i>	61		1		
Crimson Rosella <i>Platycercus elegans</i>	135	9			

APPENDIX 1 (continued)

Species	Weight (g)	1993–2005		2006–2019	
		Br	Non-br	Br	Non-br
Crimson Rosella juv	131	6			
Eastern Rosella <i>Platycercus eximius</i>	106	12		1	
Eastern Rosella juv	106	4			
Rosella sp.	119			1	
Superb Fairy-wren <i>Malurus cyaneus</i>	9		2		
Fairy-wren <i>Malurus</i> sp.	10	3			
Spotted Pardalote <i>Pardalotus punctatus</i>	9	1			
Striated Pardalote <i>Pardalotus striatus</i>	12	3			
Red Wattlebird <i>Anthochaera carunculata</i> juv	99	1			
Noisy Miner <i>Manorina melanocephala</i>	67	1			
Noisy Miner juv	52	1			
Noisy Friarbird <i>Philemon corniculatus</i>	109	1			
White-browed Babbler <i>Pomatostomus superciliosus</i>	40	1			
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	116	1			
Olive-backed Oriole <i>Oriolus sagittatus</i>	96	1			
Grey Fantail <i>Rhipidura albiscapa</i>	8	1			
Magpie-lark <i>Grallina cyanoleuca</i>	82	5			
Scarlet Robin <i>Petroica boodang</i>	13	3			
Robin <i>Petroica</i> sp.	15	2			
Silvereye <i>Zosterops lateralis</i>	11	7	1		
Common Blackbird <i>Turdus merula</i>	94		1		
Common Blackbird imm	94	1			
Common Starling <i>Sturnus vulgaris</i>	83	4	12		
Common Starling imm	75	2			
Common Myna <i>Acridotheres tristis</i>	126	3	3		
Common Myna juv	87	1			
Fairy Martin <i>Petrochelidon ariel</i>	11	1			
House Sparrow <i>Passer domesticus</i>	28	4	9		
Sparrow <i>Passer</i> sp.	26	2	2		
Red-browed Finch <i>Neochmia temporalis</i>	10	7	7		
Australasian Pipit <i>Anthus novaeseelandiae</i>	26	1			
Small passerine (Passeriformes)	10	23	1	1	8
Medium passerine	50	1		2	
Bird sp.	70	16	5	17	21
Nestling bird	5	1			
Skink sp. (Scincidae)	2	3			
Unidentified vertebrate	50		1		
Millipede (Diplopoda)		1			
Cockroach (Blattodea)		30	12		
Mantis <i>Tenodera</i> sp.			1		
Mantis (Mantidae)		4			
Cricket (Gryllidae)		8	7		
Mole cricket (Gryllotalpidae)			1		
Grasshopper (Tettigoniidae)		1			
Yellow-winged Locust <i>Gastrimargus musicus</i>			1		
Locust sp. (Acrididae)		46	16		
Grasshopper (Orthoptera)		637	179	3	2
Red-eye Cicada <i>Psaltoda moerens</i>		6			
Cicada sp. (Cicadidae)		8	1		
Leafhopper (Cicadellidae)		1			
Bug (Homoptera)		2			
Bug (Hemiptera)		6			
Ground beetle (Carabidae)		82	4		
Beetle (Passalidae)		3			
Pie-dish beetle (Tenebrionidae)		2			

APPENDIX 1 (continued)

Species	Weight (g)	1993–2005		2006–2019	
		Br	Non-br	Br	Non-br
Beetle (Tenebrionidae)		1	1		
Christmas beetle <i>Anoplognathus viriditarsus</i>		2			
Christmas beetle <i>Anoplognathus olivieri</i>			1		
Christmas beetle <i>Anoplognathus</i> sp.		367	12		
Black Beetle <i>Heteronychus arator</i>		11			
Scarab <i>Diaphonia dorsalis</i>		2			
Dung beetle (Scarabaeinae)		11	2		
Scarab (Dynastinae)		12	1		
Scarab (Scarabaeidae)		478	54		
Click beetle (Elateridae)		9	1		
Longicorn beetle <i>Phoracantha semipunctata</i>		8			
Longicorn <i>Phoracantha tricuspa</i>		2			
Longicorn <i>Phoracantha</i> sp.		403	73		
Longicorn <i>Copterus thoracicus</i>		1			
Longicorn (Cerambycidae)		157	16		
Leaf beetle (Chrysomelidae)		2			
Weevil (Curculionidae)		20	1		
Beetle (Coleoptera)		328	57	61	18
Moth (Lepidoptera)		381	88	1	2
Sugar ant <i>Campanotus</i> sp.		4			
Bull ant <i>Myrmecia</i> sp.		1			
Ant (Formicidae)		5			
Insect sp. (Insecta)		10	11		
Scorpion (Scorpiones)		2			
Wolf spider (Lycosidae)		453	320		
Huntsman spider (Heteropodidae)		52	20		
Spider <i>Uloborus</i> sp.		1			
Spider (Araneae)		37	16		