Regional variation in the composition and structure of mixed-species bird flocks in the Western Ghats and Sri Lanka

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Mixed-species bird flocks are attractive models for the investigation of geographical variation in animal communities, as they represent a subset of the avifauna in most forested regions of the world. Yet studies of the regional variation in flock size and the composition of flocks are few, due to the predominance of studies carried out at single study site. Here, we review nine studies of mixed-species flocks conducted at 16 sites along the Western Ghats in India and in Sri Lanka. We find that flock size varies as much within this region as it does globally, with observation time being a confounding variable. Flock composition, however, is predictably related to elevation. Flocks at high elevations (>1200 m) in the Western Ghats strongly resemble flocks at high elevations in the mountain ranges of Sri Lanka in their composition, especially at the family level. We compare these flocks to flocks of other regions and make recommendations on study methodology that can facilitate comparisons across studies.

Keywords: Bird communities, biogeography, mixed-species flocks, Western Ghats.

MIXED-species flocks are a characteristic feature of bird communities throughout the world, especially in birds of forested regions and in the tropics[1,2]. Flocks are defined as an association of two or more species that move consistently without respect to the location of specific food resources in contrast to aggregations[2]. Most studies of mixed-species flocks have focussed on the adaptive benefits to flocking[3–5]. Less is known about the degree of co-evolution among members in flocks[6], and whether flocks represent a structured community with some species always or never found together[7–9].

Studies of the biogeography of flocks have the potential to address questions of community organization, but are rare, especially at the regional scale. Most studies gather data at one site; for example, Buskirk[10] and Thiollay and Jullien[11] compared the ecology of birds at one site to investigate why some species are found in flocks and some are not. On the opposite extreme of the scale, Thiollay[1] has compared mixed-species flocks systems in multiple sites on several continents; in such a case, different study sites contain different species, and often different families of birds. In contrast, at an intermediate geographical scale, regional studies can ask whether some species play similar roles in flocks in different areas, or whether associations between species or families can be found repeatedly in flocks. Regional studies can be conducted by one researcher[12–14] or can be reviews of multiple studies[2,15]; as yet they have been largely restricted to the Neotropics (but see Diamond[16] for work in Papua New Guinea).

The flocks of South Asia present an interesting opportunity to study questions of flock variation on the regional scale. Although mixed-species flocking is widespread in the area[17], few systematic studies of flocks were conducted until the 1990s (but see Partridge and Ashcroft[18], MacDonald and Henderson[19], and Vijayan[20]). Over the last decade and a half, however, there has been a growing interest in the subject, and a flurry of activity particularly along the Western Ghats and Sri Lankan mountain ranges[21–27]. We review this literature and synthesize and reanalyse this data to investigate geographical variation within this region. Specifically, we ask whether (a) similar flock systems can be found in areas with similar environments, (b) whether there are distinct flock systems in different environments, and (c) what occurs in intermediate environments – do systems blend together, or co-exist? For environmental gradients, we focus on elevation, and

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we compare flock systems both in their size (number of species, number of individuals), and composition.

Study region

The Western Ghats mountain range runs approximately 1600 km along India's west coast from the Gujarat–Maharashtra (21°N) border to the southern tip of India (8°N). Sri Lanka is a continental island separated from India by the shallow 20 m deep and 64–137 km wide Palk Strait; the Sri Lankan highlands are isolated from the Western Ghats by approximately 400 km. In India, the western slopes of the Western Ghats catch much of the precipitation, leaving the eastern slopes drier; consequently, the western slopes and the high altitudes are covered by tropical wet evergreen and semi-evergreen forests, whereas the eastern slopes are dominated by dry deciduous forest and thorn scrub vegetation[28]. There is also a north–south gradient of precipitation with the south having a shorter dry season and a higher level of species richness and endemism, particularly of moist forest taxa[29,30]. Likewise, in Sri Lanka, precipitation and biodiversity are concentrated in the southwestern part of the country and the central mountains[31,32].

Together, the Western Ghats and Sri Lanka have been designated as one of the 34 biological diversity hotspots, due to the high endemism of the fauna and flora and the threats to biodiversity[30,33,34]. Despite repeated occurrences of land bridges between Sri Lanka and India, with the most recent one being ~10,000 years ago, the fauna of the Western Ghats and Sri Lanka remain quite distinct, as species have had difficulty traversing the dry environments between the two wetter mountain areas[35]. Probably due to their isolation from other rainforest regions, the Western Ghats and Sri Lanka are relatively depauperate in their avifauna, having many fewer land-bird species than similar areas in the Eastern Himalayas[36]. The area is, however, a centre of bird endemism[37], with at least 25 Sri Lankan[38,39] and 16 Western Ghats endemics[40] (see also Rasmussen and Anderton[41]). Many of these endemic species are threatened: nine of the endemic Sri Lankan species are listed as 'vulnerable or endangered', as are four of the Western Ghats endemics[42]. Loss of habitat is the primary threat[43]. It is estimated that between 1976 and 1995, the Western Ghats lost over 25% of its forest cover[44]. In Sri Lanka, forest cover dropped from 44% of the country in 1956, to 27% by 1980, and deforestation continues at an annual estimated rate of 1.5% (ref. 43).

Methods

Within the region, nine studies of mixed-species published between 1976 and 2008 were considered for analysis. Some of these studies were designed to compare different sites which were either far from each other, such as Trivedi[23], or differed in elevation, such as Nizam *et al.*[21], or land-use type, such as Pramod[25] and Robin and Davidar[24]. Sridhar and Sankar[27] looked at many forest fragments and the effect of fragment size; we have included here only the three largest fragments studied that were adjacent to large tracts of forest, as they had the largest sample sizes. Altogether, we analysed 16 sites, ranging from tropical deciduous to evergreen forest, and spanning a wide north–south range from approximately 6°N to 21°N (Table 1, Figure 1).

We used the published studies and additional information, and data from the authors to assess the size of flocks and flock composition for these sites, and what species led flocks. Some studies did not have estimates of the total number of species found at a site (inside and outside of flocks) and for these studies we used available checklists from that area. For all estimates of total species numbers, we did not count some groups of birds that would not be expected in mixed-species flocks (see footnotes to Table 2). Nomenclature and taxonomy follow BirdLife International[45].

Some variations in the studies' methodology should be noted here.

(i) *Definition of a flock.* Most of the studies we reviewed used a simple definition of a flock as a group of two or more species moving together in the same direction, although some studies required more than two species[27]. Some definitions also included a minimum time period[24,25,27], or a proximity criterion[23].

(ii) *Observation time.* Most of the studies reviewed here would watch a flock for as long as it took to ensure that all the species or individuals were counted. Four of the nine studies recorded observation time.

(iii) *Sampling design.* Most of the surveys were conducted from a series of walking paths, although some studies at times followed flocks away from such paths[24].

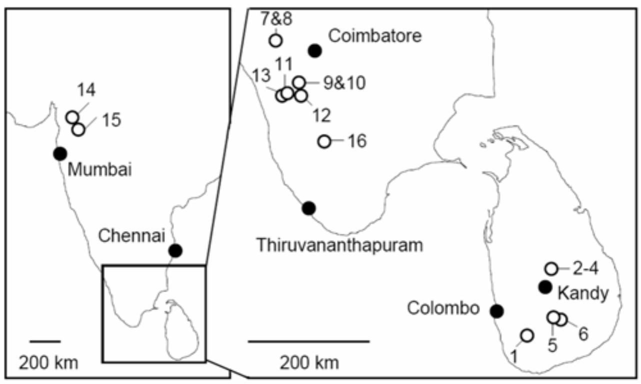

Figure 1. The 16 study sites in India and Sri Lanka. Site numbers are included in Table 1. Map information from Google Maps (www.google.com/maps).

Table 1. The location and the habitat in which mixed-species were studied. Nine studies (ordered alphabetically by author) are reviewed; some studies had multiple sites, for a total of 16 sites

Name	Study authors	Latitude (°N)	Longitude (°E)	Elevation (m)	Rain-fall (mm)	Landuse type	Vegetation type	Season and year of fieldwork (month/year)	Definition of flock
Lowland Sri Lanka, Sinharaja	Kotagama and Goodale[22]	6°26′	80°21′	400–600	4000	Selectively logged forest	Evergreen	1/81–1/82; 5/83–5/84; 6/95–8/95; 7/96–8/96; 11/97–6/98; 9/98–10/98	Moving associations, >2 species
Knuckles Range, Sri Lanka – Low	Nizam *et al.*[21]	7°32′	80°47′	300–450	3000–3450	Forest	Evergreen	1/06–12/06	Moving associations, >2 species, 3 birds
Knuckles Range, Sri Lanka – Middle	Nizam *et al.*[21]	7°32′	80°45′	800–1000	n/a	Forest	Evergreen	1/06–12/06	Moving associations, >2 species, 3 birds
Knuckles Range, Sri Lanka – High	Nizam *et al.*[21]	7°31′	80°44′	1300–1450	2400	Forest	Evergreen	1/06–12/06	Moving associations, >2 species, 3 birds
Horton Plains, Sri Lanka	Partridge and Ashcroft[18]	6°48′	80°48′	2200	n/a	Forest	Evergreen	8/70–9/70	Not specified
Montane Sri Lanka – Tangamalai eastern Fragment	Perera[26]	6°46′	80°56′	1600	2750	Forest fragment	Evergreen	10/94–3/95	Moving associations, >2 species
Nilgiri Hills, India – Forest	Pramod[25]	11°4′	76°24′	1000	4000	Forest	Evergreen	10/94–1/95	Moving associations, >10 min
Nilgiri Hills, India – Forest buffer	Pramod[25]	11°4′	76°24′	600	2500	Forest buffer	Semi-evergreen	10/94–1/95	Moving associations, >10 min
Western Anamalai Range, India – Forest	Robin and Davidar[24]	10°23′	76°43′	400–1000	1700	Forest	Deciduous	12/99–3/00	Moving associations, >2 min
Western Anamalai Range, India – Teak Plantation	Robin and Davidar[24]	10°23′	76°43′	400–1000	1700	Teak plantation	Deciduous	12/99–3/00	Moving associations, >2 min
Valparai Plateau, India: Andiparai	Sridhar and Sankar[27]	10°14′	76°35′	1270	3500	Forest	Evergreen	12/04–4/05	Moving associations, >5 min, >3 species
Valparai Plateau, India: Iyerpadi-Akkamalai	Sridhar and Sankar[27]	10°12′	76°48′	1250–1550	3500	Forest	Evergreen	12/04–4/05	Moving associations, >5 min, >3 species
Valparai Plateau, India: Manamboli	Sridhar and Sankar[27]	10°12′	76°32′	785	3500	Forest	Evergreen	12/05–4/05	Moving associations, >5 min, >3 species
Northern Western Ghats: Purna	Trivedi[23]	21°11′	73°40′	130–574	2100	Forest	Deciduous	6/01–3/03	Moving associations, >2 species, within 10 m of each other[9]
Northern Western Ghats: Ratanmahal	Trivedi[23]	20°34′	74°07′	230–670	1000	Forest	Deciduous	9/99–1/01	Moving associations, >2 species, within 10 m of each other[9]
Kerala, India: Thekkady, Periyar Tiger Reserve	Vijayan[20]	9°34′	77°10′	900–1000	1700	Partially disturbed forest	Deciduous	3/80–2/81	Moving associations within 5 m of each other

(iv) *Data collected.* The studies varied according to the data collected, as the objectives of the studies differed. Some studies collected information of foraging techniques or heights[24]. Other studies were more interested in species associations[20], or relationship to vegetation or land-use[27]. Four studies published quantitative data on leadership[18,21,22,25], although the type of data varied (see discussion).

We return in the discussion to these factors, where we suggest some aspects of methodology that should, in our opinion, be used in future studies.

Analysis of flock size and comparison to flocks from other biogeographical regions

Before comparing flock sizes among sites, we analysed the effect of observation time on flock size. Species accumulation curves can be modelled through asymptotic or non-asymptotic curves[46]. Because the different studies followed different observation methods and were in different environments, we did not force the same model through the data from different sites but followed a systematic method to determine the appropriate model for each site. First, we tested whether there was a relationship between the number of species in flocks and observation time, through simple linear regression. If there was, we determined whether the relationship was improved by transforming the minutes observed using the square root function (implicating a power regression fit was appropriate), or if it was better improved by changing the response variable to be minutes/species (implicating a strong asymptote). For power transformations, we fit the equation S (observation time) = a (observation time)^B. For asymptotic relationships, we fit the Michaelis–Menten equation, S (observation time) = $S_{\max}$ (observation time)/(K + observation time), where $S_{\max}$ represents a maximum number of species found in flocks, and K is the minutes in which $S_{\max}/2$ is observed[46]. These nonlinear functions were fitted using the nonlinear least squares (nls) function in *R* (ref. 47).

To compare these flocks to flocks of other regions, we surveyed the descriptive literature on mixed-species flocks for data on the average number of species and the average number of individuals per flock. We found 18 studies (covering 24 sites) in the Neotropics, and 11 studies (19 sites) in the Old World tropics that had information on the number of species per flock (Appendix A). Of these, only 13 studies (18 sites) in the Neotropics and 8 studies (12 sites) in the Old World tropics also had information on the number of individuals per flock. While we graphically investigate the relationship between the number of species and the number of individuals in the different biogeographic regions (see Figure 2), we do not analyse this data statistically, because it is not clear whether sites within studies are independent of each other, or even whether studies located in the same region are independent of each other.

Analysis of patterns in flock composition

To investigate patterns in flock composition, we randomly selected up to 30 flocks per site from those sites that had full information on the species composition of flocks (sites 1–4 and 9–15). To better represent the montane Sri Lankan flocks, we included in the dataset 30 flocks observed by EG and SWK from the region near Nuwara Eliya, Sri Lanka (elevation ~1800 m), less than 12 km from site 5, and about 400 m less in elevation (Goodale and Kotagama, unpublished data). We analysed this dataset at the species level and also at the family level, with a family counted as being present in a flock if at least one species in that family was observed in it.

To statistically analyse this data, we performed Mantel tests, using the ecodist package of *R* (ref. 48), which compared three matrices representing Euclidean dissimilarities among sites: (a) distances from each other, (b) elevations, and (c) flock compositions (at species and family level). The Mantel tests assume that the records of flock composition at the different flock sites are independent from each other, and thus that the observers' identity did not influence the flock composition data.

To illustrate similarities among flocks, we conducted detrended correspondence analysis (DCA)[49,50] on MSVP (Version 3.13, Copyright 2007, Kovach Computing). We included in the final graph only five flocks from each site and only those species or families seen in at least 10% of the sample of 60 flocks; larger analyses gave similar results but produced more cluttered graphs. Complementary analyses included hierarchical cluster analyses, conducted by calculating Pearson's correlation coefficients for all species pairs and then constructing dendrograms using average linkage[51]. From this analysis, we discuss only those species pairs that were repeatedly found to be each other's closest neighbour on dendrograms of separate sites.

Results

Analysis of flock size and comparison to flocks from other biogeographical regions

It should first be noted that correcting flock size for observation time may considerably change the interpretations of variation in flock size among sites. We found that for seven of nine sites in which the information was available, flock size was significantly correlated with observation time (Table 2). Those sites that had longer observation times best fit asymptotic equations, whereas sites with short observation times best fit power curves (Figure 2). Corrections for observation time can dramati-

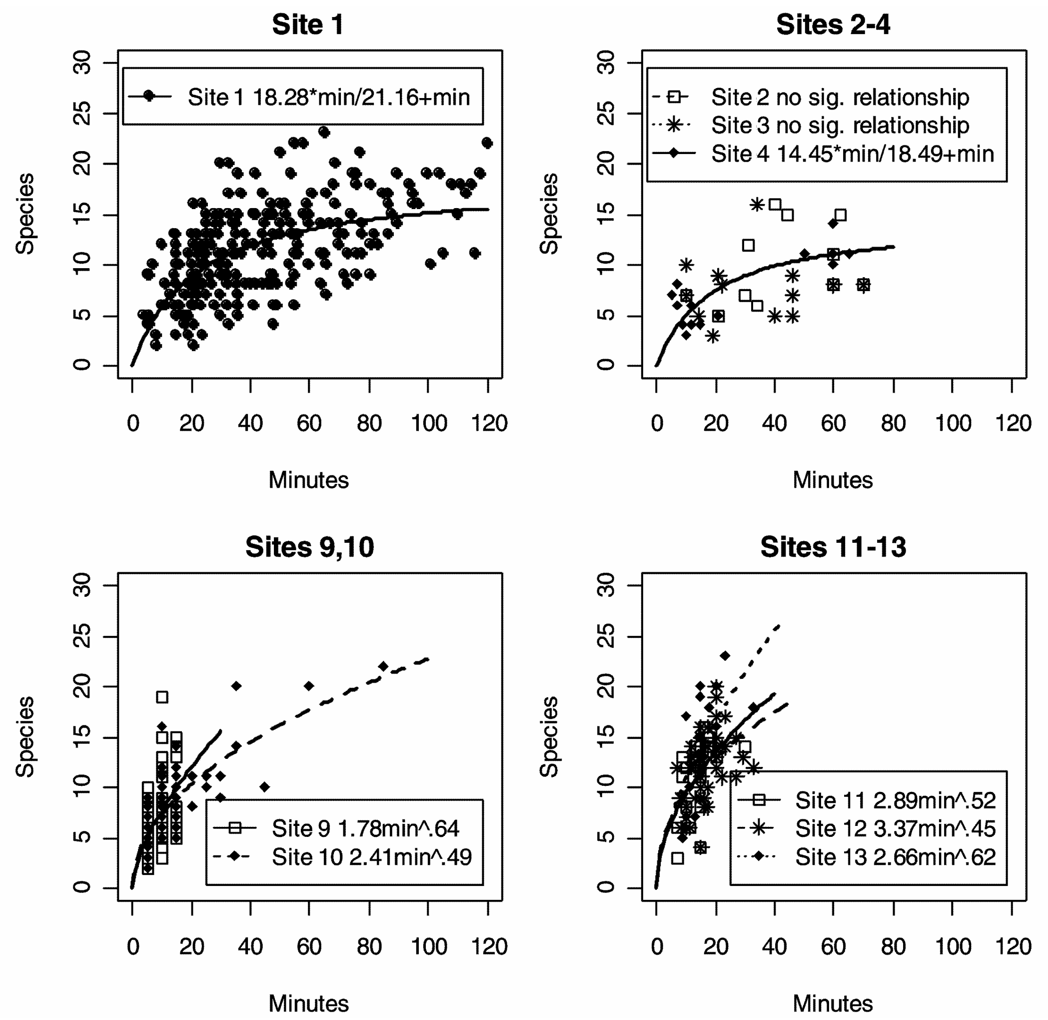

Figure 2. The relationship between observation time and number of species in flocks from four studies (nine sites). See text for methodology of nonlinear regression and Table 2 for fit statistics.

cally change comparisons between sites. For example, based on the published information, the flocks in the Sinharaja forest of lowland Sri Lanka (site 1, 10.6 ± 0.2 SE species) would seem to be considerably larger than those of the Western Anamalai Range, India forest (site 10, 8.1 ± 0.4). But the mean observation time was more than three times as long for site 1 (45.1 ± 1.8) than it was for site 10 (13.5 ± 1.3). Hence, the estimated species richness, at an observation time found in both studies, 15 min, was lower at site 1 (8.3 ± 0.4, based on linear model species = sqrt(min)), than at site 10 (9.0 ± 0.3), and the Michaelis–Menten estimate for the maximum species number in flocks, S_{max}, was lower for site 1 (18.3 ± 1.0) than for site 10 (20.9 ± 2.3).

The comparison between the average number of species per flock in the Western Ghats and Sri Lanka versus other biogeographical regions, which by necessity used uncorrected values, demonstrated that there is nearly as much variation within the region as there is across regions of the world overall. For example, the Anamalai hills flocks at the Manamboli forest rank as the 5th most specious system in the world, whereas the montane Sri Lankan flock system seen in the eastern Tangamalai forest fragment rank 54th (of the total of 58 sites).

Across the Western Ghats and Sri Lankan region, few trends in flock size based on habitat are evident. Flock sizes are smallest in deciduous forests and in the montane region of Sri Lanka, and largest at intermediate altitudes such as the Manamboli forest in the Anamalai Hills.

The flocks of the Western Ghats and Sri Lanka are generally large in terms of individuals. When compared to other systems, five of the sites described here rank as 2nd to 6th in the world (of 45 sites compared). This is due to the fact that South Asian flocks include several families of birds (particularly the Timaliidae and Zosteropidae) that are highly gregarious. The comparison to the Neotropics is particularly clear, because Neotropical flocks usually contain only one or two individuals per species[2]. In Figure 3, one can see that most of the Western Ghats and Sri Lankan flocks, as well as the flocks of

Table 2. Flock size and its relationship to observation duration. The number of species, the number of individuals, and the mean observation time are shown in the first three columns. The next three columns give the fit statistics for the relationships between observation time and flock size, where applicable, for (a) simple linear regression, (b) regression where minutes was square-root transformed, and regression where minutes/species was the response variable. The next two columns show values of S_{max} and B from the Michaelis–Menten equation, where applicable. Finally the percentage of avifauna percent of the avifauna found in flocks is shown for each site, and the source of the data

Name	Mean species ± std err, *n*	Mean individ ± std err, *n*	Mean observ. time (min) ± std err, *n*	Spec = min: R^2, *P*	Spec = sqrt (min): R^2, *P*	Min/Spec = min: R^2, *P*	S_{max}	*B*	# Flocks participants/ checklist[a]	Source of checklist
Sinharaja	10.6 ± 0.2, 476	41.3 ± 1.3, 298	45.1 ± 1.8, 256	0.32, <0.0001	0.35, < 0.0001	0.45, 0.0001	18.3 ± 1.0	21.2 ± 3.4	59/107 (55%)	From outside source FOGSL[75]
Knuckles Range – Low	9.6 ± 0.8, 22	25.0 ± 3.0, 22	42.0 ± 5.8, 11	0.13, 0.28	0.16, 0.23	n/a	n/a	n/a	50/117 (43%)	From study[57]
Knuckles Range – Middle	8.22 ± 0.8, 18	23.72 ± 2.4, 18	33.69, ± 5.4, 13	0.00, 0.85	0.00, 0.83	n/a	n/a	n/a	36/111 (32%)	From study[57]
Knuckles Range – High	6.9 ± 0.5, 30	26.6 ± 2.6, 18	28.1, ± 6.5, 14	0.73, 0.0001	0.67, 0.0003	0.76, < 0.0001	14.5 ± 2.6	18.5 ± 8.7	31/80 (39%)	From study [57]
Horton Plains	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	10/103 (10%)	From outside source FOGSL[76]
Tangamalai	3.9 ± 0.2, 51	12.5 ± 1.0, 51	n/a	n/a	n/a	n/a	n/a	n/a	13/36 (36%)	From study
Nilgiri Hills – Forest	7.9 ± 0.4, 25	40.4 ± 3.3, 25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Nilgiri Hills – Buffer	7.4 ± 0.5, 20	35.7 ± 3.0, 20	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
W. Anamalai – Forest	6.4 ± 0.3, 117	8.1 ± 0.5, 117	7.61 ± 0.3, 117	0.31, < 0.0001	0.31, < 0.0001	0.11, < 0.0003	19.6 ± 4.8	14.8 ± 5.8	59/156 (38%)	From outside source[77]
W. Anamalai Teak	8.1 ± 0.4, 88	14.7 ± 1.5, 88	13.5 ± 1.3, 88	0.54, < 0.0001	0.57, < 0.0001	0.49, < 0.0001	20.9 ± 2.3	17.9 ± 3.7	57/156 (36%)	From outside source[77]
Valparai: Andiparai	11.4 ± 0.8, 25	34.6 ± 2.6, 25	14.4 ± 1.1, 22	0.29, 0.01	0.32, 0.006	0.04, 0.35	n/a	n/a	34/52 (65%)	From study
Valparai: Iyerpadi	11.8 ± 0.4, 67	37.4 ± 1.6, 67	15.9 ± 0.7, 55	0.22, 0.0002	0.26, <0.0001	0.23, 0.0003	22.0 ± 4.5	13.8 ± 6.1	48/58 (83%)	From study
Valparai: Manamboli	15.0 ± 1.0, 30	37.3 ± 3.3, 30	15.8 ± 1.3, 18	0.37,0.008	0.41, 0.004	0.04, 0.43	n/a	n/a	59/72 (82%)	From study
N.W. Ghats: Purna	4.2 ± 0.3, 29	11.3 ± 1.7, 23	n/a	n/a	n/a	n/a	n/a	n/a	31/97 (32%)	From study
N.W. Ghats: Ratanmahal	5.0 ± 0.5, 32	10.5 ± 1.4, 23	n/a	n/a	n/a	n/a	n/a	n/a	32/95 (34%)	From study
Periyar	8.7 ± n/a 2119[c]	26 ± n/a 2119[c]	15	n/a	n/a	n/a	n/a	n/a	75/10 6 (71%)	From study

[a]Figures adjusted so as not to include raptors (hawks/owls/vultures), water birds (shorebirds/waders/rails/waterfowl/cormorants/gulls/terns), aerial species (swallow/swifts) or aerial/night species (nightjars/frogmouths).
[b]Only including 1995–1998 data.
[c]Number of 15-min periods in which species was present when following mixed-species flocks.

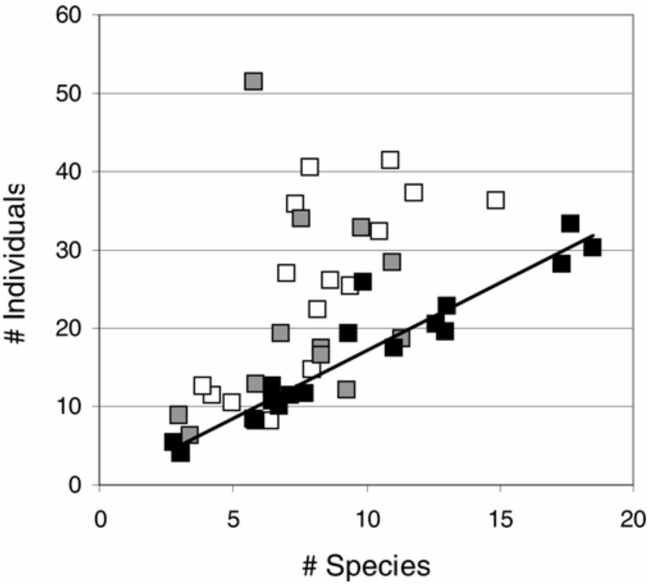

Figure 3. The relationship between the number of species and the number of individuals in flocks. White boxes represent Western Ghats and Sri Lankan systems discussed here. Grey boxes are other Old World tropical systems, and black boxes are Neotropical systems (see Appendix A). The line represents the relationship between the number of species and the number of individuals in the Neotropics.

the Old World tropics more generally, lie above the line representing the relationship between species and individuals in flocks of the Neotropics (see also Appendix A).

In most studies 30–45% of the avifauna is found in flocks, except for those studies in which there was particularly heavy sampling[20,22]. Again, the flocks of the Anamalai Hills stand out, with the forests on the Valparai Plateau having a high percentage of birds in flocks (77% on average).

Analysis of patterns in flock composition

Elevation is a stronger predictor of flock composition than is distance between the locations. The Mantel test shows a non-significant effect of distance (Mantel $r = 0.03$, $P = 0.40$), and a significant effect of elevation (Mantel $r = 0.34$, $P = 0.02$) on the species composition of flocks. The effects are stronger at the family level, but the trend for elevation to predominate is the same (Mantel r for distance = 0.19, $P = 0.06$, Mantel r for elevation = 0.44, $P = 0.002$). These results, however, are complicated by the fact that sites 14 and 15 (the northern Western Ghats) are the most remote sites, much farther apart than the other sites (see Figure 1). If these sites are removed, the analysis then compares short distances within a country versus long distances between countries. For such an analysis, distance is a stronger determinant than elevation for species (Mantel r for distance = 0.41, $P = 0.009$, Mantel r for elevation = 0.28, $P = 0.04$). For families, however, elevation still predominates (Mantel r for distance = 0.18, $P = 0.13$, Mantel r for elevation = 0.36, $P = 0.02$).

The DCA illustrates the powerful influence of elevation on flock composition. In the analysis of composition by species, elevation is the major factor influencing axis 1 of the DCA, so that montane flocks and species have low scores whereas lowland flocks and species have high scores (Figure 4 *a*). Axis 1 explained 13.1% of the variation, whereas axis 2 explained a further 9.0% of the variation and was related to the country – Sri Lankan species had high values, whereas Indian species had lower values. The family analysis showed, however, that montane flocks from the two countries are indistinguishable at this higher taxonomic level (Figure 4 *b*; axis 2 on this graph represents differences between the family composition of flocks particularly in lowland Sri Lanka).

The distinctive montane system is evident when looking at the species which were most abundant in flocks at the different sites (Appendix B). All of the flocks observed in this review that were above 1200 m included white-eyes (*Zosterops* spp.) and/or the grey-headed canary flycatcher (*Culicicapa ceylonensis*). The Indian flocks of high altitude described here appeared to be led by the brown-cheeked fulvetta (*Alcippe poioicephala*), a small babbler found only in India[27], but at even higher elevations this babbler drops out (VVR, pers. obs.).

In lowland flocks, flocks usually include larger species in the babbler family and drongos. Often large woodpeckers (e.g. *Dinopium* sp.) are also found in these flocks[52]. There seems to be a particular affinity between drongos and *Turdoides* babblers, as these species were each other's closest neighbours in dendrograms at a site in the Sri Lankan lowlands (site 1) and in sites of the Indian lowlands (sites 14–15).

Another group of species consists of a canopy contingent that can join either lowland or montane flocks, and includes members of the families Aegithinidae, Campephagidae, Chloropseidae and Sittidae, although rarely does this group form separate flocks of its own. A widespread species, the scarlet minivet (*Pericrocotus flammeus*) was observed to be a leader of flocks in three sites (see Appendix B). This minivet is often closely associated with another canopy species, the velvet-fronted nuthatch (*Sitta frontalis*); the two species were each other's closest neighbours in two Indian sites (10 and 11).

One factor that differed between studies was the season in which the fieldwork was conducted (see Table 1). However, only one study[18] was conducted exclusively in seasons when migrants were not present. Migrants showed considerable variation in their participation in flocks, probably influenced by latitude. In particular *Phylloscopus* sp. play a generally small role in Sri Lanka, but were much more common in the Western Ghats (e.g. the western crowned warbler *Phylloscopus occipitalis* and the large-billed warbler *P. magnirostris* were among the most abundant species in the higher altitudes of the Anamalai Hills; see Appendix B).

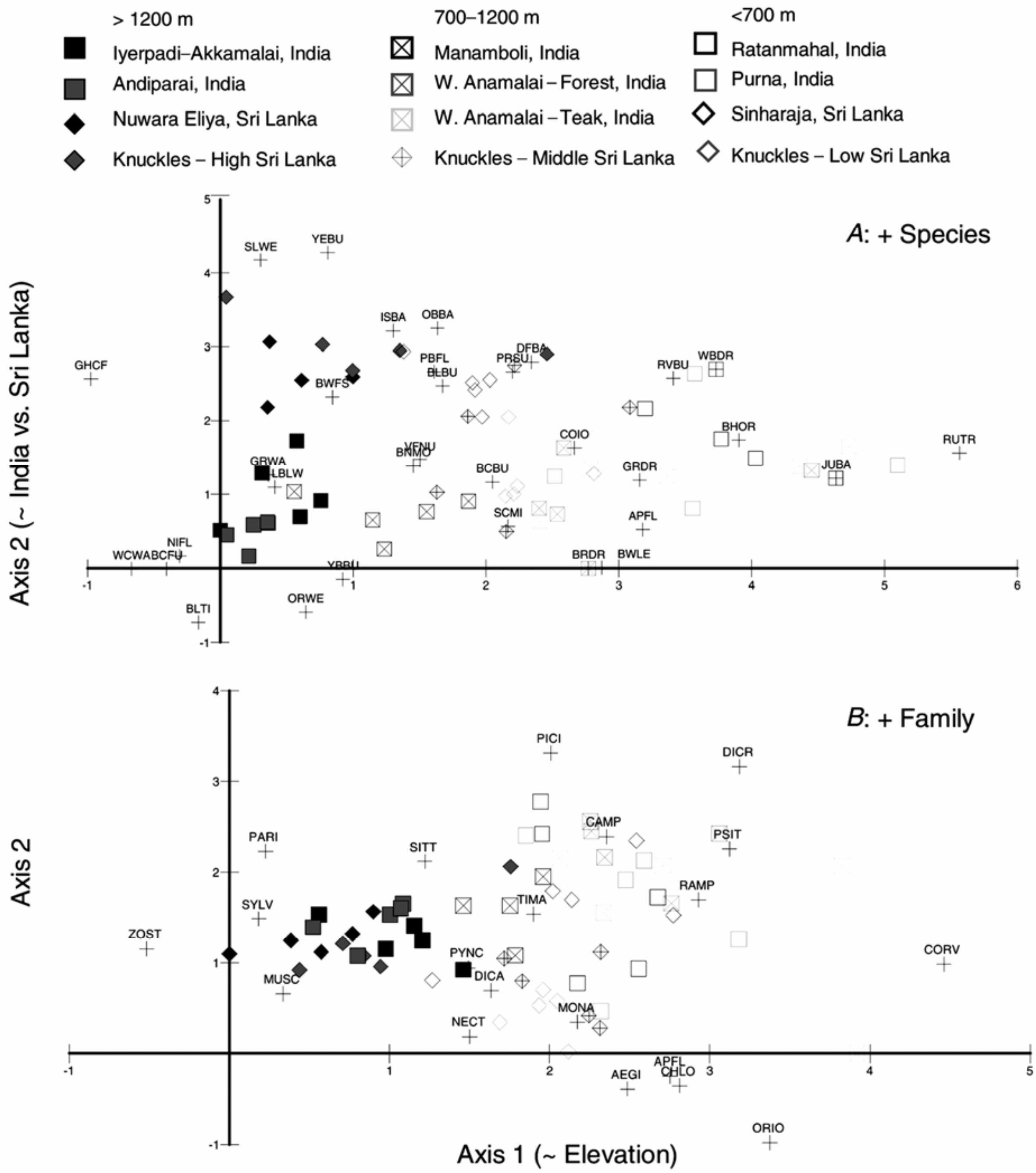

Figure 4. The composition of flocks by country and elevation, as described by detrended correspondence analysis (DCA) graphs. Squares are Indian flocks, diamonds are Sri Lankan flocks. (A): DCA is subjected on species, (B) DCA is subjected on families. Species abbreviations: APFL, Asian Paradise-flycatcher *Terpsiphone paradisi*; BWFS, Bar-winged Flycatcher-shrike *Hemipus picatus*; BLBU, Black Bulbul *Hypsipetes leucocephalus*; BCBU, Black-crested Bulbul *Pycnonotus melanicterus*; BCFU, Brown-cheeked Fulvetta *Alcippe poioicephala*; BHOR, Black-hooded Oriole *Oriolus xanthornus*; BLTI, Black-lored Tit *Parus xanthogenys*; BNMO, Black-naped Monarch *Hypothymis azurea*; BWLE, Blue-winged Leafbird *Chloropsis cochinchinensis*; BRDR, Bronzed Drongo *Dicrurus aeneus*; COIO, Common Iora *Aegithina tiphia*; DFBA, Dark-fronted Babbler *Rhopocichla atriceps*; GRDR, Greater Racket-tailed Drongo *Dicrurus paradiseus*; GRWA Greenish Warbler *Phylloscopus trochiloides*; GHCF, Grey-headed Canary Flycatcher *Culicicapa ceylonensis*; ISBA, Indian Scimitar Babbler *Pomatorhinus horsfieldii*; JUBA, Jungle Babbler *Turdoides striatus*; LBLW, Large-billed Leaf Warbler *Phylloscopus magnirostris*; NIFL, Nilgiri Flycatcher *Eumyias albicaudata*; OBBA, Orange-billed Babbler *Turdoides rufescens*; ORWE, Oriental White-eye *Zosterops palpebrosus*; PBFL, Pale-billed Flowerpecker *Dicaeum erythrorhynchos*; PRSU, Purple-rumped Sunbird *Nectarinia zeylonica*; RVBU, Red-vented Bulbul *Pycnonotus cafer*; RUTR, Rufous Treepie *Dendrocitta vagabunda*; SCMI, Scarlet Minivet *Pericrocotus flammeus*; SLWE, Sri Lanka White-eye *Zosterops ceylonensis*; VFNU, Velvet-fronted Nuthatch *Sitta frontalis*; WCWA, Western Crowned Warbler *Phylloscopus occipitalis*; WBDR, White-bellied Drongo *Dicrurus caerulescens*; YBBU, Yellow-browed Bulbul *Iole indica*; YEBU, Yellow-eared Bulbul *Pycnonotus penicillatus*. Family abbreviations: AEGI, Aegithinidae; CAMP, Campephagidae; CHLO, Chloropseidae; CORV, Corvidae; DICA, Dicaeidae; DICR, Dicruridae; MONA, Monarchidae; MUSC, Muscicapidae; NECT, Nectariniidae; ORIO, Oriolidae; PARI, Paridae; PICI, Picidae; PSIT, Psittacidae; PYCN, Pycnonotidae; RAMP, Ramphastidae; SITT, Sittidae; SYLV, Sylviidae; TIMA, Timaliidae; ZOST, Zosteropidae.

Discussion

Biogeographical variation in mixed-species flocks within the Western Ghats/Sri Lankan region

In this review, we show that similar flock systems in terms of their composition can be found in the montane areas of Sri Lanka and the Western Ghats hill ranges, locations that are isolated from each other by approximately a minimum of 400 km. The flocks of Sri Lanka and the Western Ghats are more similar to each other when judged at the family level than the species level, due to the presence of some endemic species in Sri Lanka (e.g. Sri Lanka white-eye *Zosterops ceylonensis*, yellow-eared bulbul *Pycnonotus penicillatus*, dull-blue flycatcher *Eumyias sordida*) and some species that are found only in India (e.g. brown-cheeked fulvetta, black-lored tit *Parus xanthogenys*, Nilgiri flycatcher *Eumyias albicaudata*). Congeneric species may be playing similar roles in the different systems: the gregarious Sri Lanka white-eye may be replaced by the equally gregarious oriental white-eye in India, whereas the dull-blue flycatcher in Sri Lanka, a species with relatively low propensity to flock, may be replaced by the similar Nilgiri flycatcher in India. Lowland flocks systems, in contrast, varied more widely in composition, with the exception of usually including drongos, and often including large babbler species. Perhaps this is due to a high level of variation in precipitation, and, consequently, forest types, in these different areas.

The total numbers of species per flock are widely variable throughout the region, with as much variation within the region as there is on the global scale. Partly, variation among studies is due to the effects of a confounding variable, observation time. Although observation time is an issue all studies must address, we know of no previous work that has investigated the issue quantitatively, and only one that has depicted the relationship graphically[53]. The ecological variables controlling flock size require further analysis; even important gradients such as land use[24,25] and fragment size[27], have not been shown to have a large effect on flock size. Further research should determine whether flock size is best correlated with predator density, as suggested by Thiollay[1].

These results raise several questions that we hope will be answered by further studies. First, does the similarity between montane flocks in the Western Ghats and Sri Lanka merely represent similarities between the general avifaunas at these elevations, or is there a distinct flock system, with the birds of the two areas outside of flocks being less similar to each other than the birds inside flocks? Several of us (EG, SWK, BZN, UKGKP, T. R. S. Raman and Swati Sidhu) are currently conducting a flock sampling effort in both Sri Lanka and the Western Ghats that collects information on birds inside and outside of flocks.

A second, related question involves whether lowland and montane flock systems blend together at intermediate elevations. There were several sites at intermediate elevations in our sample here: flocks at the Manamboli forest on the Valparai Plateau were interesting in that they included both elements of the lower elevation flocks (e.g. drongos) and elements of the higher elevation flocks (e.g. grey-headed canary flycatcher), and were particularly diverse. At an intermediate elevation in the Knuckles range of Sri Lanka, however, the flocks resembled those at lower elevations, and were sharply distinct with those at higher elevations. A small scale study of flocks over an elevation gradient in the Kalawana–Rakwana range of Sri Lanka, has shown that in some places lowland and highland flock systems co-exist separately for much of the day, although they do merge together when they meet[54]. Thus all three different possibilities – blending, co-existence, and distinctness – appear to occur in different areas of the region.

Finally, it should be noted that although the composition of flocks was quite similar in the highlands of the Western Ghats and Sri Lanka, the leadership can vary, with the brown-cheeked fulvetta apparently serving as the leader on the Valparai Plateau, rather than white-eyes or the grey-headed canary flycatcher, even though the latter species were still present[27]. This result adds to a number of studies that have shown that species can change roles in flocks in different areas[8,12,55,56], or that primary leaders can become secondary leaders when they are associated with other species[16]. However, we need to caution that the type of information on leadership provided in the different studies vary: in some it is the horizontal organization of flocks from front to back[18,22], whereas for others it is the first species to move in a certain direction[22,25,57], or the species that appears to play an important function in flock formation[27], and more research needs to be directed towards investigating flock leadership in the region.

Comparison to flocks in nearby regions

Some components of flocks observed in this study have similarities to flock systems in other parts of south or southeast Asia. Flocks dominated by large babblers of the *Garrulax* genus, and including drongos, are found in lowland areas of Arunachal Pradesh (northeast India), Myanmar and Thailand[51,58,59]. These *Garrulax* flocks inhabit the understorey and midstorey of both evergreen and deciduous forests. They coexist with canopy flocks, in which the families of Campephagidae, Sittidae, and Aegithinidae dominate, and which are similar to the minivet-led component of flocks described here. Flocks dominated by Campephagidae, Sittidae, and Aegithinidae as well as Chloropseidae are also found further to the east and south, in Malaysia[60–62].

There is little information on flocks of higher elevation in eastern India, Myanmar and Thailand. Interestingly, in the study in Arunchal Pradesh[59], which was conducted at elevations of 500–650 m, the grey-headed canary flycatcher was a member of an understorey and midstorey flock system that coexisted with the *Garrulax*-led flock system in the same vegetation layer (the species may be an altitudinal migrant in the area, T. R. S. Raman, pers. commun.). This group also included many *Phylloscopus* warblers. At higher elevations in Arunachal Pradesh, one of the authors (H.S.) has observed a predominance of warbler-dominated flocks. Flocks of several species of *Phylloscopus* were also described in Kashmir by MacDonald and Henderson[19].

Comparison to flocks from other biogeographical regions

From the data reviewed here, we can make some comparison between the flocks of the Western Ghats/Sri Lanka region to those from other biogeographical regions of the world. One clear result is that the flocks of this region, and the Old World tropics generally, have more individuals per flock and per species than those of the Neotropics (Figure 2)[2]. This result is of importance because the high number of species with only a few individuals per flock, and interspecific flock territoriality[63,64], have been discussed as factors promoting high species diversity in Neotropical avifaunas[65]. Such a factor would not seem to be applicable to the avifauna of the Western Ghats/Sri Lanka, or even that of the Old World tropics. Generally, the flocks that we have observed have many characteristics of ‘bird waves’[61], as birds are picked up and dropped off as the flock moves through the forest. Although there do tend to be some areas where flocks are seen more than others, there is yet no definitive evidence for interspecific territoriality in flocks of the Old World tropics. Perhaps ‘bird waves’ is not actually an adequate description for flocks of this region: some species of mammals are occasionally seen in flocks and squirrels in the genus *Funambulus* can be in some cases quite common[18,22]; to our knowledge the participation of mammals in bird flocks is unique to the south and southeast Asian region (see also Nimnuan *et al*.[58]).

One pattern that does seem to be repeated in the Neotropics and the Old World tropics is an increase in the importance of migrant species in the subtropics relative to the tropics. In the Neotropics, the flocks of tropical south and central America are generally aseasonal[2] (but see Deverley and Peres[66]), whereas flocks in the subtropics often include many migrants, and sometimes are led by them[9,12]. A similar trend appears from this study: the flocks of Sri Lanka generally include few migrants, but there is more migrant participation in India, with the extreme migrant-dominated flocks being found in temperate/subtropical Kashmir[19]. More generally, the issue of seasonality in flocks of the region requires more study: in some systems the size and the composition of flocks do not vary much throughout the year (e.g. Kotagama and Goodale[22]), but in other systems, particularly in India, the composition and frequency of flocks may change quite radically (e.g. Vijayan[20] and V. V. Robin, pers. obs.). An extreme example of seasonality in flocks not involving migrants was observed by Santharam[52], who showed that woodpeckers were largely absent in mixed flocks at his field site in Kerala during the late dry season (March–May), but were common at other times of the year.

How does the organization of flocks differ between the Western Ghats/Sri Lanka and other regions? Similar to other areas, there is a general tendency for gregarious species to lead flocks[8,9]. In the case of Western Ghats/Sri Lanka, such leaders included highly gregarious white-eyes and babblers, as well as slightly less gregarious species such as minivets. However, there is one family of birds that are not particularly gregarious yet play an important role in the flock systems of the Western Ghats and Sri Lanka – the drongos (Dicruridae). Drongos are well known to make alarm calls[67,68], and thus may play a role analogous to ‘sentinel’ species in the Neotropics such as ant-shrikes and shrike tanagers in Peru[63,64], or one of several species in the Campo-Cerrado region of Brazil[69,70]. Indeed, the close association between drongos and large babblers such as those of the *Turdoides* genus may be due to an exchange of benefits: drongos provide better vigilance to the babblers, and in return sally for insects beat-up by leaf-gleaning babblers[23,59,71]. It would be interesting to inquire whether there are distinct functional roles in flocks: leaf-gleaning gregarious species, and alarm calling sallying species. An excellent opportunity to test this hypothesis would be to study the alarm calling behaviour of the sallying grey-headed canary flycatcher, which is clearly an important component of high elevation flocks in the Western Ghats/Sri Lankan region.

Methodological recommendations

As new studies are started, we hope researchers will adhere to similar methodologies, so that the studies can be easily compared. Here we offer some recommendations (ordered as in the methodology section above):

Definition of a flock: While the traditional definition of two or more species moving together is applicable for most studies, it may be also useful to record non-moving associations, as some groups of territorial omnivores often seem to travel together, without much net movement (Eben Goodale, pers. obs.).

Observation time: We recommend that there be a minimum observation length preferably greater than 25 min, an observation time greater than any of the estimates of the Michaelis–Menten parameter K in all of our studies

Appendix A. References used in comparison of flock sizes to other biogeographical regions

Reference	Place	Site or stratum	Species	Individuals
Old World tropics				
Bell[78]	Papua New Guinea	Understorey	3.0	8.8
	Papua New Guinea	Canopy	3.4	6.3
Chen and Hsieh[79]	Taiwan		5.8	32.2
Croxall[62]	Sarawak Malaysia	Primary forest	11.3	18.6
	Sarawak Malaysia	Secondary forest	8.3	16.5
Eguchi[80]	Madagascar		5.7	n/a
Greig-Smith[81]	Ghana		8.3	17.4
King and Rappole[51]	Mynamar		6.8	19.3
Laman[53]	Kalimantan Indonesia		9.3	12.2
Lee *et al.*[60]	Penisular Malaysia	Forest interior	9.3	n/a
	Penisular Malaysia	Forest edge	8.4	n/a
	Penisular Malaysia	Urban	5.1	n/a
McClure[61]	Penisular Malaysia	Mile 13	7.6	34.0
	Penisular Malaysia	Mile 22	9.8	32.7
	Penisular Malaysia	Subang	11	28.3
Nimnuan *et al.*[58]	Thailand		5.9	12.8
Winterbottom[82]	Zambia	Baroste Province	9.9	n/a
	Zambia	Eastern Province	7.7	n/a
	Zambia	Southern Province	7.8	n/a
Neotropics				
Bohórquez[83]	Columbia		5.8	8.3
Botero[84]	Columbia		4.3	n/a
Davis[85]	Atlantic Forest Brazil		6.8	10.0
Develey and Peres[66]	Atlantic Forest Brazil		6.6	n/a
Develey and Stouffer[86]	Amazonian Brazil		10.9	n/a
Ewert and Askins[87]	U.S. Virgin Islands		3.1	4.0
Gram[12]	Northeastern Mexico	Dry pine-oak forest	9.9	25.9
	Northeastern Mexico	Humid oak-pine/cloud forest	9.3	19.3
	Northeastern Mexico	Tropical semi-deciduous forest	6.5	10.7
Graves and Gotelli[7]	Peru		18.5	30.3
Herzog *et al.*[88]	Bolivia		2.8	5.4
Hutto[9]	Western Mexico		7.7	11.6
Hutto[89]	Western Mexico	Highlands	18.6	n/a
	Western Mexico	Lowlands	4.7	n/a
Jones[90]	Panama		5.9	8.1
King and Rappole[91]	Highlands of Guatemala, Hondurus, southern Mexico		12.6	20.4
Latta and Wunderle[92]	Dominican Republic		7.2	11.3
Maldonado-Coelho and Marini[93]	Atlantic Forest Brazil		6.5	12.6
Poulsen[94]	Ecuador		17.7	32.2
Stotz[14]	Amazonian Brazil	Roraima	13.1	17.4
	Amazonian Brazil	Rondônia	13.0	19.6
	Amazonian Brazil	Amazonas	17.4	28.2
	Atlantic Forest Brazil	Espírito Santo	11.1	17.4
Tubelis *et al.*[95]	Cerrado region, Brazil		4.6	n/a

(see Table 2). Repeated scans of the same flock at regular intervals might give an idea of the turnover and nature of participation by different species.

Sampling design: Point counts are not as practical as transects for flock work because of the rarity of finding a flock at a particular point (but note that Lee *et al.*[60] did use one hour long point hours to survey flocks). We recommend working on transects, because information on the density of flocks can also be obtained while increasing the likelihood of encountering flocks. When walking transects, it is also helpful to estimate the distance to detected birds, as this will help in accounting for differences in detectability, an essential aspect for density estimation[72]. Yet other methods will also have their uses: for example, following flocks for longer periods of time can give important information on species turnover.

Another aspect of study design that should be discussed is choice of location(s). Traditionally, most studies of mixed-species flocks were conducted using one site. One disadvantage with such a design is that the independence of the flock records is sometimes question-

Appendix B. The composition of flocks. The most numerous species per family is shown for five common flocking families. Three of these families (Campephagidae, Timaliidae and Zosteropidae) are often described as flock leaders; Dicruidae and Picidae are often found associating in flocks. Other species in these same families are listed as long as they are amongst the most frequent 10 species for the site. Species outside of these families are listed in 'Other', as long as they are amongst the most frequent 5 species for the site. Species that were observed to lead the majority of the flocks at a site are in boldface. Only four studies[18,21,22,25] published data on leadership, other data are from personal observations of authors; leadership was unclear in sites without boldface. Numbers in parentheses represent the percent of flocks in which the species was found.

Name	Campephagidae	Dicruridae	Picidae	Timaliidae	Zosteropidae	Other
Lowland Sri Lanka	*Pericrocotus flammeus* (48%)	*Dicrurus paradiseus* (89%)	*Picus chlorolophus* (41%)	***Turdoides rufescens* (92%)**, *Garrulax cinereifrons* (47%), *Pomatorhinus horsfieldii* (45%), *Rhopocichla atriceps* (45%)	*Zosterops ceylonensis* (29%)	Trogonidae (*Harpactes fasciatus*, 62%) Pycnonotidae (*Iole indica*, 53%) Monarchidae (*Hypothymis azurea*, 49%) Cuculidae (*Phaenicophaeus pyrrhocephalus*, 49%)
Knuckles Range, Sri Lanka – Low	***Pericrocotus flammeus* (50%)**	*Dicrurus paradiseus* (18%) *Dicrurus caerulescens* (18%)	*Dendrocopos nanus* (5%)		*Zosterops palpebrosus* (23%)	**Chloropseidae (*Chloropsis cochinchinensis*, 73%)** Pycnonotidae (*Pycnonotus melanicterus*, 64%) Aegithinidae (*Aegithina tiphia*, 64%) Pycnonotidae (*Iole indica*, 41%) Pycnonotidae (*Hypsipetes leucocephalus*, 41%)
Knuckles Range, Sri Lanka – Middle	***Pericrocotus flammeus* (28%)**	*Dicrurus caerulescens* (28%)			*Zosterops palpebrosus* (21%)	**Aegithinidae (*Aegithina tiphia*, 72%)** Chloropseidae (*Chloropsis cochinchinensis*, 61%) Dicaeidae (*Dicaeum erythrorhyncus*, 56%) Pycnonotidae (*Pycnonotus luteolus*, 53%) Pycnonotidae (*Pycnonotus melanicterus* 39%)
Knuckles Range, Sri Lanka – High	*Pericrocotus flammeus* (27%)	*Dicrurus caerulescens* (17%)		*Pomatorhinus horsfieldii* (27%), *Rhopocichla atriceps* (27%)	***Zosterops ceylonensis* (80%)**	Pycnonotidae (*Pycnonotus penicillatus*, 83%) **Muscicapidae (*Culicicapa ceylonensis*, 73%)** Sittidae (*Sitta frontalis*, 53%) Paridae (*Parus major*, 40%)
Montane Sri Lanka – Western Forest	*Hemipus pictatus* (5%)			*Rhopocichla atriceps* (55%), *Pomatorhinus horsfieldii* (39%), *Turdoides rufescens* (3%)	***Zosterops ceylonensis* (71%)**	Pycnonotidae (*Pycnonotus penicillatus*, 82%) Paridae (*Parus major*, 74%) **Muscicapidae (*Culicicapa ceylonensis*, 45%)**
Montane Sri Lanka – Eastern Fragment	*Pericrocotus flammeus* (43%), *Hemipus pictatus* (20%)			*Pomatorhinus horsfieldii* (24%), *Rhopocichla atriceps* (22%)	*Zosterops ceylonensis* (76%)	Muscicapidae (*Culicicapa ceylonensis*, 69%) Muscicapidae (*Eumyias sordida*, 57%)
Nilgiri Hills, India – Forest[a]	*Pericrocotus flammeus* (n/a), *Tephrodornis virgatus* (n/a)	*Dicrurus adsimilis* (n/a)	*Dinopium javanense* (n/a)	***Turdoides striatus* (n/a)**, *Alcippe poioicephala* (n/a)	*Zosterops palpebrosus* (n/a)	Sylviidae (*Phylloscopus occipitalis*, n/a) Nectariniidae (*Nectarinia minima*, n/a)
Nilgiri Hills, India – Forest buffer[b]	n/a	n/a		n/a	n/a	n/a

(*Contd*)

Appendix B. (*Contd*)

Name	Campephagidae	Dicruridae	Picidae	Timaliidae	Zosteropidae	Other
Western Anamalai Range, India – Forest	*Pericrocotus flammeus* (56%), *Tephrodornis virgatus* (28%), *Pericrocotus cinnamomeus* (20%)	*Dicrurus aeneus* (71%), *Dicrurus paradiseus* (56%)	*Dinopium* sp., 31%	*Turdoides striatus* (19%)		
Western Anamalai Range, India – Teak Plantation	*Pericrocotus flammeus* (63%), *Pericrocotus cinnamomeus* (30%)	*Dicrurus aeneus* (85%), *Dicrurus paradiseus* (66%), *Dicrurus caerulescens* (47%) *Dicrurus leucophaeus* (25%)	*Dinopium* sp., 50%	*Turdoides striatus* (34%)		Sittidae (*Sitta frontalis*, 56%)
Valparai Plateau, India: Andiparai	*Pericrocotus flammeus* (36%)		*Picumnus innominatus* (21%)	***Alcippe poioicephala* (93%)**	*Zosterops palpebrosus* (75%)	Muscicapidae (*Culicicapa ceylonensis*, 86%) Pycnonotidae (*Iole indica*, 71%) Sylviidae (*Phylloscopus magnirostris*, 71%)
Valparai Plateau, India: Iyerpadi–Akkamalai	*Hemipus pictatus* (49%)	*Dicrurus paradiseus* (19%)	*Picumnus innominatus* (15%)	***Alcippe poioicephala* (94%)**	*Zosterops palpebrosus* (84%)	Muscicapidae (*Culicicapa ceylonensis*, 85% Sylviidae (*Phylloscopus occipitalis*, 84%) Pycnonotidae (*Iole indica*, 72%)
Valparai Plateau, India: Manamboli	*Pericrocotus flammeus* (63%), *Hemipus pictatus* (50%)	*Dicrurus paradiseus* (83%), *Dicrurus aeneus* (70%)	*Dinopium javanense* (37%)	***Alcippe poioicephala* (73%)**	*Zosterops palpebrosus* (37%)	Sittidae (*Sitta frontalis*, 80%) Pycnonotidae (*Iole indica*, 63%)
Northern Western Ghats: Purna	*Tephrodornis pondicerianus* (38%)	*Dicrurus paradiseus* (62%), *Dicrurus caerulescens* (31%)	*Dinopium benghalense* (21%)	*Turdoides striatus* (59%)		Chloropseidae (*Chloropsis aurifrons*, 21%)
Northern Western Ghats: Ratanmahal	*Tephrodornis pondicerianus* (38%)	*Dicrurus caerulescens* (69%), *Dicrurus paradiseus* (50%)	*Dinopium benghalense* (28%)	*Turdoides striatus* (59%)	*Zosterops palpebrosus* (13%)	Corvidae (*Dendrocitta vagabunda*, 34%)
Lowland Kerala, India[c]	*Pericrocotus flammeus* (76%)	*Dicrurus paradiseus* (80%), *Dicrurus aeneus* (63%)	*Dinopium benghalense* (63%)	*Turdoides striatus* (38%)		Sittidae (*Sitta frontalis*, 71%) Paridae (*Parus major*, 61%)

[a]Species ranked by relative abundance in flocks, not percent of flocks. [b]Data combined with site 7, above. [c]Number of 15-min periods in which species was present when following mixed-species flock.

able. Multi-site designs may improve statistical issues related to data independence and provide more external validity.

Information collected: One kind of data that is easy to collect, and helps in comparing flocking in different areas is flocking propensity, defined as the number of individuals of a particular species that were observed inside flocks divided by the total number of birds observed of that species[9,64,73]. Having propensity data allows one to detect species that are common in flocks simply because they are abundant in an area, or rare in flocks because they are rare in an area. It should be noted that propensity data, while useful, may also be biased if the bird's detection rate differs inside and outside of flocks (T. R. S. Raman, pers. comm.).

Another kind of information that is difficult to collect, but very important to the organization of flocks, is leadership information[5a,74,74a]. Finally, it should be mentioned that studies with marked birds would be a great boon for flock studies in South Asia. As discussed above, excellent studies of territoriality have been conducted in the Neotropics, but such studies have yet to be conducted in the Old World tropics.

Conclusion

Our conclusions are preliminary due to the differences in methodology amongst the studies and some large gaps where the studies have taken place (most noticeably, the large distance between the northernmost part of the Western Ghats and the Nilgiri Hills, as well as the most southern areas of the Western Ghats, high elevation areas >1500 m in the Anamalai and Nilgiri Hills, and dry-zone deciduous forests of Sri Lanka). However, the number of studies on mixed-species bird flocks in the Western Ghats/Sri Lanka region is large enough now to show some general patterns, including strong similarities between flock systems on isolated mountain ranges. We are particularly interested to see if studies of flocks at higher elevations in northeast India and Myanmar will find similar elevational patterns in flock composition. Also, more detailed studies of what birds are outside of flocks are necessary to determine whether this montane flock system is really a co-evolved distinctive system, or whether it is simply reflective of similarities in the general pool of species found in the different areas. Finally, we have been silent in this review about the important variables of habitat complexity and land-use, as few studies investigated these variables (but see Robin and Davidar[24] and Pramod[25] regarding land-use, and Sridhar and Shankar[27] regarding fragmentation). Studies on the effects of these variables, and management plans that consider the conservation of flocks, are particularly needed in the region. We hope this review sparks interest in these types of questions, and helps in promoting compatible and comparable studies on the biogeographical variation of mixed-species flocks.

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