

The benefits of joining mixed-species flocks for Greater Racket-tailed Drongos *Dicrurus paradiseus*

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Drongos are well known to participate in mixed-species bird flocks, but it is not clear whether they are mostly commensalists, catching insects that other species disturb, or kleptoparasites, stealing food directly from other species. We studied the foraging ecology of Greater Racket-tailed Drongos *Dicrurus paradiseus* inside and outside mixed-species flocks in seven areas of a lowland rainforest in Sri Lanka. We found that drongos in all seven areas fed at a higher rate when in flocks. Kleptoparasitism was practised at a low rate (4% of observations); more often, drongos captured insects disturbed by other species (41% of observations). To accrue these benefits, drongos adjusted the height at which they perched to match the foraging height of Ashy-headed Laughingthrush *Garrulax cinereifrons*, a species that forages lower than drongos normally do, and those of Orange-billed Babbler *Turdoides rufescens*, a species that forages higher than drongos normally do. We conclude that drongos are better classified as commensalists than as parasites, as they exact only a small cost on other species in flocks; they may even be mutualists, because they make sensitive and reliable alarm calls to which other species react.

INTRODUCTION

The benefits of mixed-species flocking, whether reduced predation risk or increased foraging efficiency, are often analysed as they apply to the flock as a whole (Morse 1977, Terborgh 1990). Different species, however, may benefit from flocking in different ways (Hino 1998). Furthermore, species differ in the benefits they provide to others, with some 'nuclear' species being particularly important to flock formation and cohesion (Moynihan 1962, Hutto 1994). A full description of a mixed-flock system would therefore depict the flow of different benefits among a web of species.

The complexity of interspecific relationships within mixed-species flocks is exemplified by the role of drongos Dicruridae, which are frequent members of such flocks in the Old World tropics and Australasia. Drongos may benefit other species by giving alarm calls and serving as flock 'sentinels', because their sallying foraging technique makes them particularly vigilant for predators (Munn 1984, Goodale and Kotagama 2005a). Alternatively, they may neutrally affect other species, but accrue benefits themselves, by catching insects disturbed ('beat-up') by other species (Swynnerton 1915, Hino 1998). Or they may negatively affect other species through kleptoparasitism (Brockmann and Barnard 1979, King and Rappole 2001). To understand whether drongos are respectively mutualists, commensalists or parasites in a flock system, all possible interactions must be measured.

A mixed-flock system in the rainforests of Sri Lanka provides an opportunity to understand fully the relationship between drongos and other species within a flock. It has previously been argued that Greater Racket-tailed Drongos *Dicrurus paradiseus* play a sentinel, nuclear role in this flock system, because they are sensitive in detecting predators and make reliable alarm calls (Goodale and Kotagama 2005a), and because other birds are attracted to a random sample of their vocalisations (Goodale and Kotagama 2005b). Here, we investigate the benefits gained by drongos from being in such flocks. First, we compare the foraging rate and success of drongos inside and outside flocks. Second, we assess how these foraging benefits arise; specifically whether drongos act as commensalists, capturing insects disturbed by other

species in the flock, or as kleptoparasites, stealing prey items from other flock members. Finally, we examine whether drongos enhance their likelihood of these foraging benefits by increasing their proximity to other flock members. In particular, we investigate whether drongos adjust their perch height to match that of two leaf-gleaning species: Ashy-headed Laughingthrush *Garrulax cinereifrons*, which forages lower than drongos, and Orange-billed Babbler *Turdoides rufescens*, which forages higher than drongos (Kotagama and Goodale 2004). We predicted that the closer drongos were horizontally to these species, the closer they would be vertically.

METHODS

Study site

The study was conducted in the north-western sector of the Sinharaja World Heritage Reserve, a rainforest in Sri Lanka (6°26'N 80°21'E, 400–600 m). Sinharaja is an evergreen lowland rainforest, with the canopy dominated by trees of *Mesua* spp. and *Shorea* spp. (Gunatilleke and Gunatilleke 1981). The mixed-species flocks of the reserve are large (averaging 12 species and 40 individuals), and are characterised by two species that are found in >90% of flocks: Greater Racket-tailed Drongo and Orange-billed Babbler (Kotagama and Goodale 2004).

Data collection

As all observations were made on unmarked birds, flocks were studied at several different sites within the forest to enhance sample independence. A previous radio-telemetry study of Greater Racket-tailed Drongos showed that they had home ranges less than 1.5 km in diameter (Goodale and Kotagama 2006b). We selected seven areas of the forest within walking distance of the Sinharaja Research Station that were each c. 1.5 km in diameter and 1.5 km from each other.

Observations were carried out by SHKS and field assistants. An observation began when a perched drongo was detected and ended when that drongo flew to a perch from where it could not be seen; observations therefore varied in length and so were timed. For each observation, the following were noted: (a) whether a bird was inside a

babbler-led flock (defined as within 10 m of an Orange-billed Babbler) or not (drongos outside such flocks were sometimes loosely associated with other species, but such associations fell apart quickly and were very different from typical babbler/drongo flocks); (b) the height, at the start of the observation, of the drongo's perch and the horizontal and vertical distance to the closest Ashy-headed Laughingthrush and to the closest Orange-billed Babbler; and (c) how many foraging trips the focal bird made, a foraging trip being either a 'sally' (a circuitous flight obviously directed towards an aerial insect) or a 'hover' (a foraging attempt to capture an insect on a substrate while hovering in the air). After each observation, the observer noted whether the drongo had performed any of the following behaviours during the last foraging trip of the observation: (a) kleptoparasitised another species by taking food directly from the bill; (b) chased an insect another species was chasing (also considered kleptoparasitism); or (c) captured an insect that was disturbed by another species (if the path of the insect was seen or the drongo foraged in an area where vegetative debris was falling). These three categories were mutually exclusive. The observer also recorded whether this last foraging trip was successful in capturing an insect (if a captured insect was seen or if the drongo was seen manipulating an insect in its bill).

Analysis

In the original design of the study, the unit of replication was the seven different areas in which we sampled. However, because not all data were available from all areas, sample sizes were sometimes too small for statistical analysis between areas. Hence, we also investigated the strength of relationships within areas. To test whether drongos adjust their foraging height to match leaf-gleaning

species, we compared the vertical and horizontal distances between the drongo and the other species using simple linear regressions for each area separately. Whenever we made tests on multiple areas, we adjusted the α -level of the test accordingly.

RESULTS

Greater Racket-tailed Drongos foraged at a significantly higher rate inside flocks (mean \pm SE foraging trips per minute = 0.43 ± 0.04) than they did outside flocks (0.12 ± 0.04 ; Wilcoxon test: $W_{pos} = 28$, $W_{neg} = 0$, $N = 7$, $P < 0.025$). This relationship was apparent in all seven areas, although significant in only five of them (Table 1). Foraging success was also significantly higher inside flocks (175 successes in 303 observations that included foraging trips, 58%) than outside flocks (8 successes in 24 observations that included foraging trips, 33%, Fisher's Exact Test, $P = 0.03$). This trend was found in the five areas for which it could be calculated, but was not significant in any of them.

When in mixed-species flocks, 41% of drongo foraging trips involved the capture of insects disturbed by other species (Table 2). In a large majority of these cases, insects were disturbed by Orange-billed Babblers (81%); the remainder were dominated by trunk-gleaning or probing species, such as Indian Scimitar Babblers *Pomatorhinus horsfieldii* (6%), Velvet-fronted Nuthatches *Sitta frontalis* (4%), Lesser Yellownapes *Picus chlorolophus* (3%) and Black-rumped Flamebacks *Dinopium benghalense* (3%). Compared with the capture of disturbed insects, drongos showed a very low rate (3%) of kleptoparasitism (Table 2). Eighty-five percent of the 20 kleptoparasitic events involved food taken directly from the bill of another bird;

Table 1. The foraging rate of Greater Racket-tailed Drongos inside and outside mixed-species flocks.

Area	Number of observations	Mean foraging rate (number of trips per minute)		Mann Whitney U test
		Inside	Outside	
Camp to West Main	129	0.35	0.09	$U = 809$ $P = 0.04$
Deniya to Heendola	89	0.45	0.25	$U = 144$ $P = 0.47$
Lankagama	35	0.44	0	$U = 27$ $P = 0.005$
Murakelle	78	0.35	0	$U = 168.5$ $P = 0.01$
Pitakelle	61	0.64	0.10	$U = 94.5$ $P < 0.001$
Sinhagala	69	0.37	0.31	$U = 337$ $P = 1.00$
Waturava	120	0.42	0.10	$U = 796.5$ $P < 0.001$

Table 2. Methods of prey capture by Greater Racket-tailed Drongos foraging in mixed-species flocks. Figures shown are the number (and percentage) of observations which involved kleptoparasitism, the disturbance of prey by another species, or in which no other species was involved.

Area	Number of observations	Kleptoparasitism	Disturbance by another species	No other species involved
Camp to West Main	129	5 (4%)	46 (36%)	78 (60%)
Deniya to Heendola	89	3 (4%)	52 (58%)	34 (38%)
Lankagama	35	1 (3%)	14 (40%)	20 (57%)
Murakelle	78	2 (3%)	32 (42%)	44 (55%)
Pitakelle	61	3 (5%)	32 (52%)	26 (43%)
Sinhagala	69	1 (1%)	21 (30%)	47 (69%)
Waturava	120	5 (4%)	39 (33%)	76 (63%)
Total	581	20 (3%)	236 (41%)	325 (56%)

Table 3. The relationships between the vertical distance (VD) and the horizontal distance (HD) from a Greater Racket-tailed Drongo to the nearest Orange-billed Babbler and Ashy-headed Laughingthrush. No Ashy-headed Laughingthrushes were present in three of the areas. Symbols after area names correspond to those in Fig. 1.

Area	Orange-billed Babbler	Ashy-headed Laughingthrush
Camp to West Main Δ	VD = 1.43 + 1.07 HD $F_{1,100}=23.21$ $P=0.007$	VD = 1.87 + 1.07 HD $F_{1,54}=44.35$ $P=0.004$
Deniya to Heendola \blacktriangle	VD = 2.71 + 0.27 HD $F_{1,81}=0.48$ $P=0.99$	VD = 5.19 + 0.36 HD $F_{1,22}=5.59$ $P=0.72$
Lankagama \square	VD = 1.19 + 0.68 HD $F_{1,24}=12.43$ $P=0.01$	—
Murakelle \diamond	VD = 1.29 + 0.16 HD $F_{1,65}=3.08$ $P=0.46$	—
Pitakelle \blacklozenge	VD = 0.99 + 0.63 HD $F_{1,39}=6.42$ $P=0.10$	—
Sinhagala \bullet	VD = 1.24 + 0.42 HD $F_{1,49}=17.50$ $P=0.007$	VD = 2.31 + 0.26 HD $F_{1,11}=1.56$ $P=0.67$
Waturava \circ	VD = 1.59 + 0.51 HD $F_{1,67}=10.32$ $P<0.01$	VD = 3.52 + 0.53 HD $F_{1,26}=28.60$ $P=0.004$

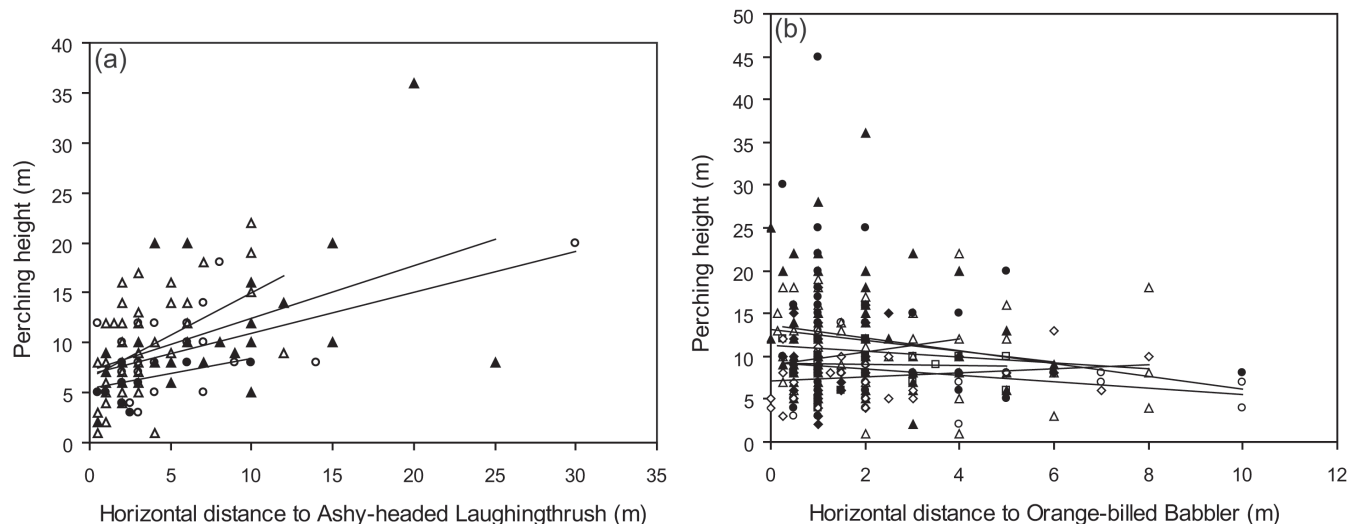


Figure 1. The tendency for Greater Racket-tailed Drongos to match the foraging heights of leaf-gleaning species led to drongos perching lower when close to the ground- and understory-feeding Ashy-headed Laughingthrushes (a), and perching higher when close to the subcanopy-feeding Orange-billed Babblers (b). Regression lines are for the separate areas; symbols correspond to areas listed in Table 3. Note that the y-variable here (perching height) is not the same as the response variable (vertical distance) in Table 3.

in the remainder, drongos caught an insect another bird had been chasing. In the majority of kleptoparasitism cases, the victim was a leaf-gleaning babbler (75% Orange-billed Babbler, 10% Ashy-headed Laughingthrush); the remainder of incidences involved Malabar Trogon *Harpactes fasciatus* (10%) and Indian Scimitar Babblers (5%).

Drongos tended to match their perching height to the foraging height of leaf-gleaning species. Drongos that were closer horizontally to Ashy-headed Laughingthrushes were also closer to them vertically in all four areas that could be tested, and significantly so in two areas (Table 3). The same trend held for Orange-billed Babbler: the closer drongos were horizontally to babblers, the closer they were vertically in all seven areas tested, and significantly so in four areas (Table 3). This behaviour resulted in drongos foraging lower when horizontally close to Ashy-headed Laughingthrushes, and higher when horizontally close to Orange-billed Babblers (Fig. 1).

DISCUSSION

This study adds to the considerable body of evidence that drongos, and sallying species more generally, benefit from associating with other animals. Drongos have been reported to follow a wide variety of animals from ungulates (Herremans and Herremans-Tonnoeyr 1997) to

woodpeckers (Styring and Ickes 2001), and may even make use of phenomena that disturb insects such as wildfires (Ali and Ripley 1987). We found that Greater Racket-tailed Drongos in Sri Lanka rainforests foraged at a higher rate and were more successful when they joined mixed-species bird flocks. This is consistent with earlier studies in India, where Veena and Lokesha (1993) showed that drongos increased their foraging rate and success when associating with mynas, and in Madagascar, where Hino (1998) showed that drongos and another sallying species (Madagascar Paradise Flycatcher *Terpsiphone mutata*) foraged more successfully when in mixed-species flocks. Drongos in Sri Lanka rarely foraged alone and thus seem to be quite dependent on their association with other species in flocks.

Two mechanisms have been proposed by which sallying species, such as drongos, benefit from mixed-species flocks: the beating effect (Swynnerton 1915), in which these species capture flushed insects, or kleptoparasitism (Brockmann and Barnard 1979). In some earlier studies, kleptoparasitism was argued to be important (Hino 1998,), whereas in others the benefit of beating predominated (Veena and Lokesha 1993, Herremans and Herremans-Tonnoeyr 1997, Styring and Ickes 2001). Our study showed that Greater Racket-tailed Drongos use both mechanisms, but that kleptoparasitism is relatively infrequent in comparison with beating. Greater Racket-tailed Drongos in the mixed-species flocks of the

Sinharaja World Heritage Reserve in Sri Lanka can therefore be considered more commensal than parasitic with respect to their foraging ecology.

Greater Racket-tailed Drongos appeared to adjust their spatial position in flocks to increase their proximity to other species. The Ashy-headed Laughingthrush is one of the few species in Sri Lankan flocks that tends to forage at a lower height than drongos (Kotagama and Goodale 2004), and drongos foraged lower when associated with laughingthrushes. Similarly, drongos matched their height to that of nearby Orange-billed Babblers, which forage higher on average than drongos (Kotagama and Goodale 2004). One explanation for these results is that drongos may benefit from a dilution effect, in which proximity to another individual reduces the risk of predation (Terborgh 1990). Our impression, however, is that other sallying species, such as Asian Paradise Flycatcher *Terpsiphone paradisi* and Malabar Trogon, also forage lower when laughingthrushes are present, whereas leaf-gleaning species such as Orange-billed Babbler do not adjust their height. This suggests that the primary reason why drongos adjust their foraging height is to maximise the benefit from the beating effect.

Drongos use their vocal behaviour to increase their proximity to other species, by vocally mimicking the songs and contact calls of other species (Goodale and Kotagama 2006a). Since drongos benefit from associating with other species, this mimicry could be an adaptive, manipulative behaviour. The reason why other species have not evolved an ability to detect and avoid being attracted to such mimicry, and why other species did not act aggressively towards drongos may be because the costs of associating with drongos are low: the rate of kleptoparasitism in this study was only 3%. Moreover, other species may benefit from the presence of drongos, owing to their sensitive and reliable alarm calls (Goodale and Kotagama 2005a). Future studies should investigate whether other species adjust their behaviour to avoid being close to drongos, so avoiding being vulnerable to kleptoparasitism, or whether they lower their vigilance when drongos are present, relying instead on the drongos' alarm calls.

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