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Shrewd alliances: mixed foraging associations between treeshrews, greater racket-tailed drongos and sparrowhawks on Great Nicobar Island, India

Meera Anna Oommen^{1,†} and Kartik Shanker^{2,*}

¹Centre for Herpetology/Madras Crocodile Bank Trust, Post Bag 4, Mamallapuram, Tamil Nadu 603104, India

²Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

*Author for correspondence (kshanker@ces.iisc.ernet.in).

[†]Present address: Dakshin Foundation, C-305, Samvridhi Gardenia, 88/3 Bytarayanapura, Bangalore 560065, India.

Mixed-species foraging associations may form to enhance feeding success or to avoid predators. We report the costs and consequences of an unusual foraging association between an endemic foliage gleaning tupaid (Nicobar treeshrew *Tupaia nicobarica*) and two species of birds; one an insectivorous commensal (greater racket-tailed drongo *Dicrurus paradiseus*) and the other a diurnal raptor and potential predator (*Accipiter* sp.). In an alliance driven, and perhaps engineered, by drongos, these species formed cohesive groups with predictable relationships. Treeshrew breeding pairs were found more frequently than solitary individuals with sparrowhawks and were more likely to tolerate sparrowhawks in the presence of drongos. Treeshrews maintained greater distances from sparrowhawks than drongos, and permitted the raptors to come closer when drongos were present. Treeshrew foraging rates declined in the presence of drongos; however, the latter may provide them predator avoidance benefits. The choice of the raptor to join the association is intriguing; particular environmental resource states may drive the evolution of such behavioural strategies. Although foraging benefits seem to be the primary driver of this association, predator avoidance also influences interactions, suggesting that strategies driving the formation of flocks may be complex and context dependent with varying benefits for different actors.

Keywords: mixed foraging associations; predator avoidance; context dependence; treeshrews; drongos; sparrowhawks

1. INTRODUCTION

Mixed-species flocks of birds are hypothesized to occur either to improve foraging efficiency or to reduce

predation risk to flock members (Greenberg 2000; Sridhar *et al.* 2009). Although extensive observations of mixed flocks have been reported from across the world, there are few recorded reports of birds of prey participating in foraging associations. In the rare cases where raptors have been observed, the interactions have typically been with taxa that are larger and not at risk of predation, such as the association between double-toothed kites and capuchin monkeys (e.g. Boinski & Scott 1988). The presence of birds of prey in mixed avian and mammalian groups has not been reported before nor explored in the context of small mammals such as treeshrews where the predator–prey size ratio is larger, a factor that may increase relative predation risk. Here, we report a mixed-species association between a raptor (*Accipiter* sp.) and two other species; namely the greater racket-tailed drongo (*Dicrurus paradiseus*) and the Nicobar treeshrew (*Tupaia nicobarica*), and report on the costs and benefits to different species. We address this by examining: (i) frequencies and patterns of organization and occurrence of different species combinations, (ii) distances of species from each other in different combinations, and (iii) foraging rates.

2. MATERIAL AND METHODS

(a) Study area

The study was carried out on Great Nicobar Island (6°45' to 7°15' N, 93°38' to 93°55' E, 995 km²) in the Andaman Sea. The mixed foraging association was observed in all survey locations (the southern, eastern and western parts of Great Nicobar). A low-lying mixed-species littoral woodland of 5 km² at South Bay in Galathea National Park in the southern portion of Great Nicobar was selected for intensive study as this location was relatively more accessible than the rest of the island.

(b) The mixed flock

The Nicobar treeshrew, *T. nicobarica*, is a small endangered range-restricted mammal confined to Little and Great Nicobar islands (combined area of approx. 1000 km²). It is a small tupaid (75 g) characterized by extreme arboreality and a high degree of insectivory. The species was largely encountered as solitary individuals (hereafter singletons) or as breeding pairs that typically foraged and rested together. There have been few studies on wild treeshrews, a notable exception being a detailed study of several species in Borneo (Emmons 2000). Greater racket-tailed drongos (*D. paradiseus*, 74–124 g) play various roles in foraging associations, ranging from mutualists and commensal feeders to occasional kleptoparasites (Satischandra *et al.* 2007). Accipiters (300–350 g) are known to feed on large insects, small reptiles and amphibians, birds and occasionally small mammals (Gamauf *et al.* 1998). Several accipiters are reported from Great Nicobar Island (Nicobar sparrowhawk *Accipiter butleri*, Besra *Accipiter virgatus*, Chinese sparrowhawk *Accipiter soloensis* and Japanese sparrowhawk *Accipiter gularis*); uncertainty regarding plumage characteristics and distribution precluded species-level identification (see the electronic supplementary material for details).

(c) Field methods

Instantaneous scans and focal animal/group observations were the two main sources of data that were collected over a period of three and a half months (see the electronic supplementary material for details). Instantaneous scans were employed to understand group composition, distances between individuals of the group and to record primary activities of members of the group. We recorded a total of 360 scans (totalling 25 h) during the study, distributed through the period of the day when treeshrews are active. On locating a group, we noted the activities of group members at 3 or 5 min intervals until the group was lost; the interval for each successive scan was picked randomly. In addition, we also employed focal animal/group sampling where a group once located was followed until it disintegrated or was lost in the canopy. Focal sampling (totalling 13 h, 25 min) was used to assess foraging rates (the interval between two feeding events) and to collect additional data on distances between individuals. Observations of solitary drongos and sparrowhawks were recorded outside the mixed flock for 63 and 30 min, respectively.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0945> or via <http://rsbl.royalsocietypublishing.org>.

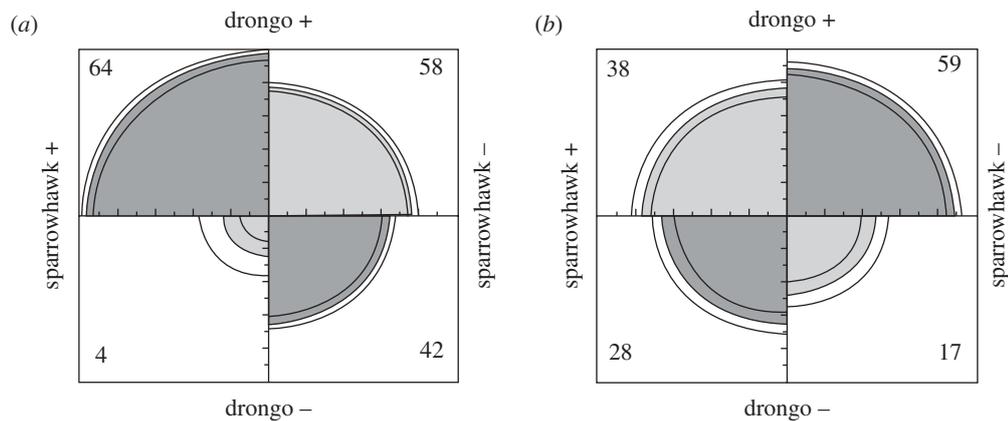


Figure 1. Number of occurrences (count) of members of the foraging association during instantaneous scans: (a) solitary individuals; (b) pairs. Presence of a particular species is denoted by 'plus' and absence by 'minus'. The three-way interaction between treeshrews (solitary and pairs), drongos (presence and absence) and sparrowhawks (presence and absence) was highly significant.

(d) Data analysis

To examine the significance of the presence and absence of species in different group combinations, occurrence data pertaining to the association between treeshrews, sparrowhawks and drongos were explored by fitting a generalized linear model to the count data for a $2 \times 2 \times 2$ contingency table with two factors for each species: treeshrew (solitary/pair), drongo (present/absent) and sparrowhawk (present/absent) (Crawley 2007). First, a saturated model was fitted to the data including all interactions. The second model removed the effect of the three-way interaction between treeshrews, drongos and sparrowhawks. The significance of the deviation between models was tested using a χ^2 -test. As data were not normally distributed, comparisons between foraging rates as well as foraging distances between species were carried out using the Wilcoxon rank-sum test on independent samples. All analyses were carried out using R and S-PLUS software (see the electronic supplementary material for details).

3. RESULTS

(a) Frequencies of occurrence

Treeshrews were observed to forage extensively with greater racket-tailed drongos and sparrowhawks; drongos were present in 70.6 per cent of the combinations and sparrowhawks in 43.2 per cent. The occurrences of the three species in the association, examined using a generalized linear model, proved to be highly significant (deviance = -33.68 , $p < .0001$) (figure 1). Single treeshrews were more likely to be found with sparrowhawks in the presence of drongos (52.4%) than in the absence of drongos (8%). When drongos were absent, pairs were more likely to be found in the presence of sparrowhawks (19.7%) than single treeshrews (2.4%).

(b) Distances between species

Both species of birds followed the treeshrews and fed on prey that were flushed. Average distances between treeshrews and sparrowhawks were significantly greater than the distances between treeshrews and drongos (Wilcoxon $Z = -7.2258$, $p < 0.001$, $n = 306$) (figure 2). Distances between treeshrews and sparrowhawks were significantly greater for groups where drongos were absent (Wilcoxon $Z = -2.0411$, $p < 0.05$, $n = 144$; table 1).

(c) Foraging rates

Over 97 per cent of treeshrew feeding events were on insects and the remaining were on fruits. Treeshrew foraging rates declined in the presence of drongos

with individuals feeding every 71 s in the absence of the birds and 201 s when the birds were present (Wilcoxon $Z = -2.6357$, $p < 0.01$, $n = 44$). Obvious kleptoparasitism from drongos and aggression from treeshrews were observed when there were more than two drongos in a group (a rare occurrence). In the absence of sparrowhawks, treeshrews fed every 47 s when drongos were also absent and every 230 s when drongos were present (Wilcoxon $Z = -3.1846$, $p < 0.001$, $n = 31$). Overall foraging rates of treeshrews were not significantly affected in the presence of sparrowhawks (Wilcoxon $Z = -0.5918$, $p = 0.55$, $n = 44$). Foraging rates of drongos ranged from 69 to 221 s in six different treeshrew–drongo–sparrowhawk combinations, while that of sparrowhawks ranged from 4 to 23.6 min in interspecific groups. During brief observations of solitary drongos (63 min) and sparrowhawks (30 min), the former were only observed to feed twice, and the latter not at all.

4. DISCUSSION

Our results suggest that foraging efficiency is the primary driving force behind the formation of this unique association. There is a decline in foraging efficiency for the treeshrew which may have little ability to ward off attendant species (although they display aggression when there are more than two drongos and obvious food stealing by drongos). Drongos and sparrowhawks avail of insect and vertebrate prey, respectively, that are flushed by treeshrews; our limited data point to improved foraging rates for these species. There is considerable literature which supports the theory that drongos join mixed flocks for enhanced food benefits (Goodale & Kotagama 2006; Satishchandra *et al.* 2007). The role of raptors in mixed flocks in general also seems to point towards increased food benefits (Boinski & Scott 1988; Sridhar 2007).

Although foraging rates for treeshrews declined in the presence of drongos, these birds may reduce the predation risk for treeshrews from the sparrowhawk within the association or from other raptors or predators. In general, sallying birds are known to be extremely vigilant as a result of their habitual scanning for insects. Drongos are known to be adept at

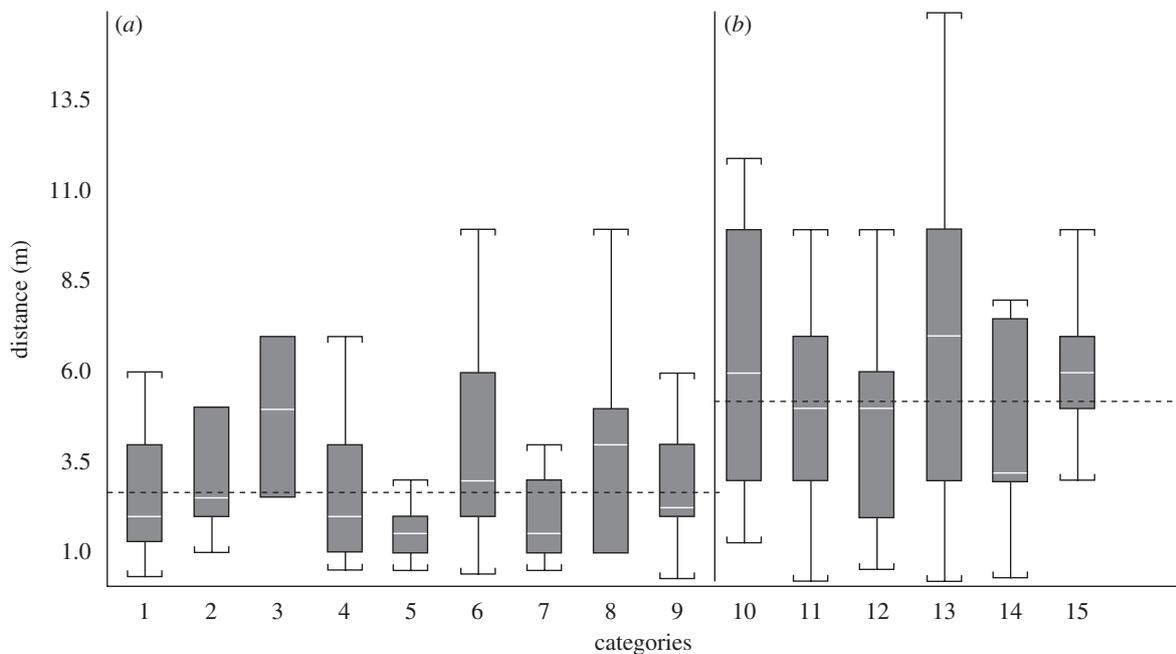


Figure 2. Average distance (dotted line) maintained between (b) treeshrews and sparrowhawks was significantly greater than between (a) treeshrews and drongos. Distances were significantly greater for groups where drongos were absent. Individual box and whiskers plots denote different combinations of individuals. (a) $x' = 3.09$ m, $n = 195$; (b) $x' = 5.75$ m, $n = 111$. Legend for categories: (a) 1, (1ts, 1dr); 2, (1ts, 2dr); 3, (1ts, 3dr); 4, (1ts, 1dr, 1sh); 5, (1ts, 2dr, 1sh); 6, (2ts, 1dr); 7, (2ts, 2dr); 8, (2ts, 1dr, 1sh); 9, (2ts, 2dr, 1sh); (b) 10, (1ts, 1sh); 11, (1ts, 1dr, 1sh); 12, (1ts, 2dr, 1sh); 13, (2ts, 1sh); 14, (2ts, 1dr, 1sh); 15, (2ts, 2dr, 1sh). ts, treeshrew; dr, drongo; sh, sparrowhawk.

Table 1. Average distances from the nearest treeshrew to the sparrowhawk; distances were significantly greater for groups where drongos were absent (Wilcoxon $Z = -2.0411$, $p = 0.041$, $n = 144$). (ts, treeshrew; dr, drongo; sh, sparrowhawk.)

drongo	mean distance of nearest treeshrew from the sparrowhawk (m)	group composition	mean distance of the nearest treeshrew from the sparrowhawk for individual groups (m)
absent	7.35	1ts, 1sh	6.8
		2ts, 1sh	7.45
present	5.44	1ts, 1dr, 1sh	5.62
		1ts, 2dr, 1sh	4.66
		2ts, 1dr, 1sh	5.33
		2ts, 2dr, 1sh	5.74

perceiving threats and to be especially vigilant during *Accipiter* attacks (Goodale & Kotagama 2005). Foliage gleaning species (like treeshrews), which are the most conspicuous as well as the least vigilant foragers, may be the most likely to benefit from flocks (Thiollay 1999). In our study, when drongos were absent, treeshrews maintained greater distances from the sparrowhawk and displayed greater alertness, indicating that they did consider the raptor as a potential predator. Thus, the high degree of association between drongos and treeshrews may be owing to both foraging efficiency for the former and predator avoidance for the latter.

Sparrowhawk presence in mixed groups was strongly correlated to that of drongos. The pair-singleton dichotomy of the treeshrews plays a role in detection as breeding pairs, unlike singletons, exchange frequent contact calls even when foraging close by. Drongos may depend either on mimicry to access solitary individuals or track down the pairs on the basis of their contact calls. For the sparrowhawks, the drongos may serve as a signal for finding the treeshrews. Our occurrence data suggest that either sparrowhawks cannot trace singletons

without the help of drongos or singletons do not tolerate sparrowhawks in the absence of drongos. In limited observations on flock formation, sparrowhawks were always found to join treeshrew breeding pairs or groups with drongos, suggesting support for the former hypothesis. Out of 310 scans, only four records were of a sparrowhawk with a singleton, and these were remnants of groups abandoned by drongos.

The sparrowhawk diverges from typical hunting techniques displayed by accipiters and exhibits a local, context-dependent foraging preference. *Accipiter* species in general are known to supplement about 10 per cent of their diet with small mammals (Gotmark & Post 1996) and to attack the most vulnerable group of mammals that are present in the area (Cresswell & Quinn 2004). However, the lowered chance of predation success in the presence of drongos may have led to the choice of the predator to join the group as a commensal. Other mammal species that are known to be followed by raptors are much larger and at lower risk of predation (e.g. ungulates, primates, armadillos) compared with treeshrews.

Whereas most studies on mixed foraging flocks have examined benefits in terms of foraging efficiency, reduced predation risk or vigilance as fixed states for species or flocks, our results suggest that strategies driving flock formation are more complex and context dependent with varying benefits for different actors. What makes this association unusual is the cohesiveness and stability of the group as a whole, with the drongos and sparrowhawks actively seeking out these small mammals and the different group members receiving varied benefits. Unlike opportunistic associations that are reported in the literature, these associations are consistent, last longer periods of time and have predictable outcomes (e.g. obvious kleptoparasitism when there are more drongos; treeshrews feeding further away from sparrowhawks when drongos are absent). To conclude, the complexity of interspecific relationships in the context of mixed foraging is increased by new observations where predators join potential prey as foraging commensals and need to be examined further in the light of evolution of context-dependent strategies. At a broader scale, the dynamics of associations such as these has the potential to shed light on both ecological resource states and ethological adaptations of species.

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