

Seasonal variation in naturally occurring mobbing behaviour of drongos (*Dicruridae*) towards two avian predators

VINCENT NIJMAN

Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands (E-mail: nijman@science.uva.nl)

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I tested the hypothesis that mobbing chiefly functions as a nest defence mechanism by studying the mobbing behaviour of two species of drongo (black drongo *Dicrurus macrocercus* and ashy drongo *D. leucophaeus*) towards two species of raptor in rain forest of western Java, Indonesia. It was predicted that firstly mobbing would occur more frequent and more intense during the drongo's breeding season and secondly that it would be more frequently and more intensely directed towards the nest and egg predating black eagle *Ictinaetus malayensis* compared to the relatively harmless Javan hawk-eagle *Spizaetus bartelsi*. I found a seasonal difference in mobbing frequency and intensity in the predicted direction for the Javan hawk-eagle but not for the black eagle. Black eagles were not more frequently or more intensely mobbed than Javan hawk-eagles. In the tropics, mobbing to repel a predator may be adaptive at both seasons due to the year-round residency of drongos. Furthermore, if black eagles use the frequency or intensity of mobbing as a clue to locate nests, a lack of seasonal difference in mobbing behaviour by drongos may be an evolutionary adaptive strategy.

KEY WORDS: anti-predator behaviour, black eagle, Indonesia, Javan hawk-eagle, mobbing.

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INTRODUCTION

Many bird species from diverse orders exhibit mobbing behaviour. This can be directed towards potential predators, but also to competitors and apparently

innocuous species (ARNOLD 2000). Mobbing can cause profound distress, may lead to significant changes in time-budgets, and even abandonment of the area (FLASSKAMP 1994). The widespread occurrence of the behaviour is somewhat surprising, for it often involves the bird seeking out a potentially dangerous animal and performing conspicuous displays near it, or even attacking it. That mobbing does involve a serious risk is attested by several reports of mobbing birds being seized by predators (SORDAHL 1990). The adaptive significance of mobbing has for a long time remained an enigma, but it may serve as a nest (or offspring) defence mechanism (CURIO 1978). For instance, in species where the female builds the nest and incubates the eggs, the nesting-defence hypothesis predicts sexual differences in mobbing intensity, i.e. a higher level of mobbing initially by the female, whereas the male's response should increase when he starts feeding the nestling, a result indeed found in meadow pipits *Anthus pratensis* (PAVEL & BURES 2001). We would expect mobbing to be (largely) confined to the breeding season and it should increase in intensity during the breeding season, a pattern that has been found in some species (e.g. American robin *Turdus migratorius*, SHEDD 1982, chaffinch *Fringella coelebs*, KRAMS & KRAMA 2002). Other species, however, display mobbing behaviour even in the non-breeding period, albeit at lower intensity (black-capped chickadee *Poecile atricapilla*, SHEDD 1983). In yet other species, such as the noisy miner *Manorina melanocephala*, a large proportion of the mobbers apparently do not make another type of contribution to the nest, possibly indicating unrelatedness to the nestlings, suggesting other benefits such as a display of social status or individual quality (ARNOLD 2000, cf. ZAHAVI & ZAHAVI 1997).

Given that several bird species have been reported to mob a large range of other species, mobbing towards different species may serve different functions. The possible functions and adaptive significance of mobbing in birds are mostly studied experimentally by placing real or stuffed potential predators, or by playing their calls, in the territories of the mobbing species (e.g. SHALTER 1978; SHEDD 1982, 1983; FLASSKAMP 1994; HALUPKA & HALUPKA 1997; ARNOLD 2000; PAVEL & BURES 2001). In most of the studies using real predators these are normally either tethered or caged, precluding direct conclusions on the context of the mobbing behaviour and the interaction between mobber and mobbed (but see e.g. ZAHAVI & ZAHAVI 1997). Furthermore, mobbing of stationary predators may have different proximate functions than mobbing when under immediate threat by e.g. a nearby raptor in flight (DESROCHERS et al. 2002). Here I explore the possible function of naturally occurring mobbing behaviour by drongos (Dicruridae) to two similar-sized, large, free-living avian predators, the Javan hawk-eagle *Spizaetus bartelsi* and the black eagle *Ictinaetus malayensis* in the rainforests of western Java, Indonesia.

Drongos are a largely (sub)tropical family of insectivorous birds. Although weighing only 40-90 g, they are well-known for their aggressive behaviour towards larger birds, especially raptors (NIJMAN & SÖZER 1995, FREY et al. 2000).

The Javan hawk-eagle hunts mainly from perches, and a wide range of prey is taken, including birds (NIJMAN et al. 2000). However, when birds were involved it mainly comprised ground-perching birds and the relatively short second toe is evidence that the eagle is not adapted to catch birds in flight. In contrast, the black eagle chiefly hunts on nestlings, eggs, and birds (HOGERWERF 1949). Its small wing-loading (the ratio of body mass to surface area of the wing), elongated tail, and pronounced slotting of the primaries make it capable of manoeuvring along the forest edges slowly, soaring in search of prey. Its elongated and only slightly curved claws effectively enlarge its grasp area and enable the eagle to handle eggs,

whereas its relatively large gape allows it to carry eggs away from the nest in the beak. Hence, in all likelihood, the Javan hawk-eagle is not a significant predator of drongos, and poses little threat to their eggs and nestlings. The black eagle, however, is expected both to hunt the drongos themselves and to pose an especially large threat to the eggs and nestlings.

If the hypothesis that mobbing serves as a nest (or offspring) defence mechanism is correct, it is expected that (a) mobbing should be more intense towards the egg and nest predating black eagle compared to the relatively harmless Javan hawk-eagle and (b) mobbing should be more intense during the drongo's breeding season.

METHODS

Data acquisition

I studied mobbing behaviour of drongos towards eagles at three study areas in western Java, i.e. Mt Gede-Pangrango (107°00'E, 06°45'S: 1994-2001), Mt Slamet (109°15'E, 07°15'S: 1994-1995), and Mts Dieng (109°35'E, 07°06'S: 1994-2001) (for a description of the study areas, see VAN BALEN et al. 2001). Observations were made from ridges, vantage points and watchtowers with a total effort of > 300 days inside forested areas. The eagles occur at low population densities and in all, I had 110 contact hr with Javan hawk-eagles (73 hr during the breeding season of drongos; see below) and 84 with black eagles (37 hr during the breeding season).

Mobbing behaviour is only one phase in a continuum of behavioural response to a predator that ranges from fleeing to attacking (SIMMONS 1952). Visual displays and vocalisation in combination with closely approaching a predator are widely considered to constitute mobbing (e.g. SHEDD 1982), but the context in which e.g. physical attacks are performed differ from those when mobbing is restricted to just vocalising. In the analysis, I therefore only included direct attacks in which physical contact with the eagle was made. Attacks consist of short dashing flights, and/or repetitive strikes, performed by one or several birds (NIJMAN & SÖZER 1995). The intensity of the attack was measured directly by the duration of the attack and indirectly by the response of the eagle. For analysis the duration of the attack was ordered along an ordinal scale from *short* (1-5 sec), to *medium* (5-20 sec) to *long* (> 20 sec). Likewise, the response of the eagle to the attack was subjectively classified on an ordinal scale: *indifferent* (the eagle appears to ignore the attack with almost no change in flight pattern noted, although the bird may be vocalising), *actively avoiding* (the eagle maintains its flight in a straight line but responds to each attack by a drop in height), or *defending* (the eagle actively defends itself by losing height and turning on its back to deter the attack). Although the drongos were not individually recognisable, the study was conducted at a great number of localities throughout the study areas over a period of 8 years, so most observations can be assumed to be of different drongos, and therefore are independent.

Analysis

In the study areas four species of drongo are present. Analysis was restricted to the two most common species, i.e. black drongo *Dicrurus macrocercus* and ashy drongo *D. leucophaeus*. These two species are very similar morphologically and ecologically. On Java, they occur over a similar altitudinal range with, however, ashy drongo having a greater preference for forest and black drongo for more open habitats (S. VAN BALEN pers. comm.). Breeding in western Java occurs largely from April to June (Fig. 1), coinciding with the beginning of the

dry (or less wet) season. Given an incubation period of about 16-17 days, and a nestling period of about 17-18 days (data from *D. adsimilis*: FREY et al. 2000), and while acknowledging the occurrence of nests at all times of the year, the period April-August was considered the breeding season for drongos on Java and, subsequently, September-March as the non-breeding period.

I used a log-likelihood analysis (G-test) to test for differences in the distribution of occurrences, with the expected values generated based on a random distribution proportional to sampling effort per species or season (cf. NIJMAN & VAN BALEN 2003). To obtain a better approximation to χ^2 William's correction to G was applied (G_{adj} : SOKAL & ROHLF 1995). G_{adj} values were compared with critical values of the χ^2 distribution. Significance was assumed when $P < 0.05$ in a two-tailed test.

RESULTS

Differential mobbing by drongos towards avian predators

Mobbing of one of the two species of eagle by one of the two species of drongo was a relatively rare occurrence, and especially those mobbing attempts that involved physical contact. In all, I documented 27 mobbing attempts by drongos that included an attack with physical contact, i.e. 17 towards Javan hawk-eagles and 10 towards black eagles. Ten attacks were performed by ashy drongos and 7 by black drongos. For 10 attacks the birds were not identified to the species level but were by either ashy or black drongos (and not one of the two other species of (racket-tailed) drongo present in the study areas). All but one of the attacks were towards flying eagles; once a black eagle perched in a tree was attacked for several

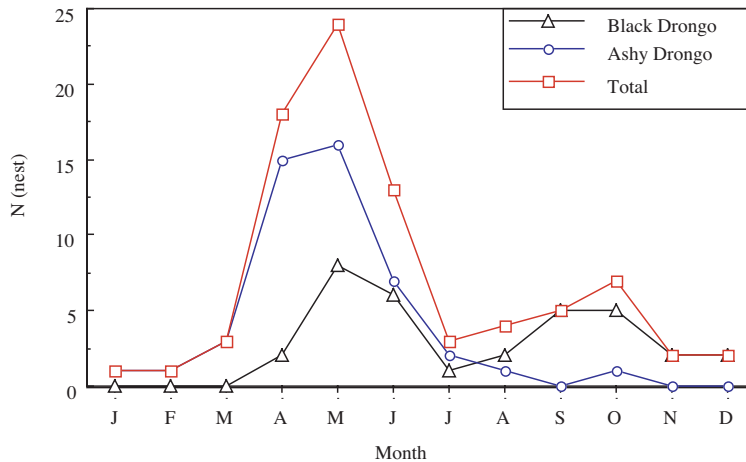


Fig. 1. — The breeding season of Dicruridae (black drongo *Dicrurus macrocercus* [N = 33], ashy drongo *D. leucophaeus* [N = 47]) in western Java, Indonesia based on the number of nests observed per month (data from HOOGERWERF 1949 and HELLEBREKERS & HOOGERWERF 1967). Months during which a nest was found but no eggs were collected were included conservatively as a single nesting attempt.

minutes by two black drongos. Attacks ranged from short single strikes with a duration of only a few seconds, to a series of repetitive attacks lasting up to five minutes.

Black eagles were not more frequently attacked than Javan hawk-eagles ($G_{\text{adj}} = 0.3$, $df = 1$, $P = 0.60$). Duration of attacks (*short, medium, long*) did not differ between the two species of eagle (Mann-Whitney U, $N_1 = 8$, $N_2 = 12$, $P = 0.93$), nor did the two eagles differ significantly in their response to the attack (Mann-Whitney U, $N_1 = 6$, $N_2 = 11$, $P = 0.28$). Thus the prediction that black eagles should be more frequently or more vigorously attacked is not supported by the data.

Seasonal variation in mobbing behaviour by drongos

Combining data from both eagles, no association between mobbing and season was apparent ($G_{\text{adj}} = 0.3$, $df = 1$, $P = 0.60$). There is however a significant seasonal difference between the two species in the number of attacks received (Fig. 2: $G_{\text{adj}} = 5.6$, $df = 1$, $P = 0.018$). The black eagle tended to be more frequently mobbed during the non-breeding season than during the breeding season of drongos (8 attacks during 44 observation hours vs 2 attacks during 37 observation hours), but the difference is not significant ($G_{\text{adj}} = 2.5$, $df = 1$, $P = 0.11$). For the Javan hawk-eagle significantly more attacks were documented during the breeding season (15 attacks during 73 observation hours) compared to the non-breeding season (2 attacks during 36 observation hours) ($G_{\text{adj}} = 4.0$, $df = 1$, $P = 0.045$).

The intensity of the attacks measured directly by its duration did not differ with season (Mann-Whitney U, $N_1 = 2$, $N_2 = 10$, $P = 0.19$ and $N_1 = 4$, $N_2 = 6$, $P =$

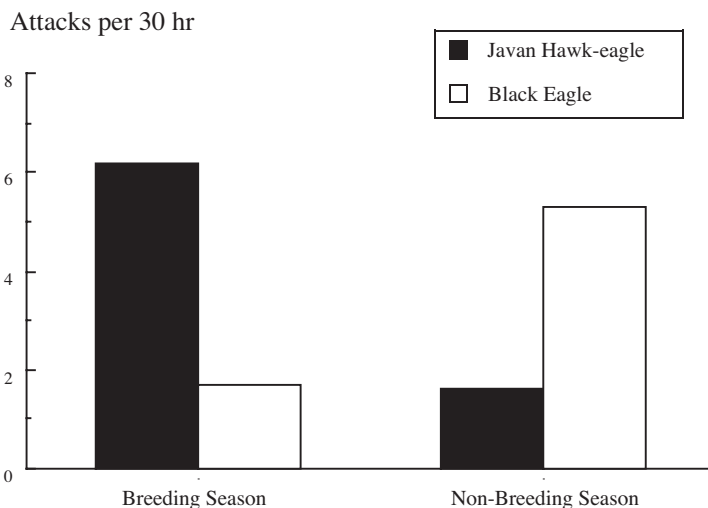


Fig. 2. — Seasonal differences in mobbing intensity by drongos towards two avian predators (Javan hawk-eagle *Spizaetus bartelsi* and black eagle *Ictinaetus malayensis*) as indicated by the number of attacks per 30 hr of observation.

0.86 for Javan hawk-eagle and black eagle respectively). However, the response of the Javan hawk-eagle towards the mobbing behaviour of the drongos showed a tendency to differ between the seasons (Mann-Whitney U, $N_1 = 2$, $N_2 = 9$, $P = 0.08$), with *actively avoiding* and *defending* being relatively more common during the breeding season. This may suggest either more intense mobbing during the breeding season by drongos or, alternatively, a seasonal difference of motivation of Javan hawk-eagles towards attacks.

DISCUSSION

Both species of eagle range over large areas, with homeranges in the order of 10-30 km² (VAN BALEN et al. 2001, NIJMAN 2004) and occur at low population densities. During the 300-days in the field, on average 39 min day⁻¹ were in contact with the eagles during which, on average, 0.14 mobbing attacks hr⁻¹ were recorded. Hence, although drongos are widely reported to frequently mob raptors, mobbing of Javan hawk-eagle and black eagle was a relatively rare occurrence. As a consequence, sample sizes in the present study were small, but nevertheless allow the main research questions to be answered. Due to difficulties associated with studying mobbing in free-living species in a rainforest environment larger sample sizes will be difficult to obtain.

Contrary to the prediction from the nest/offspring defence hypothesis, black eagles were not more frequently attacked than Javan hawk-eagles, nor was there a difference apparent in the intensity of the attacks by drongos towards the two eagles. Other studies have found clear differences in mobbing response towards different predators. ARNOLD (2000) found a higher mobbing intensity for noisy miners towards a stuffed predator of nests and adults (brown falcon *Falco berigora*) and a novel bird (brown dove *Macropygia amboinensis*) compared to a predator on nests only (Torresian crow *Corvus orru*). Likewise, SLAGSVOLD (1985) found mobbing response of hooded crow *C. corone* to differ between three different stuffed predators.

Several studies of mobbing behaviour have noted an association between this behaviour and reproductive activity (CURIO 1978, SHEDD 1982). Only for the Javan hawk-eagle did the number of attacks increase during the drongo's breeding season. The willingness of drongos to mob Javan hawk-eagles more during the breeding season than during the non-breeding season, probably stems from at least three factors: (1) drongos are more aggressive at this time than during other times of the year and lack the option of easy relocation away from predators on their territories, (2) birds are likely to have eggs or young on their territories (cf. SHEDD 1982) and (3) if the Javan hawk-eagles have a greater need for prey to feed their offspring during the drongo's breeding season, they in fact may pose a greater threat to drongos than at other times of the year (S. VAN BALEN in litt.). It should be noted, however, that although significantly more nests were found during April-June, breeding has been observed during all months. Attacks during the "non-breeding period" may reflect a small number of birds having a nest or may indicate a base-line level of mobbing that is present all-year round.

Black eagles seem to be attacked all-year round, and the number of attacks was actually higher during the non-breeding season, albeit non-significantly. Unlike many temperate areas, many species in the tropical rain forests of Java are proba-

bly year-round residents. More sedentary animals should mob more intensely than less sedentary ones (SHERMAN 1977). Living continuously on a territory or home range may mean that mobbing to force a predator away is adaptive at all times of the year, because relocation to avoid further predator encounters is not possible. Thus, for sedentary species, the benefits of causing a predator to 'move on' would maintain mobbing at some baseline level that will be increased in the breeding season, as mobbing serves an additional function of protecting the young. Since black eagles may pose a larger year round threat than the Javan hawk-eagle, vigorously attacking them at any time may make evolutionary sense.

Counterintuitively this study suggest that black eagles may actually be less frequently mobbed during the drongo's breeding season. An explanation for either the lack of seasonality in mobbing towards black eagles, or even a decrease in mobbing intensity during the drongo's breeding season, may be due to the specific threat that this eagle poses. Unlike most other bird-predating raptors, black eagles mainly predate on eggs and nestlings, and less so on fledglings or adults. If black eagles make use of the intensity of mobbing in order to locate nests, as has been suggested for cuckoos (CRAIB 1994) and cowbirds (SMITH et al. 1984, but see GILL et al. 1997), reduced mobbing during the breeding season may actually enhance the fitness of the drongos. The data from the present study are consistent with that of BURES & PAVEL (2003) and the hypothesis warrants further investigation.

In conclusion, as noted in other studies, drongos are frequent mobbers towards potential predators, but possibly in response to different selection pressures certain predators are more intensely mobbed than others during different phases of the breeding cycle. This study suggests that mobbing may also be related to the type of threat posed by the predator to the birds and/or their offspring.

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REFERENCES

- ARNOLD K.E. 2000. Group mobbing and nest defense in a cooperatively breeding Australian bird. *Ethology* 106: 385-393.
- BALEN S. VAN, NIJMAN V. & SÖZER R. 2001. Conservation of the endemic Javan Hawk-eagle *Spizaetus bartelsi*, Stresemann, 1924 (Aves: Falconiformes): density, age structure, and population numbers. *Contributions to Zoology* 70: 161-173.
- BURES S. & PAVEL V. 2003. Do birds behave in order to avoid disclosing their nest site? *Bird Study* 50: 73-77.
- CURIO E. 1978. The adaptive significance of avian mobbing: I Teleonomic hypothesis and predictions. *Zeitschrift für Tierpsychologie* 48: 175-183.

- CRAIB J. 1994. Why do common cuckoos resemble raptors. *British Birds* 87: 78-79.
- DESROCHERS A., BELISLE M. & BOURQUE J. 2002. Do mobbing calls affect the perception of predation risk by forest birds? *Animal Behaviour* 64: 709-714.
- FLASSKAMP A. 1994. The adaptive significance of avian mobbing 5: an experimental test of the move on hypothesis. *Ethology* 96: 322-333.
- FREY C.H., KEITH S. & URBAN E.K. 2000. Birds of Africa. Vol. VI. London: Academic Press.
- GILL S.A., GRIEF P.M., STAIB L.M. & SEALY S.G. 1997. Does nest defence deter or facilitate cowbird parasitism? A test of the nesting-cue hypothesis. *Ethology* 103: 56-71.
- HALUPKA K. & HALUPKA L. 1997. The influence of reproductive season stage on nest defense by Meadow Pipits (*Anthus pratensis*). *Ethology Ecology & Evolution* 9: 89-98.
- HELLEBREKERS W.P.H.J. & HOGERWERF A. 1967. A further contribution to our oological knowledge of the island of Java (Indonesia). *Zoologische Verhandelingen, Leiden* 88: 1-164.
- HOGERWERF A. 1949. Bijdrage tot de oölogie van Java. *Limosa* 22: 1-320.
- KRAMS I. & KRAMA T. 2002. Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *Proceedings of the Royal Society London (B)* 269: 2345-2350.
- NIJMAN V. 2004. Habitat segregation in two congeneric hawk-eagles (*Spizaetus bartelsi* and *S. cirrhatous*) in Java, Indonesia. *Journal of Tropical Ecology* 20: 105-111.
- NIJMAN V. & SÖZER R. 1995. Aggressive behaviour displayed towards the Javan Hawk-eagle *Spizaetus bartelsi*. *Kukila* 7: 152-154.
- NIJMAN V. & VAN BALEN S. 2003. Wandering stars: age-related habitat use and dispersal in Javan Hawk-eagles. *Journal für Ornithologie* 144: 451-458.
- NIJMAN V., VAN BALEN S. & SÖZER R. 2000. Breeding biology of the Javan Hawk-eagle *Spizaetus bartelsi* in West Java, Indonesia. *Emu* 100: 125-132.
- PAVEL V. & BURES S. 2001. Offspring age and nest defense: test of the feedback hypothesis in the Meadow Pipit. *Animal Behaviour* 61: 297-303.
- SHALTER M.D. 1978. Effect of spatial context on the mobbing behaviour of Pied Flycatchers to a predator model. *Animal Behaviour* 26: 1219-1221.
- SHEDD D.H. 1982. Seasonal variation and function of mobbing and related anti-predator behaviors of the American Robin (*Turdus migratorius*). *Auk* 99: 342-346.
- SHEDD D.H. 1983. Seasonal variation in mobbing intensity in the Black-capped Chickadee. *Wilson Bulletin* 95: 343-348.
- SHERMAN P.W. 1977. Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253.
- SIMMONS K.E.L. 1952. The nature of predator reactions in breeding birds. *Behaviour* 4: 161-171.
- SLAGSVOLD T. 1985. Mobbing behaviour of the Hooded Crow *Corvus corone cornix* in relation to age, sex, size, season, temperature and kind of enemy. *Fauna Norvegica (C)* 8: 9-17.
- SMITH J.N.M., ARCESE P. & MACLEAN J.G. 1984. Age, experience and enemy recognition by wild song sparrows. *Behavioral Ecology and Sociobiology* 14: 101-106.
- SOKAL R.R. & ROHLF F.J. 1995. Biometry. The principles and practice of statistics in biological research, 3rd ed. New York: W.H. Freeman.
- SORDAHL T.A. 1990. Risk of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bulletin* 102: 349-352.
- ZAHAVI A. & ZAHAVI A. 1997. The Handicap Principle, a missing piece of Darwin's puzzle. Oxford: Oxford University Press.