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Western striped squirrel *Tamiops mcclellandii*: A non-avian sentinel species of bird waves

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Abstract. The presence of "avian sentinels" in bird waves (mixed-species foraging flocks), which mob or alarm-call in response to predators, is widely recognised. Yet in the highly threatened lowland deciduous forests of South-east Asia, a mammal, the western striped squirrel *Tamiops mcclellandii*, which usually accompanied bird-waves, was a more obtrusive sentinel than any bird. It called most often in response to predators (40 out of 70 observations) and was the first species to emit alarm calls on 24 occasions (60%) where studied in Huai Kha Khaeng Wildlife Sanctuary, western Thailand. The squirrels fed in close proximity to drongos (*Dicrurus* spp.), suggesting they may benefit from the drongos' tendency to mob predators. Additionally, the drongos actively followed the bark-foraging squirrels in order to capture flushed arthropods. The presence of the western striped squirrel both helped reduce the need for vigilance among avian flock members and contributed to flock cohesion.

Key words. mixed-species flock, squirrel, anti-predator alarm call, anti-predator vigilance, sentinel species, interspecific interactions

INTRODUCTION

An avian mixed-species foraging flock (or bird-wave) is a coalition of two or more bird species foraging together and consistently moving in the same direction (Morse, 1970; Bell, 1982; Berner & Grubb, 1985). Participants benefit through flocks providing "safety in numbers", contributing to better anti-predator vigilance (Terborgh, 1990), thus more time can be allocated by flock members for other activities such as foraging (Roberts, 1995). Some mixed-species flock members, particularly flycatching species, benefit from capturing arthropods flushed by movements of other flock participants (Satischandra et al., 2007). Such a lifestyle, which often involves the use of prominent, elevated perches, is also thought to enable these flycatching species to act as "sentinels", which spot predators at the same time as scanning for prey (Lima & Bednekoff, 1999; Greenberg, 2000). Sentinels may not only mob predators themselves, but through their utterance of alarm calls may stimulate other flock members to join them in mobbing (Terborgh, 1990; Ragusa-Netto, 2002; Templeton & Greene, 2007; Goodale & Kotagama, 2008). In Asian forests, drongos (fam. Dicruridae) appear to be especially prominent as sentinels. Mixed-species flock members in Sri Lanka were attracted to playback of random segments of vocalisations of a sentinel species, the Sri Lanka drongo *Dicrurus lophorinus* (formerly treated as a subspecies of greater racket-tailed drongo *D. paradiseus*), which included alarm calls (Goodale & Kotagama, 2005).

The participation of non-avian species, especially arboreal and semi-arboreal diurnal mammals, which are relatively small in body size, has also been documented in avian mixed-species flocks. Three species of squirrels, western striped squirrel *Tamiops mcclellandii*, grey-bellied squirrel *Callosciurus caniceps*, and variable squirrel *C. finlaysoni*, were all recorded traveling with bird flocks in Khao Yai National Park, Thailand (Nimnuan et al., 2004). Three species of palm squirrels *Funambulus* spp. in Sri Lanka foraged and moved in the same direction as mixed flocks of birds (Kotagama & Goodale, 2004), contributing alarm calls in the presence of potential predators, although this was not quantified (Goodale & Kotagama, 2005). In the Neotropics, Amazonian red squirrel *Urosciurus spadiceus* (Della-Flora et al., 2013) and dwarf squirrels *Microsciurus* spp. (Thorington et al., 2012) participated in avian mixed-species flocks. Many instances of birds and mammals mutually recognising and responding to each other's anti-predator alarm calls have been documented (Seyfarth et al., 1980; Rainey et al., 2004; Randler, 2006; Lea et al., 2008; Schmidt et al., 2008; Oommen & Shankar, 2010). However, the participation of mammal species in avian mixed-species flocks has nowhere been thoroughly investigated or quantified.

Treeshrews (Scandentia: Tupaiidae) and diurnal squirrels (Rodentia: Sciuridae) are among the potential mammalian participants in South-east Asian avian mixed species flocks. While most arboreal squirrels are mainly herbivorous, with invertebrates and small vertebrates also contributing to

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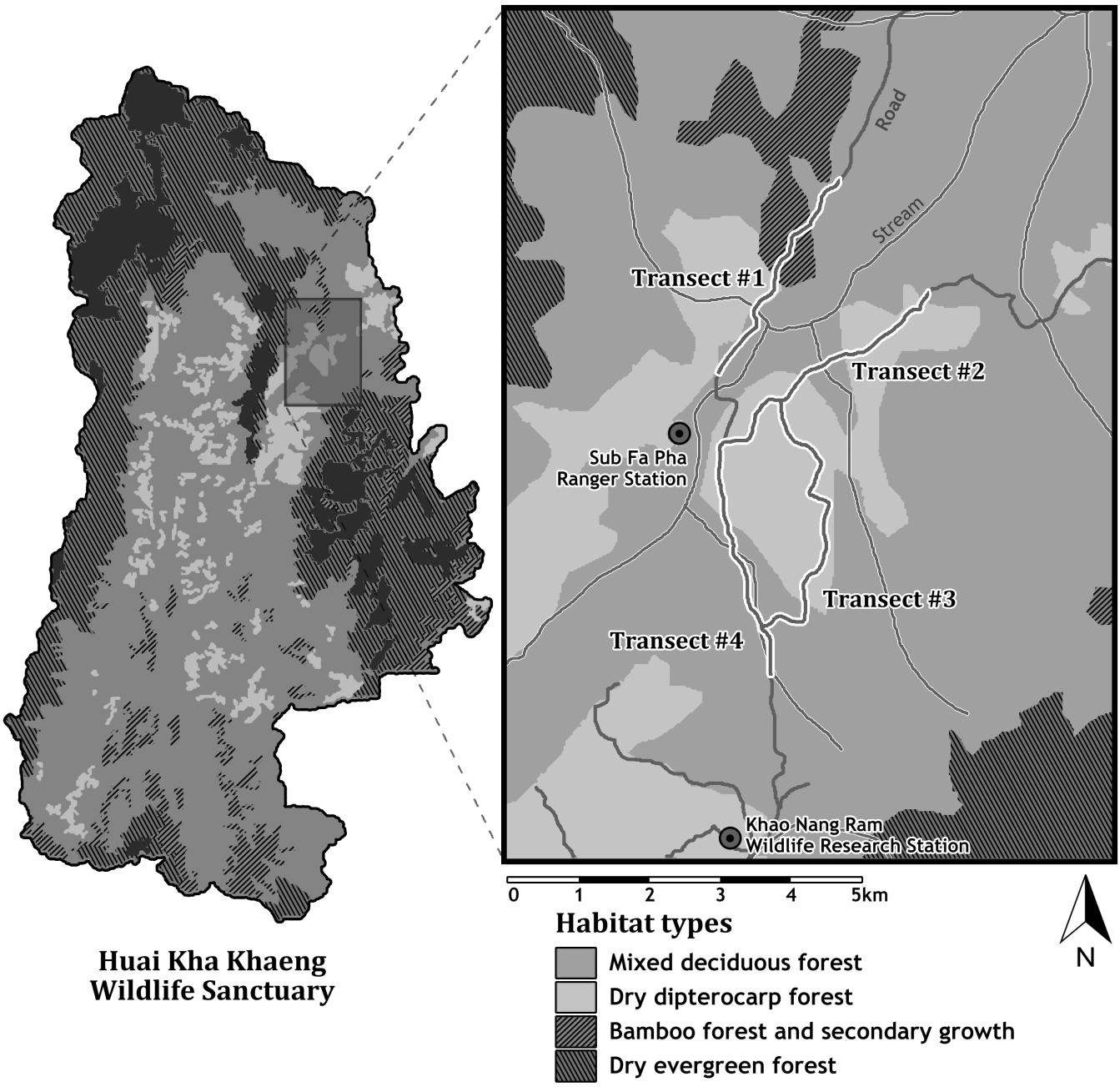

Fig. 1. Transects and habitat types at the study site.

Fig. 2. Close-association between *Dicrurus paradiseus* and *Tamiops mcclellandii.*

Fig 3. Close-association between *Dicrurus annectens* and *Tamiops mcclellandii*.

their diet, *Tamiops*, abundant in South-east Asian forests, is primarily insectivorous (Casanovas-Vilar & van Dam, 2013). The core food resources of insectivorous *Tamiops* may therefore be rather more uniformly distributed, like those of insectivorous birds, suggesting the need to travel constantly to search for food instead of lingering in specific stations around clumped fruit resources. As a bark-gleaner that runs along tree trunks and larger limbs, *Tamiops* might be expected to flush arthropods making it an ideal associate for flycatching birds to follow. Potential avian flycatching sentinels might therefore associate preferentially with squirrel bark-gleaners. *T. mcclellandii* (western striped squirrel, Himalayan striped squirrel, Burmese striped squirrel) inhabits a variety of forested habitats from the Himalayas eastwards to northern Vietnam and southwards to the Thai–Malay Peninsula (Chang et al., 2011), and is the most widespread *Tamiops* species in Thailand. The main objective of this study was to investigate the behaviour of mammals in avian mixed-species foraging flocks and examine the evidence for possible mutualistic relationships with birds. It was predicted that the western striped squirrel would be a frequent anti-predator alarm caller.

MATERIAL & METHODS

Study site. The study was carried out in a deciduous forest composed largely of dry dipterocarp and old-growth mixed deciduous forest surrounding Sub Fa Pha Ranger Station (15°32′18″N 99°18′00″E) at elevations 210–300 m above sea level in the UNESCO Thung Yai–Huai Kha Khaeng Wildlife Sanctuaries World Heritage site (Fig. 1) (Namwong & Gale, 2015). This area is part of a contiguous forested area covering 18,630 km^2 adjoining Myanmar, known as Thailand's Western Forest Complex, which is one of the largest protected forest remnants in mainland South-east Asia (UNESCO, 2014).

Methods. Field observations and data collection were made while slowly walking transects along laterite roads inside the forest during the first four hours and the last four hours of daylight. There was a total of four transects (Fig. 1). The average walking distance per transect was 5.0 km. Two transects were alternately walked per day (one morning and one evening). Data were collected for at least 12 days monthly during January to December 2012.

Flock types. All individual birds and mammals associating in a flock were identified and counted. Flock types were categorised according to body size of the majority of members within. Birds with a body length under 19 cm were considered small-sized (Morrison & Ross, 1989). Very few potential mixed-flocking species exceeded 35 cm in body length and could be considered large-sized. Therefore, every mixed-species flock was categorised as being composed of either small-sized birds or medium-sized birds. Avian sentinel species, to which particular attention was given in this study, included the ashy drongo *Dicrurus leucophaeus*, greater racket-tailed drongo *D. paradiseus*, crow-billed drongo *D. annectens*, and black-naped monarch *Hypothymis azurea*. While several other presumed avian sentinel species were present at the study site, only these four species provided sufficient observations for analysis. The identities and foraging modes of the associated species were recorded. The main foraging modes of flock members were categorised into four different foraging guilds: arboreal foliage-gleaners, bark-gleaners, terrestrial foragers, and flycatching foragers. The mixed-flocking propensity of a species was defined as its frequency of occurrence in mixed-species flocks (the number of occasions that species was seen in mixed-species flocks relative to the total number of encounters with that species).

Early anti-predator alarm calls. The chronological order of species heard emitting alarm calls in the presence of predators was recorded. It was assumed that the more rapidly a species responded to a predator's presence, the more important was its role as a sentinel. The species of predator was also identified and recorded whenever possible. The most visible and likely predators of mixed-species flock members were mainly raptorial birds (Accipitriformes, Strigiformes, Falconiformes). However, non-avian predators such as monitor lizards *Varanus* spp. and snakes were also noted if they instigated alarm calls from mixed-species flock members.

Cross-species associations among birds and mammals. Encounters with mammals such as squirrel or treeshrews were categorised as either (1) solitary or with conspecifics, (2) accompanying a flock of small-sized birds or (3) accompanying a flock of medium-sized birds. In all cases where an avian sentinel species was present in a flock, apparently cohesively following a different species, either another bird or a mammal, both the sentinel and the species it was following were identified and recorded. Such an interspecific relationship was referred to in this study as a close-association.

RESULTS

Occurrence of mammals in mixed-species bird flocks. Three mammal species (northern treeshrew *Tupaia belangeri*, western striped squirrel, and Pallas's squirrel *Callosciurus erythraeus*) showed a significantly greater tendency to join flocks of medium-sized birds (in which laughingthrushes and woodpeckers predominated) than flocks of small-sized birds, which consisted predominantly of black-naped monarch *Hypothymis azurea*, grey-headed canary-flycatcher *Culicicapa ceylonensis*, dark-necked tailorbird *Orthotomus atrogularis*, pin-striped tit babbler *Mixornis gularis*, velvet-fronted nuthatch *Sitta frontalis*, ioras *Aegithina* spp. and leaf warblers *Phylloscopus* spp. (Pearson's Chi-square p-values < 0.05; Table 1). The western striped squirrel and the semi-terrestrial northern treeshrew showed the highest mixed-flocking propensity among mammals (67%, n=367; and 61%, n=61 respectively; Table 2). Other flock joiners were Indochinese ground squirrel *Menetes berdmorei*, Pallas's squirrel, and grey-bellied squirrel *Callosciurus caniceps* (mixed-flocking propensity of 38%, 31%, and 21%, respectively; Table 1). The occurrence of the largest species, black giant squirrel *Ratufa bicolor*, with avian mixed-species flocks was possibly accidental (Table 2). In most cases, no

Table 1. Numbers of occasions mammal species were encountered associating with conspecifics or bird flocks.

Species	Solitary or with conspecifics		With mixed-species foraging flock			
			Small-sized birds		Medium-sized birds	
	N	Frequency	N	Frequency	N	Frequency
Tupaia belangeri	24	0.39	4	0.07	33†	0.54
Tamiops mcclellandii	122	0.33	71	0.19	174†	0.47
Menetes berdmorei	10	0.63	0	0.00	6	0.38
Callosciurus erythraeus	291	0.69	9	0.02	120†	0.29
Callosciurus caniceps	45	0.79	2	0.04	10	0.18
Ratufa bicolor	70	0.95	0	0.00	4	0.05

† Significantly greater tendency to join medium-sized bird flocks than small-sized bird flocks (Pearson's Chi-square p-value < 0.05; null hypothesis rejected)

Table 2. Numbers of individuals per encounter and propensity of mammal species to join avian mixed-species foraging flocks.

Species	Number of individuals[a]		Total encounters[b]	Flocking propensity[c]
	Mean (± SE)	Max		
Tamiops mcclellandii	1.36 ± 0.03	4	367	0.67
Tupaia belangeri	1.05 ± 0.03	2	61	0.61
Menetes berdmorei	1.07 ± 0.02	2	16	0.38
Callosciurus erythraeus	1.18 ± 0.18	5	420	0.31
Callosciurus caniceps	1.21 ± 0.41	3	57	0.21
Ratufa bicolor	1.12 ± 0.04	2	74	0.05

[a]Number of individuals of the same species that was encountered in the same flock.
[b]Total number of occasions each species was encountered.
[c]Mixed-species flocking propensity is the number of that species seen inhabiting mixed-species flocks divided by the total number of occasions it was encountered.

more than one or two individuals of each mammal species were encountered in any one flock (Table 2).

Early anti-predator alarm calls. A total of 28 species of birds and mammals were heard to emit anti-predator alarm calls during data collection (Table 3). Two species of squirrels, the western striped and Pallas's squirrels, contributed most calls. On the 70 occasions when alarm calls were heard upon the presence of predators, the first calls were most often produced by the western striped squirrel (24 occasions; 34.3%), followed closely by the abundant Pallas's squirrel (22 occasions; 31.4%). On only 24 occasions (34.3%) were the first calls produced by birds (all species combined) rather than squirrels. The black-naped monarch provided the most frequent first alarm calls among birds (5 occasions; 7.1%) followed by greater racket-tailed drongo (4 occasions, 0.33%).

The relationship of predator species and types of alarm-callers was also identified (Table 4). The alarm-callers were classified into three groups: birds, *Callosciurus* squirrels, and the western striped squirrel. All bird alarm callers were grouped into one category because the contribution of anti-predator alarm calls of any one species was small. Among ten predatory species identified, the changeable hawk eagle *Nisaetus limnaeetus*, the largest diurnal bird-of-prey at the study site, most frequently elicited alarm calls (38 occasions). The second most common predator to instigate alarm calls was the semi-diurnal owl, Asian barred owlet *Taenioglaux cuculoides* (14 occasions; Table 4). Birds (10 observed responses) and western striped squirrels (7 responses) gave the most frequent alarm responses to the owlet.

Associations between squirrel and bird species. All avian sentinel species showed more frequent close-associations with bark-gleaners, whether birds or squirrels, than with other foraging guilds (Tables 5, 6). However, greater racket-tailed drongo was the only species in which this relationship was statistically significant (n=85; Pearson's Chi-squared p-value < 0.05; Table 6). Crow-billed drongo also showed more frequent interactions with bark-gleaning species than with species of other foraging guilds combined, although the relationship was not statistically significant (n=34; Table 6). Bark-gleaners observed being followed included woodpeckers (Piciformes: Picidae), Claudia's leaf warbler *Phylloscopus claudiae*, velvet-fronted nuthatch, western striped squirrel and Pallas's squirrel. Of the four sentinel species on which the present study focused, three (the three species of drongos) most frequently associated with the western striped squirrel. The (smaller-sized) black-naped monarch differed in that it showed its highest frequency of association with the similar-sized velvet-fronted nuthatch

Table 3. Frequency of first utterance of predator alarm calls.

Alarm calling species	First		Second		Later		Total
	N	Frequency	N	Frequency	N	Frequency	
Anthracoceros albirostris	–	0.00	1	0.50	1	0.50	2
Picus erythropygius	–	0.00	1	0.33	2	0.67	3
Dinopium javanense	–	0.00	1	0.50	1	0.50	2
Tephrodornis virgatus	–	0.00	–	0.00	1	1.00	1
Aegithina lafresnayei	–	0.00	1	1.00	–	0.00	1
Oriolus xanthornus	–	0.00	–	0.00	1	1.00	1
Rhipidura javanica	1	1.00	–	0.00	–	0.00	1
Dicrurus aeneus	1	0.20	4	0.80	–	0.00	5
Dicrurus paradiseus	4	0.33	5	0.42	3	0.25	12
Hypothymis azurea	5	0.63	3	0.38	–	0.00	8
Urocissa erythrorhyncha	1	0.50	1	0.50	–	0.00	2
Culicapa ceylonensis	3	0.75	–	0.00	1	0.25	4
Pycnonotus flaviventris	2	0.50	2	0.50	–	0.00	4
Pycnonotus finlaysoni	–	0.00	1	1.00	–	0.00	1
Pycnonotus conradi	–	0.00	–	0.00	1	1.00	1
Orthotomus sutorius	1	1.00	–	0.00	–	0.00	1
Prinia rufescens	–	0.00	–	0.00	1	1.00	1
Phylloscopus plumbeitarsus	1	1.00	–	0.00	–	0.00	1
Garrulax leucolophus	1	0.20	1	0.20	3	0.60	5
Garrulax monileger	–	0.00	–	0.00	1	1.00	1
Gracula religiosa	–	0.00	–	0.00	1	1.00	1
Cyornis tickelliae	–	0.00	–	0.00	1	1.00	1
Copsychus saularis	1	1.00	–	0.00	–	0.00	1
Kittacincla malabarica	1	1.00	–	0.00	–	0.00	1
Chloropsis aurifrons	2	0.50	–	0.00	2	0.50	4
Callosciurus caniceps	–	0.00	–	0.00	1	1.00	1
Callosciurus erythraeus	22	0.71	7	0.23	2	0.06	31
Tamiops mcclellandii	24	0.60	11	0.28	5	0.13	40

Table 4. Predator species observed and alarm responses detected.

Predator species	Birds[a]		*Callosciurus* spp.[b]		*Tamiops mcclellandii*		Total occasions
	N	Frequency	N	Frequency	N	Frequency	
Nisaetus limnaeetus	16	0.42	21	0.55	24	0.63	38
Taenioglaux cuculoides	10	0.71	1	0.07	7	0.50	14
Spilornis cheela	2	0.33	4	0.67	4	0.67	6
Accipiter badius	2	0.67	1	0.33	2	0.67	3
Ketupa zeylonensis	3	1.00	2	0.67	1	0.33	3
Accipiter trivirgatus	2	1.00	1	0.50	–	0.00	2
Nisaetus nipalensis	1	1.00	1	1.00	–	0.00	1
Accipiter gularis	–	0.00	1	1.00	1	1.00	1
Microhierax caerulescens	1	1.00	–	0.00	–	0.00	1
Varanus bengalensis	–	0.00	–	0.00	1	1.00	1

[a]Occasion when anti-predator alarm calls were heard emitted by bird species.
[b]Occasion when anti-predator alarm calls were heard emitted by any *Callosciurus* squirrel species. Virtually all calls belonged to Pallas's Squirrel *C. erythraeus*. Grey-bellied Squirrel *C. caniceps* only accounted for 1 occasion.

Table 5. Numbers of occasions when sentinel species were associated closely with other members of mixed-species foraging flocks.

Species closely associated with sentinel	Foraging guild[a]	*Dicrurus leucophaeus*		*Dicrurus paradiseus*		*Dicrurus annectens*		*Hypothymis azurea*	
		N	Freq.	N	Freq.	N	Freq.	N	Freq.
Phaenicophaeus tristis	AG	–	0.00	6	0.07	1	0.03	–	0.00
Yungipicus canicapillus	BG	1	0.04	–	0.00	–	0.00	1	0.02
Dinopium javanense	BG	1	0.04	12	0.14	1	0.03	–	0.00
Gecinulus viridis	BG	–	0.00	1	0.01	–	0.00	–	0.00
Chrysophlegma flavinucha	BG	–	0.00	7	0.08	1	0.03	–	0.00
Picus chlorolophus	BG	–	0.00	1	0.01	–	0.00	–	0.00
Picus erythropygius	BG	–	0.00	3	0.04	–	0.00	–	0.00
Dryocopus javensis	BG	–	0.00	1	0.01	–	0.00	–	0.00
Tephrodornis virgatus	FF	4	0.16	2	0.02	–	0.00	–	0.00
Pericrocotus roseus	AG	–	0.00	1	0.01	–	0.00	5	0.12
Pericrocotus speciosus	AG	1	0.04	–	0.00	1	0.03	–	0.00
Coracina macei	AG	1	0.04	–	0.00	–	0.00	–	0.00
Lalage polioptera	AG	1	0.04	–	0.00	–	0.00	–	0.00
Aegithina lafresnayei	AG	–	0.00	–	0.00	1	0.03	2	0.05
Aegithina tiphia	AG	2	0.08	1	0.01	4	0.12	1	0.02
Oriolus chinensis	AG	1	0.04	1	0.01	–	0.00	–	0.00
Oriolus xanthornus	AG	2	0.08	1	0.01	2	0.06	–	0.00
Hypothymis azurea	FF	–	0.00	–	0.00	1	0.03	–	0.00
Pycnonotus conradi	AG	1	0.04	–	0.00	–	0.00	–	0.00
Phylloscopus schwarzi	AG/TF	–	0.00	–	0.00	–	0.00	1	0.02
Phylloscopus inornatus	AG	–	0.00	–	0.00	–	0.00	1	0.02
Phylloscopus plumbeitarsus	AG	–	0.00	–	0.00	–	0.00	1	0.02
Phylloscopus claudiae	AG/BG	–	0.00	–	0.00	–	0.00	2	0.05
Phylloscopus ricketti	AG	–	0.00	–	0.00	–	0.00	1	0.02
Mixornis gularis	AG	–	0.00	–	0.00	1	0.03	6	0.15
Garrulax leucolophus	TF	–	0.00	2	0.02	–	0.00	–	0.00
Garrulax monileger	TF	–	0.00	15	0.18	–	0.00	–	0.00
Sitta frontalis	BG	4	0.16	–	0.00	1	0.03	19	0.46
Chloropsis cochinchinensis	AG	–	0.00	–	0.00	1	0.03	1	0.02
Tupaia belangeri	BG/TF	–	0.00	2	0.02	–	0.00	–	0.00
Tamiops mcclellandii	BG	6	0.24	28	0.33	18	0.53	–	0.00
Callosciurus erythraeus	BG	–	0.00	1	0.01	1	0.03	–	0.00
Total occasions		25		85		34		41	

[a]Abbreviations for foraging guilds: AG = arboreal foliage-gleaners, BG = bark-gleaners, TF = terrestrial foragers, FF = flycatching foragers.

Table 6. Numbers of occasions when sentinel species were associated closely (see text for description) with other members of mixed-species foraging flocks (categorised by foraging guild).

	Dicrurus leucophaeus		*Dicrurus paradiseus*		*Dicrurus annectens*		*Hypothymis azurea*	
Foraging guild	**N**	**Freq.**	**N**	**Freq.**	**N**	**Freq.**	**N**	**Freq.**
Bark-gleaner	12	0.48	56[†]	0.66	22	0.65	22	0.54
Arboreal foliage-gleaner	9	0.36	10	0.12	11	0.32	21	0.51
Terrestrial forager	–	0.00	19	0.22	–	0.00	1	0.02
Flycatching forager	4	0.16	2	0.02	1	0.03	–	0.00

[†] Significantly greater tendency to associate with bark-gleaners than other foraging guilds (Pearson's Chi-square p-value < 0.05; null hypothesis rejected).

and did not associate with squirrels. The bark-gleaning and semi-terrestrial northern treeshrew, another mammal species regularly participating in mixed-species foraging flocks, was observed in a close-association with greater racket-tailed drongo twice (Table 5).

DISCUSSION

Despite many reports of squirrels and other small mammals foraging with mixed-flocks of birds (Kotagama & Goodale, 2004; Nimnuan et al., 2004; Oommen & Shankar, 2010; Thorington et al., 2012; Della-Flora et al., 2013), the extent of their participation in bird flocks seems to not have been previously studied or quantified. Among mammals in the present study, the western striped squirrel had the highest propensity to forage in association with avian mixed-species flocks. It emitted early anti-predator alarm calls more frequently than any other mammal or bird species. The more plentiful Pallas's squirrel was the second-most frequent early emitter of anti-predator alarm calls, but rarely joined mixed flocks. Unexpectedly, the traditional presumed avian sentinel species such as the greater racket-tailed drongo and black-naped monarch emitted alarm calls much less frequently than either of the squirrels. However, in comparison with the behaviour of avian sentinel species that occupy prominent vantage points, the bark-gleaning feeding habit of the western striped squirrel should not facilitate scanning for predators. Why should squirrels be such prolific early alarm callers? Are squirrels more vigilant than birds? Are squirrels more inclined to call because they are at greater risk from large predatory birds than are small birds? Squirrels might be perceived by predators as higher quality prey because they cannot avoid predators by aerial evasion and because of their greater body mass compared with birds of similar size. Male Pallas's squirrels on average weigh 359 g and females 375 g (Hayssen, 2008), heavier even than the very large white-bellied woodpecker *Dryocopus javensis* (197–347 g; Brazil, 2009). The western striped squirrel, though not much larger than the birds with which it associated, was much heavier (average 49.4 g, male, and 51.8 g, female), compared with black-naped monarch 8.9–13.4 g and the largest *Phylloscopus* species Radde's warbler *P. schwarzi* (8–15 g; Hayssen, 2008; Brazil, 2009).

The main benefit to squirrels and squirrel-like mammals participating in avian mixed-species flocks is probably reduced predation risk. Of the two squirrels most frequently observed, the insectivorous western striped squirrel foraged more frequently with avian mixed-species flocks than did the mainly frugivorous Pallas's squirrel, most likely because arthropods, on which the former species largely forages, were generally much more uniformly distributed than fruits. The western striped squirrel's compact size could also facilitate its agility and render its foraging mode similar to that of insectivorous birds in some respects.

The traditional avian sentinel species of mixed flocks, namely drongos and monarchs, tended to show close-association with bark-gleaning species. This may be because bark-gleaners, foraging over a large surface area of substrate, should trigger movements of arthropods more frequently per feeding station than do (e.g.,) leaf-gleaners. Sentinel species could therefore follow bark-gleaners and obtain more food with a minimal need to change perches. White-browed fantail *Rhipidura aureola*, a likely sentinel species in dry dipterocarp woodlands of Myanmar, followed the bark-gleaning Burmese nuthatch *Sitta neglecta* and foraged on flushed insects (King & Rappole, 2001), just as the black-naped monarch followed velvet-fronted nuthatches in the present study. The western striped squirrel, however, proved to be the most frequent associate for all three drongo species but the relationship was statistically significant only in the greater racket-tailed drongo. While crow-billed drongo also showed a preference for associating with bark-gleaners over other foraging guilds, as a wet season breeding visitor to the study area, absent from the site for 5 months (October to February; Limparungpatthanakij et al., 2014), the association was not statistically significant due to the lower number of observations. The ashy drongo followed arboreal foliage-gleaners only slightly less frequently than it did bark-gleaners (Table 6). The association between squirrels and drongos might not only benefit drongos in improving foraging efficiency (Satischandra et al., 2007), but reduce the predation risk to the western striped squirrel because drongos usually ferociously mob predators (Payne, 1967). There were several occasions of avian predators being chased by drongos in the study site. Greater racket-tailed drongos mobbed birds as large as changeable hawk eagle and brown fish owl *Ketupa zeylonensis*. Ashy drongos mobbed *Accipiter spp.*, oriental pied hornbill *Anthracoceros albirostris*, and collared falconet *Microhierax caerulescens*. Both bronzed drongo *D. aeneus* and hair-crested drongo *D. hottentottus*, neither of which regularly associated with mixed-species flocks, were also observed mobbing.

Although the semi-terrestrial bark-gleaning northern treeshrew regularly participated in avian mixed-species flocks, with a tendency to associate with greater racket-tailed drongo, unlike the squirrels it did not give any anti-predator alarm calls. A possible mutualistic association between greater racket-tailed drongo and another species of treeshrew, Nicobar treeshrew *Tupaia nicobarica* on Great Nicobar Island, enhanced the foraging efficiency of the treeshrew (Oommen & Shankar, 2010).

Members of flocks in Sri Lanka were attracted more to the combination of sentinel and leader species' vocalisations than to those of the sentinel or leader species alone (Goodale & Kotagama, 2005). The cohesion between bark-gleaners, such as the western striped squirrel, and the avian sentinel species may likewise invite more species to join flocks. Since the western striped squirrel was a prolific early anti-predator alarm caller that associated with drongos, this mammal–bird species pair was likely influential in mixed-species flock formation.

The western striped squirrel provides an example of a mammal species playing an apparently important role in avian mixed-species foraging flocks. It provided the most frequent early anti-predator alarm calls and was the most

frequent co-forager of drongos, which are regarded as sentinel species important in mixed-flock initiation. In order to better understand the role of the *Tamiops* squirrels, playback experiments could be used to test whether its vocalisations attract mixed-flocking birds and initiate flock formation. In addition, prey capture rates of birds (especially drongos) following squirrels and other species should be examined and compared with those in other foraging situations.

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LITERATURE CITED

Bell HL (1982) A bird community of lowland rainforest in New Guinea. 5. Mixed-species feeding flocks. Emu Austral Ornithology, 82: 256–275.

Berner TO & Grubb TC Jr. (1985) An experimental analysis of mixed-species flocking in birds of deciduous woodland. Ecology, 66: 1229–1236.

Brazil M (2009) Birds of East Asia: China, Taiwan, Korea, Japan, and Russia. New Jersey: Princeton University Press, 528 pp.

Casanovas-Vilar I & van Dam J (2013) Conservatism and adaptability during squirrel radiation: What is mandible shape telling us? PLoS ONE, 8(4): e61298. doi:10.1371/journal.pone.0061298.

Chang SW, Oshida T, Endo H, Nguyen ST, Dang CN, Nguyen DX, Jiang X, Li ZJ & Lin LK (2011) Ancient hybridization and underestimated species diversity in Asian striped squirrels (genus *Tamiops*): Inference from paternal, maternal and biparental markers. Journal of Zoology, 285: 128–138.

Della-Flora F, Melo GL, Sponchiado J & Cáceres NC (2013) Association of the southern Amazon red squirrel *Urosciurus spadiceus* Olfers, 1818 with mixed-species bird flocks. Mammalia, 77: 113–117.

Goodale E & Kotagama SW (2005) Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. Journal of Tropical Ecology, 21: 669–676.

Goodale E & Kotagama SW (2008) Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. Behavioral Ecology, 19: 887–894.

Greenberg R (2000) Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. In Boinski S & Garber PA (eds.) On the Move: How and Why Animals Travel in Groups. Chicago, IL: The University of Chicago Press. Pp. 521–559.

Hayssen V (2008) Patterns of body and tail length and body mass in Sciuridae. Journal of Mammalogy, 89: 852–873.

King DI & Rappole JH (2001) Mixed-species bird flocks in dipterocarp forest of north-central Burma (Myanmar). Ibis, 143: 380–390.

Kotagama SW & Goodale E (2004) The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. Forktail, 20: 63–70.

Lea AJ, Barrera JP, Tom LM & Blumstein DT (2008) Heterospecific eavesdropping in a nonsocial species. Behavioral Ecology, 19: 1041–1046.

Lima SL & Bednekoff PA (1999) Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Animal Behaviour, 58: 537–543.

Limparungpatthanakij W, Round PD, Khudamrongsawat J, Gale GA & Brockelman WY (2014) Composition and structure of avian mixed-species foraging flocks in lowland deciduous forests, Huai Kha Khaeng Wildlife Sanctuary. In: Proceedings of Mahidol University Graduate Research. Mahidol University, Bangkok, pp. 54–68.

Morse DH (1970) Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs, 40: 119–168.

Morrison RG & Ross RK (1989) Atlas of Nearctic Shorebirds on the Coast of South America. Volumes 1 and 2. Ottawa: Canadian Wildlife Service Special Publication, 325 pp.

Namwong N & Gale GA (2015) Nest site selection and nesting ecology of red-breasted parakeet *Psittacula alexandri* in dry dipterocarp forest, western Thailand. Forktail, 31: 121–124.

Nimnuan S, Round PD & Gale GA (2004) Structure and composition of mixed-species insectivorous bird flocks in Khao Yai National Park. Natural History Bulletin of the Siam Society, 52: 71–79.

Oommen MA & Shanker K (2010) Shrewd alliances: Mixed foraging associations between treeshrews, greater racket-tailed drongos and sparrowhawks on Great Nicobar Island, India. Biology Letters, 6: 304–307.

Payne RB (1967) Interspecific communication signals in parasitic birds. American Naturalist, 101: 363–375.

Ragusa-Netto J (2002) Vigilance towards raptors by nuclear species in bird mixed flocks in a Brazilian savannah. Studies on Neotropical Fauna and Environment, 37: 219–226.

Rainey HJ, Zuberbühler K & Slater PJB (2004) Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society of London B, 271: 755–759.

Randler C (2006) Red squirrels (*Sciurus vulgaris*) respond to alarm calls of Eurasian jays (*Garrulus glandarius*). Ethology, 112: 411–416.

Roberts G (1995) Why individual vigilance declines as group size increases. Animal Behavior, 51: 1077–1086.

Satischandra SHK, Kudavidanage EP, Kotagama SW & Goodale E (2007) The benefits of joining mixed-species flocks for Greater Racket-tailed Drongos *Dicrurus paradiseus*. Forktail, 23: 145–148.

Schmidt KA, Lee E, Ostfeld RS & Sieving K (2008) Eastern chipmunks increase their perception of predation risk in response to Titmouse alarm calls. Behavioral Ecology, 19: 759–763.

Seyfarth RM, Cheney DL & Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science, 210: 801–803.

Templeton CN & Greene E (2007) Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. Proceedings of the National Academy of Sciences of the United States of America, 104: 5479–5482.

Terborgh J (1990) Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. American Journal of Primatology, 21: 87–100.

Thorington RW Jr., Koprowski JL, Steele MA & Whatton JF (2012) Squirrels of the World. Maryland: Johns Hopkins University Press, 472 pp.

UNESCO (2014) Thungyai–Huai Kha Khaeng Wildlife Sanctuaries. UNESCO World Heritage Centre. http://whc.unesco.org/en/list/591. (Accessed 24 August 2017).