Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*

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Abstract. We observed the species and numbers of mobbing birds and their effects on a large, nocturnal, bird-eating predator, the powerful owl, together with the pattern of owl predation on mobbing and non-mobbing species. Owls were mobbed on 35 occasions by seven of 44 species of forest birds at a site composed of open forest (88% by area) and rainforest (12%). The majority of bouts involved individuals of a single species, although mixed groups were observed on nine occasions. Regular mobbers were between 4 and 26% of the owls' body weight. Owls abandoned their daytime roosts during 20% of bouts and responded by calling or actively monitoring mobbers during 54% of bouts. Mobbing appeared to explain why owls roosted in rainforest significantly more often than expected by its availability, mobbing being significantly less frequent in rainforest than in open forest. Only one mobbing species regularly occupied rainforest and the canopy of roosts in rainforest was denser than that in open forest, thus reducing the chances of an owl being detected by potential mobbers. Twelve species of forest birds were within the range of prey size of the powerful owl (75–800 g): six were mobbers and six non-mobbers. The frequency of owl predation on non-mobbers was 8.75 times that on mobbers. The species in this study took a high risk by mobbing a very large predator, but benefited by greatly reducing their chances of predation.

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Mobbing is a widespread anti-predator defence behaviour among both vertebrate and invertebrate taxa, but is best understood among birds and mammals (Harvey & Greenwood 1978). When birds mob a predator they gather around it, vocalize loudly and perform conspicuous visual displays (Francis et al. 1989). Sometimes they also physically strike the predator. The mobbing calls of birds have sharp transients and broad frequency ranges (Shalter & Schleidt 1977) which enable them to be recognized by both conspecifics and a wide range of other species (e.g. Hurd 1996). Consequently, avian mobbing is generally considered a social behaviour, sometimes with large mixed-species groups involved (Francis et al. 1989; Hurd 1996).

Mobbing benefits the mobbing individuals by impairing the predation efficiency of the predator, usually by either distracting it or driving it from the vicinity of the mobbers or their eggs and young (Curio 1978; McLean et al. 1986). A study of the impact of avian mobbing on the European kestrel, *Falco tinnunculus*, established that mobbing caused the kestrels to vacate their immediate foraging area (Pettifor 1990). Both flight-hunting and perch-hunting kestrels moved significantly further between their foraging positions when they were mobbed than when they were not mobbed. Mobbing also causes owls to vacate their daytime roosts (Flasskamp 1994).

Mobbing individuals also incur costs. Prolonged mobbing calls by nesting birds can signal the presence of a nest to predators (McLean et al. 1986) and predators may attack mobbing birds and injure or kill them (Denson 1979). Most research on the benefits of mobbing has involved situations where the mobbers were of similar size to the predator. For example, European kestrels were mobbed most often by lapwing, *Vanellus vanellus*, black-headed gull, *Larus ridibundus*, carrion crow, *Corvus corone*, and rook, *Corvus frugilegus*, all large birds unlikely to be preyed on by kestrels (Pettifor 1990). Under such

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circumstances the potential costs to the mobbers will be reduced because the risk of injury or predation is low. Studies on the effects of mobbing when the risks to the mobbing birds are high, such as when the predator is a large, bird-eating species, will contribute towards further understanding of the evolutionary significance of mobbing behaviour.

We studied the interaction of forest birds with a large, nocturnal, bird-eating predator, the powerful owl, which is one of the largest owls in the world (weight 1240–1700 g, body length 45–65 cm, wing span 112–135 cm). This species is sexually dimorphic in size with males (1469–1700 g) being larger than females (1240–1308 g; Pavey et al. 1994). Mobbing powerful owls is risky because the owls are double the size of most forest birds present within their range (e.g. Schodde & Tidemann 1988). Despite the owls' large size, they can readily capture a variety of small, fast-moving prey species (Tilley 1982; Chafer 1992). Birds (size range of 75–800 g) made up 28% of all prey items taken by powerful owls during the 2 years of this study (Pavey et al. 1994).

Powerful owls do not usually hunt during the day; instead they capture diurnal birds that are active at sunset and sunrise (personal observations). The owls may also take birds that are disturbed from their perches at night. Although the owls are mostly inactive during the day, they do occasionally capture prey that are active near their day roosts (e.g. Robinson 1968).

We examined whether any forest birds risked mobbing the owls and, if so, if they did it singly, in small groups or in large groups. We studied the outcome of such behaviour by observing the immediate response of owls when mobbed and recording their roosting positions in relation to the areas where the mobbers were active. To estimate the benefits of mobbing, we compared the incidence of owl predation on species that mobbed with those that did not mob the owls.

METHODS

Our study site was located in Brisbane Forest Park (southeast Queensland, Australia; 27°29′S, 152°58′E). We conducted observations between 1 May and 15 October in 1989 and 1990, within an area of about 14 ha where a pair of owls nested and roosted with their young. Rainforest covered

12% of the site and open forest made up the remaining 88%. The majority of forest birds in the area nested between August and October of each year, whereas the owls bred during the winter with the young leaving the nest between late July and mid-August (Pavey et al. 1994). Therefore, the study period included both breeding and non-breeding seasons of forest birds.

We conducted observations on the site over 142 days (approximately every second day) for a total of 147.5 h (mean survey time per day ± $SE = 62 ± 4.26$ min), recording the species and approximate numbers of all birds seen or heard during each survey period. Both rainforest and open forest were visited during a survey until all of the roosting owls were located. We recorded the exact location of each roost and, on a subsequent visit, estimated the foliage projective cover (FPC) in a circle 1 m in diameter above the roosting bird. Foliage projective cover is defined as the percentage of an area covered by foliage (Specht 1970). When we located roosting owls, we spent the remainder of the observation period within a radius of 250 m of them.

We watched and listened for any signs of mobbing activity such as birds calling loudly, performing conspicuous visual signals or flying through the forest in groups. An interaction was considered a mobbing bout if the bird(s) called loudly and/or gave conspicuous visual displays within a radius of 3 m of a powerful owl or flew at the owl. A bout was regarded as finished when the last mobber stopped calling and displaying or when the owl flew from its roost.

We observed mobbing bouts from a distance with $10 × 40$ binoculars and recorded details of all bouts. We recorded the species involved, the number of individuals of each species, the behaviour of the owl(s), the vegetation within which the interaction occurred and the approximate length of time (in min) during which each bird species exhibited mobbing behaviour. The response of the owl(s) was categorized as: (1) no response; (2) watch and call (called and monitored activity of mobbers); and (3) move on (flew to another perch).

To estimate whether the species involved in mobbing experienced reduced predation, we compared the frequencies of capture of mobbing and non-mobbing species by the owls. We describe the methods used to obtain dietary data of owls in Pavey et al. (1994). Weights of forest birds were

Table I. Frequency of mobbing bouts, composition of groups and mean number of individuals of each bird species observed mobbing powerful owls

Family	Species*	Frequency of mobbing (conspecific/ mixed groups)	Mean no. individuals per bout $\pm$ SE
Halcyonidae	Laughing kookaburra, *Dacelo novaeguineae* (306)	5 (0/5)	1.60 ± 0.4
Meliphagidae	Noisy miner, *Manorina melanocephala* (80)	15 (6/9)	4.73 ± 0.78
Dicruridae	Grey fantail, *Rhipidura fuliginosa* (8)	1 (1/0)	2
	Spangled drongo, *Dicrurus bracteatus* (79)	18 (14/4)	2.11 ± 0.25
Campephagidae	Black-faced cuckoo-shrike, *Coracina novaehollandiae* (134)	1 (0/1)	2
Artamidae	Grey butcherbird, *Cracticus torquatus* (75)	3 (0/3)	1.33 ± 0.33
	Pied currawong, *Strepera graculina* (321)	7 (5/2)	4.57 ± 2.91

*Weights (g) are given in parentheses.

obtained from the databases of the Queensland Museum and Australian Bird and Bat Banding Scheme.

Statistical Analysis

We used an unpaired *t*-test to compare the foliage projective cover of roosts in open forest with those in rainforest. A chi-square goodness-of-fit test (Pearson's chi-square statistic) compared use of the two vegetation types as roosts by the owls with their availability in the study area. A chi-square test of independence (Pearson's chi-square statistic) with Yates' correction for continuity compared the frequency of roosting and mobbing between the two vegetation types. An important assumption that should be met for the use of both types of chi-square test is that observations are independent (Kramer & Schmidhammer 1992). Our study design, which involved mobbing observations on a pair of owls and their three offspring, might have violated this assumption. However, we consider that observations were independent, both spatially and temporally. The owls occupied a large number of roosts within the study area which included the home ranges of several pairs or social groups of each of the mobbing species. Roost location changed almost daily. The cryptic behaviour of roosting owls and the low frequency with which mobbers located them (one bout per 252 min of observation) suggest that mobbers located owls while foraging and responded to their general gestalt as a predator. We saw no evidence that mobbers searched for roosting owls and mobbing

bouts were not restricted to particular roosts, times of day or parts of the study area. Thus each bout of mobbing appeared to be independent of previous bouts of mobbing. We consider the chi-square test to be the appropriate test under these circumstances.

RESULTS

Identity and Numbers of Mobbers

We observed powerful owls being mobbed on 35 occasions, which is a rate of one interaction per 252 min of observation. Seven species were involved in mobbing (Table I), ranging in size from the grey fantail, *Rhipidura fuliginosa* (8 g) to the pied currawong, *Strepera graculina* (321 g). Forty-four species of diurnal forest birds were present at the site during the study. Ten bouts of mobbing were directed against the (larger) male owl, 17 against the female and eight against the three young owls. Five species mobbed the owls on multiple occasions and two species only once. Hereafter, we refer to the species involved in more than one bout as 'multiple mobbers'. The weight of multiple mobbers ranged from 4 to 26% of the weight range of the powerful owl (1240–1700 g).

Twenty-six of the 35 bouts involved just one species. Of the remaining nine bouts, five had two species, two had three species and two had four species. The modal number of individuals involved per bout was two (mean=4.49). Six bouts involved mobbing by a single individual. The largest number of individuals involved in
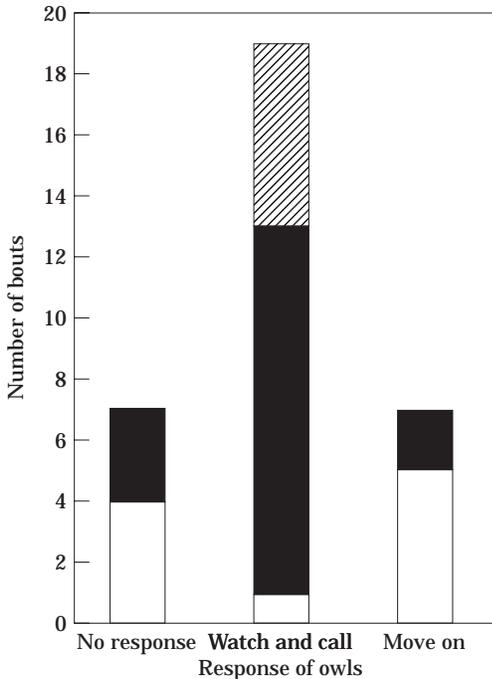
Figure 1. The response of powerful owls to mobbing by diurnal forest birds. □: Male; ■: female; ▨: young.

mobbing was a group of 22 pied currawongs. The largest mixed group consisted of 12 birds of three species.

Effects of Mobbing on Owls

Seven bouts of mobbing did not produce a vocal response from the owl or cause it to move (Fig. 1). Nineteen bouts produced a vocal response from the mobbed bird and/or active monitoring of the mobbers. Seven bouts (20%) involved the owl flying to another roost, sometimes being pursued by the mobbers. On five occasions the male flew, and on the other two the female flew. The remaining two bouts were not seen in sufficient detail to determine the effects on the owl. The female usually responded to harassment by watching the mobbers and calling, whereas the male either did not respond or flew to another roost. The young birds were always alerted by mobbing but they did not fly (Fig. 1). Either or both the spangled drongo, *Dicrurus bracteatus*, and noisy miner, *Manorina melanocephala*, were involved in all bouts that caused the owls to move roosts.

Table II. Frequency of powerful owls roosting in rainforest and open forest and the number of observations of mobbing in each vegetation type (combined for all owls and bird species)

	Roost days (*N*)	Mobbing bouts (*N*)
Rainforest	113	8
Open forest	116	27
Total	229	35

A roost day is an observation of an owl at its diurnal roost for 1 day.

Although rainforest made up only 12% of the site, owls were recorded roosting in rainforest on 113 occasions and in open forest on 116 occasions (Table II). The use of the two vegetation types as roosts by the owls was significantly different from their availability (chi-square goodness-of-fit test: $\chi^2_1 = 310.54$, $P < 0.0001$). The preference for the owls to roost in rainforest was associated with a decreased frequency of harassment by forest birds in this vegetation (Table II). Although the owls roosted with almost equal frequency in each vegetation type, 77% of bouts of mobbing took place in open forest. This difference in the frequency of roosting and mobbing between rainforest and open forest was significant (chi-square test of independence with Yates' correction for continuity: $\chi^2_1 = 7.55$, $P < 0.01$).

Mobbing may have been less frequent in rainforest for two reasons. (1) The canopy of rainforest is always denser than that of open forest, and, in our study, the mean foliage projective cover of owl roosts in rainforest ($\bar{X} \pm \text{SE} = 87.53 \pm 1.76\%$) was significantly higher than the mean of roosts in open forest ($67.73 \pm 2.51\%$; *t*-test: $t_{84} = 6.65$, $P < 0.0001$). (2) The spangled drongo was the only species that both mobbed owls and frequently occupied rainforest in the study area. It was involved in all bouts of mobbing in rainforest, and was the sole participant in all but one bout. The other multiple mobbers generally avoided rainforest and resided in open forest and adjoining parkland.

Benefits to Mobbers

The size range of birds captured by the powerful owls roosting in the study area during the

2-year period was 75–800 g (Pavey et al. 1994), a range consistent with data on avian prey of this species throughout eastern Australia (Tilley 1982; Chafer 1992). Therefore, we restricted our comparison of frequencies of capture to species of mobbing and non-mobbing birds within this size range that were resident during the study. Six species from each group fitted these criteria. These species were all the mobbers except the grey fantail (Table I) and the following non-mobbers: wonga pigeon, *Leucosarcia melanoleuca* (380 g); pale-headed rosella, *Platycercus adscitus* (145 g); rainbow lorikeet, *Trichoglossus haematodus* (116 g); scaly-breasted lorikeet, *T. chlorolepidotus* (80 g); Australian magpie, *Gymnorhina tibicen* (301 g); and torresian crow, *Corvus orru* (538 g).

The frequency of owl predation on non-mobbing species (*N*=35) was 8.75 times that of predation on mobbing species (*N*=4). Of the mobbing species, spangled drongo and black-faced cuckoo-shrike, *Coracina novaehollandiae*, were never taken and one individual of each of the other four species was captured.

DISCUSSION

The very large size of the powerful owls did not deter seven of the 44 species of forest birds in the study area from mobbing them. The weights of the multiple mobbers were between 4 and 26% of the weight range of the owl (1240–1700 g). Both the larger male and smaller female were regularly mobbed by other birds, and both sexes were harassed into changing roosts. Despite the large size difference between the mobbing species and the owls, birds did not usually mob in large numbers. A typical bout of mobbing involved two individuals of a single species. Single birds mobbed the owls on six occasions. Large conspecific and heterospecific flocks did form, but they were uncommon.

In the short term, mobbing by forest birds resulted in the owls either monitoring the behaviour of their attackers and calling (54% of bouts) or moving away from the vicinity of the interaction (20% of bouts). Mobbing appeared to influence the owls' use of vegetation as roosts. The owls roosted in rainforest as frequently as they roosted in open forest, despite the site being dominated by open forest (88% of the area). The incidence of mobbing was significantly lower in

rainforest than open forest, presumably as a consequence of both its denser canopy, which would reduce the chances of mobbers encountering the owls, and its regular occupation by only one species of multiple mobber, the spangled drongo. The long-term effect of mobbing on the owls was to move them away from the vegetation where the majority of mobbing species foraged.

When a bird mobs another species that is much heavier than it and that regularly preys on small birds, it incurs a high risk of injury or death. Theory predicts that for such a high-risk behaviour to be maintained within any population, it must in some way increase the fitness of those individuals that are involved in mobbing. This benefit will most likely result from a decreased chance of predation on the mobbing individuals or their offspring (Pettifor 1990). Our study has demonstrated that among a community of 44 bird species, six species of mobbers were captured 8.75 times less frequently than six species of similar size that did not mob owls. Therefore, the fitness benefit of engaging in predator mobbing during this study was a decreased risk of predation to the mobber itself. Previous research has shown that passerines that mob potential predators are able to reduce predation on themselves or their eggs and offspring (Hoogland & Sherman 1976; Blancher & Robertson 1982).

An obvious difference between the mobbers and non-mobbers in this study was that mobbers included only one non-passerine (Table I), whereas non-mobbers included a pigeon, three parrots and two passerines. Mobbing is recorded for a far greater number of passerine than non-passerine species (e.g. Bildstein 1982; Francis et al. 1989; Pettifor 1990; Stone & Trost 1991; Flasskamp 1994; Hurd 1996). It has been recorded among some non-passerines, including lapwings, gulls, parrots, woodpeckers and, in this study, kingfishers (Eitniear et al. 1989; Francis et al. 1989; Pettifor 1990). The taxonomic difference between mobbers and non-mobbers in our study and the increased likelihood of passerines being mobbers suggest that the predation pattern of the owls could reflect a preference for non-passerine prey rather than being a consequence of mobbing. We examined this alternative explanation by comparing the amount of predation by powerful owls on passerines and non-passerines recorded in the major dietary studies listed in Pavey et al. (1994). Passerines were captured in far greater numbers

than non-passerines (80 passerines, 11 non-passerines). Therefore, it is unlikely that the higher frequency of predation on non-mobbers reported in our study resulted from a preference of the owls for non-passerine prey.

Avian mobbing is often initiated by the sight of a hunting predator (Bildstein 1982; Pettifor 1990). As the owls were roosting when mobbed, this response clearly did not occur in our study. The mobbers were probably responding to the powerful owl's general gestalt as a predator when they engaged in mobbing behaviour. The crepuscular and nocturnal activity of the owls would prevent forest birds from observing their hunting activity, except during a short period at dusk and dawn each day. Despite the small period of overlap in activity between predator and prey, diurnal birds were a major prey item of powerful owls in our study area (Pavey et al. 1994). This predation is similar to the heavy predation by diurnal raptors on insectivorous bats emerging from their daytime roosts at sunset (Fenton et al. 1994).

ACKNOWLEDGMENTS

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