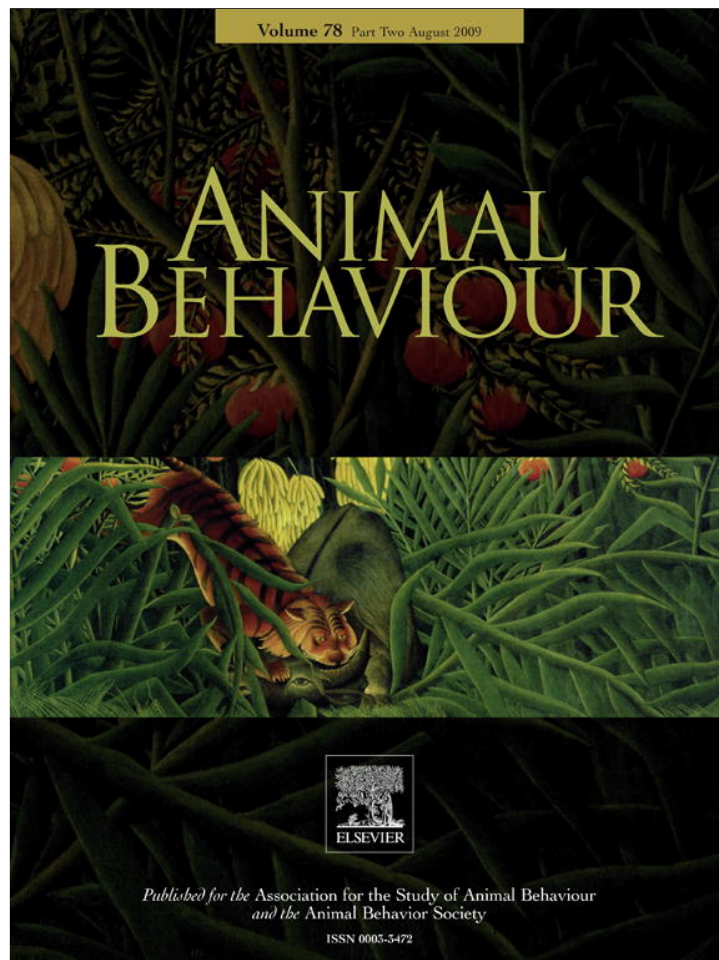


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

Why do birds participate in mixed-species foraging flocks? A large-scale synthesis

Hari Sridhar^{a,*}, Guy Beauchamp^{b,1}, Kartik Shanker^a^a Centre for Ecological Sciences, Indian Institute of Science, Bangalore^b Faculty of Veterinary Medicine, University of Montréal

ARTICLE INFO

Article history:

Received 11 November 2008
 Initial acceptance 19 January 2009
 Final acceptance 4 May 2009
 Published online 21 June 2009
 MS. number: 08-00732R

Keywords:

antipredator vigilance
 foraging
 leadership
 meta-analysis
 mixed-species flock
 pairwise comparative method

Mixed-species flocks of foraging birds have been documented from terrestrial habitats all over the world and are thought to form for either improved feeding efficiency or better protection from predators. Two kinds of flock participants are recognized: those that join other species ('followers') and are therefore likely to be the recipients of the benefits of flock participation and those that are joined ('leaders'). Through comparative analyses, using a large sample of flocks from around the world, we show that (1) 'followers' tend to be smaller, more insectivorous, and feed in higher strata than matched species that participate in flocks to a lesser extent and (2) 'leaders' tend to be cooperative breeders more often than matched species that are not known to lead flocks. Furthermore, meta-analyses of published results from across the world showed that bird species in terrestrial mixed-species flocks increase foraging rates and reduce vigilance compared to when they are solitary or in conspecific groups. Moreover, the increase in foraging rates is seen only with flock followers and not flock leaders. These findings suggest a role for predation in the evolution of mixed-species flocking. Species that are vulnerable to predation follow species whose vigilance they can exploit. By doing so, they are able to reduce their own vigilance and forage at higher rates.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Mixed-species bird flocks (flocks hereafter), roving groups of individuals from at least two species searching for food together, are found in terrestrial habitats all over the world. These flocks show large variation in size, permanence and strengths of association (Moynihan 1962; Terborgh 1990; Greenberg 2000) and include many different species in different parts of the world such as tits (Paridae), woodpeckers (Picidae) and nuthatches (Sittidae) in temperate areas; antwrens (Thamnophilidae), antshrikes (Thamnophilidae) and tanagers (Thraupidae) in the Neotropics and babblers (Timaliidae), drongos (Dicruridae) and minivets (Campephagidae) in the Palaeotropics. Two main hypotheses have been proposed to explain why birds participate in such flocks: (1) improved feeding efficiency; (2) reduced risk of predation (reviewed in Morse 1977).

Improved feeding could occur through feeding on insects flushed by other birds (Winterbottom 1943), copying foraging locations (Krebs 1973; Waite & Grubb 1988) and avoiding previously exploited areas (Cody 1971; Beauchamp 2005). Reduced predation risk can arise through the selfish-herd effect (reduced risk in relation to the position of other group members; Hamilton

1971), the dilution effect (reduced probability of being singled out by a predator; Foster & Treherne 1981), the encounter effect (reduced probability of being encountered by a predator; Inman & Krebs 1987), the confusion effect (reduced ability of a predator to single out and attack individual prey; Neill & Cullen 1974), the 'many-eyes' effect (increased probability of a predator being detected; Pulliam 1973) and physical disturbance of predators by many birds (Charnov & Krebs 1975). These two types of advantage need not be mutually exclusive; participation in flocks might allow birds to exploit the vigilance of other species, reduce their own time spent in vigilance and correspondingly increase foraging efficiency (Greenberg 2000). At the same time, it is not necessary that all participants in flocks accrue benefits; certain species that are joined by other species might in fact suffer costs from being in flocks (Zamora et al. 1992; Cimprich & Grubb 1994; Pomara et al. 2003).

Numerous approaches have been used to examine which advantages are operational in mixed-species flocks, including experiments, comparative analyses and observational methods (reviewed in Greenberg 2000). Support for both foraging and antipredator explanations has been found in one study or another (Buskirk 1976; Berner & Grubb 1985; Grubb 1987; Cimprich & Grubb 1994; Dolby & Grubb 1998; Thiollay & Jullien 1998; Thiollay 1999; Beauchamp 2004), but a consensus across a wide range of flocks has not been reached. Little is also known about the nature of the relationship between species participating in mixed-species flocks, that is, whether all or only some participants benefit through

* Correspondence: H. Sridhar, Centre for Ecological Sciences, Indian Institute of Science, Malleswaram, Bangalore-560012, Karnataka, India.

E-mail address: hari@ces.iisc.ernet.in (H. Sridhar).

¹ Guy Beauchamp is at the Faculty of Veterinary Medicine, University of Montréal, P. O. Box 5000, St-Hyacinthe, Québec J2S 7C6, Canada.

their association with other species. Given that many studies of flocks from different areas have described two types of participant in flocks, those that join other species (followers in our terminology) and those that are joined by other species (leaders in our terminology; for example see Moynihan 1962; Hino 1998; Kotagama & Goodale 2004), it is likely that the associations between species in flocks might include mutualism, commensalism and parasitism. In this paper, we attempted a large-scale analysis of why birds participate in mixed-species flocks using quantitative syntheses of pre-existing information on mixed-species flocks.

Comparative analyses have been used to examine correlates of flocking tendencies of species in Costa Rica (Buskirk 1976) and French Guiana (Thiollay & Jullien 1998). Both studies found that bird species that were more vulnerable to predation tended to have higher flocking propensities but did not distinguish between leader and follower species. In addition, these two studies were restricted to single sites and did not take into account phylogenetic relationships among species and therefore treated different species as independent units of analysis. Given that many mixed-species flocks include closely related species, the costs and benefits of flocking are probably experienced in similar fashion by many species and species are not likely to be independent statistical units. We addressed these issues by doing a comparative analysis with a broader geographical coverage and taking into account phylogenetic relationships among species.

We also carried out separate analyses for two different kinds of participant in flocks, 'followers' and 'leaders', based on the reasoning that they might be present in flocks for different reasons. Followers are species that are thought to get the benefits of flock participation while 'leaders' are species that are joined by other species and are thought to provide some of the benefits of flock participation. Through the use of comparative methods, we examined the relative importance of a candidate set of traits (explained in the following section) thought to be associated with being a flock follower and a flock leader (Buskirk 1976; Thiollay & Jullien 1998; Beauchamp 2002). This provides preliminary insights into whether direct foraging benefits or antipredator benefits (either through shared vigilance allowing for more time spent foraging or reduced predation risk) are more relevant in determining participation in flocks.

Another route to determine benefits of mixed-species flocking is to examine changes in foraging and vigilance rates of species in mixed-species flocks. Numerous studies have compared foraging and/or vigilance rates of species searching for food alone or in flocks including other species or not, but this literature has not been synthesized to examine overall patterns at a large scale. Using the tools of meta-analysis, we examined whether vigilance and foraging rates change consistently when individuals of a particular species do or do not occur in mixed-species flocks.

The overall objective of our study was to increase our understanding of the nature of the benefits of participation in mixed-species flocks and the mechanisms through which they are obtained. Our specific objectives were (1) to identify the correlates of flocking propensity and flock leadership among species and (2) to compare foraging and vigilance rates of species between mixed-species flock and solitary or conspecific group contexts.

SPECIES TRAITS AND PREDICTIONS

For the comparative analyses of flocking propensity and flock leadership we chose to focus on a suite of traits that are thought to influence participation in mixed-species flocks (Buskirk 1976; Thiollay & Jullien 1998; Beauchamp 2002). In the case of 'followers', the species traits included as independent variables were body size, diet, foraging behaviour, foraging height and intraspecific sociality.

If birds participated in mixed-species flocks for antipredator advantages we would expect small birds, which are thought to be more vulnerable to predation (Buskirk 1976; Thiollay & Jullien 1998), to join flocks more than large birds. In the case of diet, we predicted that insectivorous birds, which rarely form intraspecific groups because of competition, will participate more in flocks than plant-feeders which can obtain the benefits of group foraging through association with conspecifics (Beauchamp 2002). Bird species that forage on or close to the ground are thought to be less vulnerable to predation than those that forage arboreally (Buskirk 1976; Thiollay & Jullien 1998); we therefore expected the latter to join flocks more than the former. For the same reason, we expected bird species that forage using active methods (gleaning, bark probing, etc.) to join flocks more than sit-and-wait predators (Buskirk 1976; Thiollay & Jullien 1998). Finally, we predicted that species in which individuals can form intraspecific groups will join mixed-species flocks less than those that occur solitary or in pairs because they are not solely dependent on mixed-species flocks for group foraging (Buskirk 1976; Beauchamp 2002). These hypotheses have not been tested thoroughly but have been repeatedly discussed in the context of participation in mixed-species flocks and vulnerability to predation (Buskirk 1976; Thiollay & Jullien 1998).

In the case of leaders, we singled out one particular trait, namely cooperative breeding, which occurs frequently among leaders of mixed-species flocks (e.g. Moynihan 1962; Bell 1980, 1983; Hino 2002). Kin-selected behaviour, such as alarm calling, which might occur more frequently in cooperative breeders, may provide antipredator benefits to joining species. Earlier research has shown that leaders tend to occur in larger intraspecific groups than species that do not lead (Powell 1985). We hypothesized that if joining a leader is mainly for antipredator reasons, then, even among intraspecifically gregarious species, those that are cooperatively breeding will tend to be followed more often than those that do not breed cooperatively because the former are likely to have better-developed antipredator systems which followers can exploit (Koenig & Dickinson 2004).

METHODS

The sources that we searched to obtain the data we required for our analyses (191 published papers and three unpublished sources) were put together by us over many years and our coverage is extensive, dating back to more than 75 years. We used online search engines, using, among others, 'mixed-species flock' or 'flocking' as keywords, and backtracked references from published papers. Apart from published sources, we also wrote to researchers carrying out work on mixed-species flocking to request them to share their unpublished data (sources of data for all analyses are provided in the Appendix, Tables A1–A4). We did not include nonterrestrial and frugivorous terrestrial flocks because they seem to be formed by species independently aggregating at a resource and not based on attraction between species per se (e.g. Chilton & Sealy 1987; Hunt et al. 1988). We also did not include theoretical and review papers as they were unlikely to contain the data we required for our analyses. We included multiple papers by the same authors at the same sites because different papers could contain different measures related to mixed-species flocking that we were interested in.

Comparative Pairwise Analysis

Flock followers

We searched our database on mixed-species roving flocks in terrestrial habitats to get information on flocking propensities (the

percentage of all sightings of a species that occurred in mixed-species flocks; Jullien & Thiollay 1998) of individual bird species. Information for 14 species from two sites was obtained by directly writing to the researchers concerned and requesting them to share unpublished data (Table A1). From each site, we chose pairs of closely related species (either confamilial or congeneric), including a species with high flocking propensity and a species with low flocking propensity, with at least a 20 percentage points difference in flocking propensity between the two types of species. We chose to use flocking propensity as our measure of flocking tendency because it controls for differences in abundance between members of a pair. By choosing closely related species we made sure that the species in each pair were as similar as possible in all variables other than the ones included in the analyses. We tested differences between matched species in the following traits: body mass (g), diet (primarily insectivorous versus primarily plant-feeder), foraging behaviour (active foraging versus sit-and-wait), foraging strata (primarily terrestrial versus primarily arboreal) and intra-specific sociality (primarily gregarious vs. primarily solitary or in pairs). Wherever possible, species were assigned these trait categories based on quantitative information from the same sites from which flocking propensities were obtained. If this was not possible, species' trait information was obtained from other published literature. We were able to assign most species clearly to either of two classes for each variable, omitting the few pairs for which we were unable to do so.

We used paired *t* tests for body size and McNemar's test for all other variables. McNemar's test was only carried out for pairs of species where phenotypic traits differed within pairs; pairs that did not differ in the trait in question were ignored in the analysis. We first conducted the analysis considering all matched pairs. However, given that many pairs contained species that are closely related, we also conducted an analysis using only phylogenetically independent pairs. We conducted the phylogenetically corrected analysis by drawing a line connecting the two species of each pair on a phylogenetic tree and ensuring that no connecting lines from different pairs crossed each other (Møller & Birkhead 1992; Maddison 2000). Phylogenetic information was obtained from published literature (see Tables A1, A2).

Flock leader

We searched the previous database on mixed-species flocks to compile a list of species identified as leading flocks. We included flock leaders that were identified either using quantitative criteria (being at the forefront of flocks/was joined and followed by other species more often than it joined and followed others) or through a qualitative assessment of flock leading tendency made by the authors (Table A2). In one case, we wrote directly to the researcher concerned to obtain information.

We used a similar analytical framework to that used for flock followers. To form pairs for comparison, for every identified flock leader species, we chose the closest relative species (mostly congeneric; some confamilial) from the same site that does not lead flocks. We then used McNemar's test to see whether leaders tend to be cooperatively breeding more often than species that are not known to lead flocks. Information on cooperative breeding was obtained from a list in Koenig & Dickinson (2004). We repeated the analysis using only phylogenetically independent pairs as above.

Meta-analysis of Foraging and Vigilance Rates

Using our database, we looked for data on foraging rates (either feeding success or feeding attempts per unit time) and vigilance rates (scans per unit time; mean, SD and sample sizes) of species in

different social contexts (mixed-species flock versus solitary/intraspecific group). For both variables, we included cases for which the required measures were available for a species in mixed-species flocks and for either a solitary or an intraspecific group condition (Tables A3, A4). When measures for both solitary and intraspecific groups were available we randomly chose one for the comparison. We conducted a meta-analysis using MetaWin (Rosenberg et al. 2000) to find out whether there is an overall significant effect of social context on foraging and scanning rates across species and geographical areas. This was done in two steps. First, a standardized effect size, Hedges' d_+ , was calculated for each species in each site based on the difference in foraging or vigilance rates in two different social contexts. From these individual effect sizes, a cumulative effect size (E_{++}) was calculated, which is the average weighted by sample sizes. The analysis used a mixed-model approach given its more realistic assumption that random variation among studies exists (Gurevitch & Hedges 1993). An effect was deemed to be statistically significant if the confidence interval did not include zero. The conventional interpretation of the magnitude of effect size was used (Gurevitch & Hedges 1993): effect size of 0.2 was small, 0.5 was medium, 0.8 was large and greater than 1 was very large.

We also calculated the 'Rosenthal number' for each effect size (Gurevitch & Hedges 1993). This is a fail-safe number and indicates the number of studies of zero effect that need to be included to make the effect size obtained nonsignificant. The Rosenthal number is used to check whether there is a bias against publishing nonsignificant results. In the case of foraging rate, we also conducted the analysis including type of participant (leader or follower) as a categorical variable. This was done because we expected that the magnitude and direction of difference might vary based on whether the participant is a leader or a follower. We also repeated the analysis separately for solitary versus mixed-species flock and intraspecific group versus mixed-species flock comparisons. We could not carry out the same for vigilance rates because of inadequate sample sizes.

RESULTS

Correlates of Being a Flock Follower

We identified 66 pairs of species, in 30 bird families from 17 sites worldwide (Table A1) that met our criteria for inclusion. Measures of flocking propensity for 14 species from two sites were obtained by writing directly to the researchers concerned. In the initial analysis including all pairs, species that participated in flocks more often, in contrast to matched species from the same sites that participated less often, were significantly smaller (paired *t* test: $t_{59} = -2.3$, $N = 60$, $P = 0.023$; Fig. 1), had a more insectivorous diet (McNemar's test: $N = 6/6$ pairs, $\chi^2_1 = 4.2$, $P = 0.041$) and foraged above ground more often (McNemar's test: $N = 16/21$ pairs, $\chi^2_1 = 4.8$, $P = 0.029$). Level of activity while foraging (only one pair was different) and intraspecific gregariousness (McNemar's test: $\chi^2_1 = 0.125$, $N = 8$, $P = 0.72$) did not differ significantly between the two types of species.

Results were generally similar in the phylogenetically corrected analysis, but the sample size was reduced. Species that joined mixed-species flocks more had a more insectivorous diet than matched species that flocked less (McNemar's test: $N = 6/6$ pairs, $\chi^2_1 = 4.2$, $P = 0.041$). The effects for body size and foraging strata were of similar magnitude but not statistically significant (body size: $t_{46} = -1.8$, $N = 47$, $P = 0.082$; Fig. 1; foraging strata: $N = 12/17$ pairs, $\chi^2_1 = 2.1$, $P = 0.147$). We also did not find a significant effect for level of activity while foraging (only one pair was different) and intraspecific gregariousness ($\chi^2_1 = 0.125$, $N = 8$, $P = 0.72$).

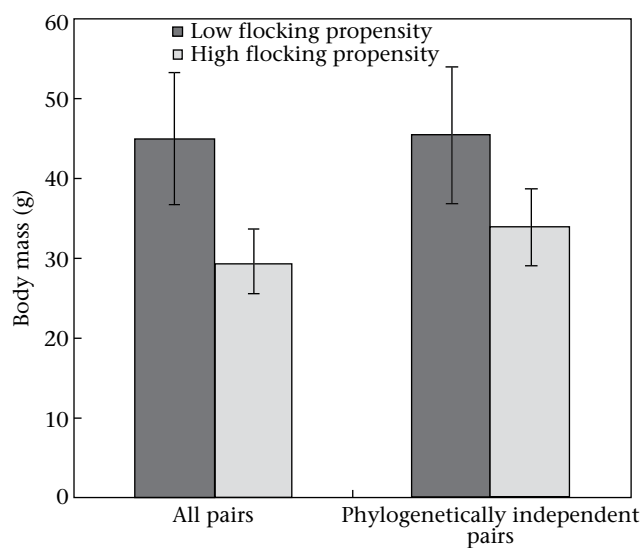


Figure 1. Comparison of average \pm SE body mass (g) between pairs of closely related species differing in flocking propensity.

Relationship Between Leadership and Cooperative Breeding

We identified 24 pairs of species in 17 families from 24 sites worldwide (Table A2) that met our criteria for inclusion. In the initial analysis including all pairs, cooperative breeding was more prevalent in leader species than in matched species that were not known to lead flocks (McNemar’s test: $N = 7/7$ pairs, $\chi^2_1 = 5.1$, $P = 0.024$). The relationship remained significant in the phylogenetically corrected analysis (McNemar’s test: $N = 6/6$ pairs, $\chi^2_1 = 4.2$, $P = 0.040$).

Influence of Social Context on Foraging and Vigilance Rates

We obtained the required foraging rate information for 27 species (22 genera, 14 families) from 14 studies (Table A3). This included 21 follower species and six leader species. Foraging rate for a given species was significantly higher when the species occurred in mixed-species flocks than when the species foraged alone or with conspecifics ($E_{++} = 0.44$, bootstrap confidence interval, CI = 0.23–0.65, $df = 26$; Rosenthal number = 150). The high Rosenthal number obtained suggests that a bias towards publication of only significant results was unlikely. When analysed

separately for flock followers and flock leaders, followers had significantly higher foraging rates in flocks ($E_{++} = 0.54$, bootstrap CI = 0.28–0.79, $df = 20$), while leaders’ foraging rates, although marginally higher in mixed-species flocks, were not significantly different between mixed-species flocks and solitary or intraspecific groups ($E_{++} = 0.13$, bootstrap CI = –0.26–0.46, $df = 5$).

We then contrasted foraging rates of species (leaders and followers together) in mixed-species flocks separately against rates when foraging alone ($N = 19$) or with conspecifics ($N = 7$). Foraging rates were significantly higher in mixed-species flocks both when compared to solitary foraging ($E_{++} = 0.40$, bootstrap CI = 0.16–0.65, $df = 18$) and when compared to intraspecific group foraging ($E_{++} = 0.55$, bootstrap CI = 0.17–0.97, $df = 6$). Small sample sizes prevented us from carrying out the same comparison for leaders and followers separately.

We obtained the required vigilance rate information for 11 species (10 genera, six families) from seven studies (Table A4). Vigilance rate was lower in mixed-species flocks than in solitary or intraspecific group conditions ($E_{++} = -1.89$, bootstrap CI = –2.68––1.17, $df = 10$; Rosenthal number = 66). The high Rosenthal number obtained again suggests that a bias towards publication of only significant results was unlikely. The sample size was too small to distinguish vigilance in mixed-species flocks from that in the solitary or intraspecific group foraging conditions separately and between leader and follower species.

DISCUSSION

The findings of our large-scale comparative analysis of mixed-species flocks suggest an important role for predation in the evolution of this behaviour in terrestrial foraging birds (Table 1). We found that higher flocking tendencies are associated with species traits thought to influence vulnerability to predation such as small size, insectivory and arboreal foraging. We also found that species that are likely to provide antipredator benefits, such as cooperative breeders, tend to be leaders of mixed-species flocks, more often. Finally, we found that foraging rates of species increase and vigilance rates decrease in mixed-species flocks, suggesting that by associating in flocks, birds are able to exploit the vigilance of the mixed-species flock and reduce their own vigilance time. Increased foraging rates in mixed-species flocks may reflect the increased time available for feeding but may also reflect direct foraging benefits such as greater food availability caused by prey flushing.

The costs and benefits of participation in mixed-species flocks have been studied using a variety of approaches. These include

Table 1
Summary of findings of different questions investigated in this study

Test	Results of analysis using all pairs	Results of analysis using only phylogenetically independent pairs
Pairwise comparison of closely related species, of which one participates in mixed-species flocks to a greater extent than the other	Smaller species participate in flocks more than large species Insectivorous species participate in flocks more than noninsectivorous species Arboreal species participate in flocks more than terrestrial species	Insectivorous species participate in flocks more than noninsectivorous species
Pairwise comparison of closely related species, of which one leads flocks while the other does not	Cooperatively breeding species lead flocks more than species that do not breed co-operatively	Cooperatively breeding species lead flocks more than species that do not breed cooperatively
Meta-analysis of difference in foraging rates of species between mixed-species flock and intraspecific group conditions	Foraging rates of species higher in flocks than when solitary or in intraspecific groups	—
Meta-analysis of difference in vigilance rates of species between mixed-species flock and intraspecific group conditions	Vigilance rates of species lower in flocks than when solitary or in intraspecific groups	—

Only results significant at $P < 0.05$ are presented.

experiments manipulating food (Berner & Grubb 1985; Grubb 1987), predation pressure (Suhonen 1993; Forsman et al. 1998), or both (Szekely et al. 1989), or removing species important for flock formation (Cimprich & Grubb 1994; Dolby & Grubb 1998), 'natural experiments' comparing foraging and vigilance behaviour in different social contexts (Popp 1988; Hino 1998), comparisons of flocking tendencies in areas differing in predation pressure (Thiollay 1999; Beauchamp 2004), and comparative analysis of flocking tendencies in relation to species traits (Buskirk 1976; Thiollay & Jullien 1998). While support for both foraging and predation-related benefits of flocking has been found from different sites, a synthesis across a range of flocks has so far been lacking. Our study provides this, using findings from a variety of approaches. We now discuss our findings in turn.

Flock Followers

Bird species that join flocks more often tended to be smaller, more insectivorous and more arboreal than matched bird species that join flocks less often. Our finding of higher participation of insectivorous birds in flocks confirms earlier suggestions based on flock composition (reviewed in Greenberg 2000). In the phylogenetically corrected analysis, diet was the only significant factor influencing joining, suggesting that this could be the most important determinant of flocking tendencies of species. The fact that smaller species and more arboreal species tended to participate more in flocks suggests a role for predation in the formation of mixed-species bird flocks. Both traits are thought to be associated with higher vulnerability to predation in terrestrial habitats (Buskirk 1976; Thiollay & Jullien 1998). However, both these traits were less significant in the phylogenetically corrected analysis although the effect was in the same direction and similar in magnitude. A larger sample size is needed to provide further insight into the effect of body size and foraging strata.

What are the benefits that insectivorous species might obtain in mixed-species flocks? Foraging advantages have been discussed in the literature and include, for instance, flushing of prey by other companions (Winterbottom 1943). Antipredator benefits have also been suggested and, given that insectivorous species rarely forage in large intraspecific groups (Beauchamp 2002), joining a mixed-species flock might allow birds to reduce time spent in vigilance. So, perhaps the effect of diet is actually confounded with group size. In this case, one could argue that less sociable species, regardless of diet, are more likely to join mixed-species flocks. However, we found no significant difference in flocking tendencies between solitary and intraspecifically gregarious species. We note that some solitary species may be prevented from joining flocks because these flocks move too rapidly or forage in an unsuitable stratum. In addition, less solitary species may also benefit from joining mixed-species flocks in terms of increased safety from predation because of an increase in group size and in predator detection ability. Therefore, intraspecific group size may not be a good predictor of joining frequency. In the end, insectivorous species those join mixed-species flocks may have a diet and feeding habits that match more closely those of other species in the group and may enjoy safety in numbers and a higher foraging efficiency once they join.

Although previous work suggested that species with a more active foraging mode are more exposed to predation and may therefore join flocks more often (Buskirk 1976; Thiollay & Jullien 1998; Beauchamp 2002), we found no evidence for this effect in mixed-species flocks. At least for the flocks that we considered, an active foraging mode was not more conducive to joining mixed-species flocks. Flocks could therefore be a mix of active foragers gaining antipredator benefits and sit-and-wait predators gaining foraging benefits.

Flock Leaders

We have shown that flock leaders tend to breed cooperatively more often than closely related species that do not lead flocks. Intraspecifically gregarious birds, which are often found to be flock leaders (Powell 1985), can provide both direct foraging benefits such as flushing insects (Kotagama & Goodale 2004) and better protection through simple dilution (Hamilton 1971), many-eyes (Pulliam 1973) or encounter effects (Inman & Krebs 1987) for flock followers. Therefore, the fact that leaders tend to be intraspecifically gregarious is not very informative in helping us understand the mechanisms through which flocks benefit participants. However, the fact that leaders tend to be cooperatively breeding more often than nonleaders does suggest an important role for antipredator behaviour. Cooperatively breeding birds live in kin groups and are likely to have well-developed intraspecific communication and alarm call systems (Koenig & Dickinson 2004). Birds that join cooperative breeders might be able to exploit this antipredator system.

A limitation of our analysis of leader traits is that most of our data came from closed forest habitats. In more open habitats, such as the 'cerrado' in Brazil, leaders often tend to be solitary 'sentinels' with well-developed alarm call systems (Ragusa-Netto 2002). Therefore, there might be more than one way of being a leader in different habitats. For example, Goodale & Kotagama (2005) found that in Sri Lankan rainforests, the calls of both the orange-billed babbler, *Turdoides rufescens*, a cooperative breeder (E. Goodale personal communication), and the greater racket-tailed drongo, *Dicrurus paradiseus*, a solitary sentinel species, attracted other species.

Influence of Social Context on Foraging and Vigilance Rates

We found that foraging rates increase and scanning rates decrease in mixed-species flocks compared to solitary or intraspecific group foraging. The effect size for foraging rate was moderate (<0.5) whereas in the case of scanning rates it was very large (>1) by conventional designations. Birds in mixed-species bird flocks might be able to reduce vigilance rates by exploiting the vigilance and antipredator systems of other species, as suggested earlier, or may simply benefit from being in a larger flock overall. Joining such flocks might be a strategy to reduce time spent vigilant and so to increase foraging efficiency. These benefits accrued through participation in mixed-species flocks could result in higher fitness; work on Neotropical flocks has shown that flock participants tended to have higher survival rates than those species that do not participate in flocks (Jullien & Clobert 2000).

We have also shown that foraging rate increases significantly only for flock followers and not for flock leaders, although the power of the test for leaders is much lower owing to the small sample size. At the moment, we do not have enough information to show how leader species might benefit from being joined by others, but it is conceivable that the balance between costs and benefits is not the same for all species in a mixed-species flock. The reduction in vigilance for species foraging in mixed-species flocks rather than alone or in intraspecific groups is in line with the common finding that vigilance in groups is usually lower (Krause & Ruxton 2002). The reduction in vigilance is in part a consequence of foraging in a larger group since mixed-species flocks are usually larger than intraspecific groups. However, there is the possibility that even for a given group size vigilance may also change depending on group composition, especially when more vigilant species are present. There is evidence that many animal species are able to recognize and use the information in the alarm calls of heterospecifics (Lea et al. 2008). Therefore, mixed-species flocks could offer additional safety because of the larger numbers and better predator detection mechanisms. Our data, however, do not allow us to tease apart the effects of group size and

composition on foraging and vigilance rates because in all our cases mixed-species flocks were larger than intraspecific groups. Also, given that many of these tests suffer from low power owing to small sample sizes, our findings are only indicative of trends.

Conclusions

Putting together our findings allows us to draw a picture of the 'why' and 'how' of mixed-species flocks: species that are vulnerable to predation join other species and benefit from their vigilance. In joining flocks, they are able to reduce their own vigilance and increase feeding rates.

We note that in the case of all the categorical species traits that we used, in most pairs the low- and high-flocking members of pairs did not differ. This could mean either that variables other than those measured are responsible for the differences in flocking tendency, or that there are finer differences between members of the pairs that were not captured at the coarse level of our categorical variables. We think the second possibility is more likely since we included the most likely candidate traits in the analysis, and that the issue could be resolved by using trait measurements of finer resolution on a continuous scale.

While we have focused on the benefits of participation in mixed-species flocks, participants also experience costs in terms of inter-specific aggression and competition. Therefore the decision whether to join a flock or not is likely to depend on what species are already present. There is, however, evidence that aggression is more common within than between species (Morse 1970; Greenberg 2000). An interesting line of enquiry would be to examine whether there are rules of association that govern species' joining of flocks.

Mixed-species groups are not restricted to terrestrial birds, but occur in a variety of taxa, including mammals (Stensland et al. 2003) and fish (Lukoschek & McCormick 2002), in different habitats, including aquatic environments, and in contexts other than foraging such as nesting (Haemig 2001). Whether the patterns we found in terrestrial avian flocks also apply in other contexts remains to be established.

Acknowledgments

We thank the Ministry of Environment and Forests, Government of India for funding this project. We are also grateful to Eben Goodale and Pranav Trivedi for sharing unpublished data and Kavita Isvaran, N.V. Joshi and Suhel Quader for useful suggestions. Finally, we thank Diego Gil and four anonymous referees for their useful suggestions.

References

- Alves, M. A. & Cavalcanti, R. B. 1996. Sentinel behaviour, seasonality and the structure of bird flocks in a Brazilian savanna. *Ornithologia Neotropical*, **7**, 43–52.
- Balda, R. P., Bateman, G. C. & Foster, F. G. 1972. Flocking associates of the pinon jay. *Wilson Bulletin*, **84**, 60–76.
- Barnard, C. J. & Stephens, H. 1983. Costs and benefits of single and mixed-species flocking in fieldfares (*Turdus pilaris*) and redwings (*T. iliacus*). *Behaviour*, **84**, 91–123, doi:10.1163/156853983X00309.
- Beauchamp, G. 2002. Higher-level evolution of intraspecific flock-feeding in birds. *Behavioral Ecology and Sociobiology*, **51**, 480–487, doi:10.1007/s00265-002-0461-7.
- Beauchamp, G. 2004. Reduced flocking by birds on island with relaxed predation. *Proceedings of the Royal Society B*, **271**, 1039–1042, doi:10.1098/rspb.2004.2703.
- Beauchamp, G. 2005. Does group foraging promote efficient exploitation of resources? *Oikos*, **111**, 403–407, doi:10.1111/j.0030-1299.2005.14136.x.
- Bell, H. L. 1980. Composition and seasonality of mixed-species feeding flocks of insectivorous birds in the Australian Capital Territory. *Emu*, **80**, 227–232, doi:10.1071/MU9800227.
- Bell, H. L. 1983. A bird community of lowland rain forest in New Guinea. 5. Mixed species feeding flocks. *Emu*, **82**, 265–275, doi:10.1071/MU9820256s.
- Benz, B. W., Robbins, M. B. & Peterson, A. T. 2006. Evolutionary history of woodpeckers and allies (Aves: Picidae): placing key taxa on the phylogenetic tree. *Molecular Phylogenetics and Evolution*, **40**, 389–399, doi:10.1016/j.ympev.2006.02.021.
- Berner, T. O. & Grubb, T. C. 1985. An experimental analysis of mixed-species flocking in birds of deciduous woodland. *Ecology*, **66**, 1229–1236, doi:10.2307/1939176.
- Brumfield, R. T., Tello, J. G., Cheviron, Z. A., Carling, M. D., Crochet, N. & Rosenberg, K. 2007. Phylogenetic conservatism and antiquity of a tropical specialization: army-ant-following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics and Evolution*, **45**, 1–13, doi:10.1016/j.ympev.2007.07.019.
- Burns, K. J. 1997. Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. *Molecular Phylogenetics and Evolution*, **8**, 334–348, doi:10.1006/mpev.1997.0430.
- Burns, K. J. & Naoki, K. 2004. Molecular phylogenetics and biogeography of Neotropical tanagers in the genus *Tangara*. *Molecular Phylogenetics and Evolution*, **32**, 838–854, doi:10.1016/j.ympev.2004.02.013.
- Buskirk, W. H. 1976. Social systems in a tropical forest avifauna. *American Naturalist*, **110**, 293–310.
- Charnov, E. L. & Krebs, J. R. 1975. Evolution of alarm calls: altruism or manipulation? *American Naturalist*, **109**, 107–112.
- Chen, C. C. & Hsieh, F. 2002. Composition and foraging behaviour of mixed-species flocks led by the grey-cheeked fulvetta in Fushan Experimental Forest, Taiwan. *Ibis*, **144**, 317–330, doi:10.1046/j.1474-919X.2002.00020.x.
- Chilton, G. & Sealy, S. G. 1987. Species roles in mixed-species feeding flocks of seabirds. *Journal of Field Ornithology*, **58**, 456–463.
- Cibois, A. 2003. Mitochondrial DNA phylogeny of babbler (Timaliidae). *Auk*, **120**, 35–54, doi:10.1642/0004-8038(2003)120[0035:MDPOBT]2.0.CO;2.
- Cicero, C. & Johnson, N. K. 2001. Higher-level phylogeny of New World vireos (Aves: Vireonidae) based on sequences of multiple mitochondrial DNA genes. *Molecular Phylogenetics and Evolution*, **20**, 27–40, doi:10.1006/mpev.2001.0944.
- Cimprich, D. A. & Grubb, T. C. 1994. Consequences for Carolina chickadees of foraging with tufted titmice in winter. *Ecology*, **75**, 1615–1625, doi:10.2307/1939622.
- Cody, M. L. 1971. Finch flocks in the Mohave desert. *Theoretical Population Biology*, **2**, 141–158.
- Croxall, J. P. 1976. The composition and behavior of some mixed-species bird flocks in Sarawak. *Ibis*, **118**, 333–346, doi:10.1111/j.1474-919X.1976.tb02024.x.
- Develey, P. F. & Stouffer, P. C. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology*, **15**, 1416–1422.
- Dolby, A. S. & Grubb, T. C. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behaviour*, **56**, 501–509, doi:10.1006/anbe.1998.0808.
- Ewert, D. N. & Askins, R. A. 1991. Flocking behaviour of migratory warblers in winter in the Virgin Islands. *Condor*, **93**, 864–868.
- Forsman, J. T., Monkkonen, M., Inkeroinen, J. & Reunanen, P. 1998. Aggregate dispersion of birds after encountering a predator: experimental evidence. *Journal of Avian Biology*, **29**, 44–48.
- Foster, W. A. & Treherne, J. E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, **293**, 466–467, doi:10.1038/293466a0.
- Goodale, E. & Kotagama, S. W. 2005. Testing the roles of species in mixed-species bird flocks of a Sri Lankan rainforest. *Journal of Tropical Ecology*, **21**, 669–676, doi:10.1017/S0266467405002609.
- Gradwohl, J. & Greenberg, R. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. *Auk*, **97**, 385–395.
- Greenberg, R. 2000. Birds of many feathers: the formation and structure of mixed-species flocks of forest birds. In: *On the Move: How and Why Animals Travel in Groups* (Ed. by S. Boinski & P. A. Gerber), pp. 521–558. Chicago: University of Chicago Press.
- Greig-Smith, P. W. 1978. The formation, structure and function of mixed-species insectivorous bird flocks in West African savanna woodland. *Ibis*, **120**, 284–297, doi:10.1111/j.1474-919X.1978.tb06789.x.
- Grubb, T. C. 1987. Changes in the flocking behaviour of wintering English titmice with time, weather and supplementary food. *Animal Behaviour*, **35**, 794–806, doi:10.1016/S0003-3472(87)80116-1.
- Gurevitch, J. & Hedges, L. V. 1993. Meta-analysis: combining the results of independent experiments. In: *Design and Analysis of Ecological Experiments* (Ed. by S. M. Scheiner & J. Gurevitch), pp. 378–398. New York: Chapman & Hall.
- Haemig, P. 2001. Symbiotic nesting of birds with formidable animals: a review with applications to biodiversity conservation. *Biodiversity and Conservation*, **10**, 527–540, doi:10.1023/A:1016654326822.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.
- Hart, P. J. & Freed, L. A. 2003. Structure and dynamics of mixed-species flocks in a Hawaiian rain forest. *Auk*, **120**, 82–95.
- Hart, P. J. & Freed, L. A. 2005. Predator avoidance as a function of flocking in the sexual dichromatic Hawaii akapea. *Journal of Ethology*, **23**, 29–33, doi:10.1007/s10164-004-0124-4.
- Hino, T. 1998. Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar. *Journal of Avian Biology*, **29**, 17–24.
- Hino, T. 2002. Breeding bird community and mixed-species flocking in a deciduous broad-leaved forest in western Madagascar. *Ornithological Science*, **1**, 111–116.
- Hughes, J. M. 2000. Monophyly and phylogeny of cuckoos (Aves, Cuculidae) inferred from osteological characters. *Zoological Journal of the Linnean Society*, **130**, 263–307, doi:10.1111/j.1096-3642.2000.tb01632.x.
- Hunt, G. L., Harrison, N. M., Hamner, W. M. & Obst, B. S. 1988. Observations of a mixed-species flock of birds foraging on Euphausiids near St-Matthew Island. *Auk*, **105**, 345–349.

- Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. *Condor*, **96**, 105–118.
- Inman, A. J. & Krebs, J. 1987. Predation and group living. *Trends in Ecology & Evolution*, **2**, 31–32, doi:10.1016/0169-5347(87)90093-0.
- Irestedt, M., Fjeldsa, J. & Ericson, P. G. P. 2004a. Phylogenetic relationships of woodcreepers (Aves: Dendrocolaptinae): incongruence between molecular and morphological data. *Journal of Avian Biology*, **35**, 280–288, doi:10.1111/j.0908-8857.2004.03234.x.
- Irestedt, M., Fjeldsa, J., Nylander, J. A. A. & Ericson, P. G. P. 2004b. Phylogenetic relationships of typical antbirds (Thamnophilidae) and test of incongruence based on Bayes factors. *BMC Evolutionary Biology*, **4**, 23, doi:10.1186/1471-2148-4-23.
- Irestedt, M., Fjeldsa, J. & Ericson, P. G. P. 2006. Evolution of the ovenbird-wood-creeper assemblage (Aves: Furnariidae): major shifts in nest architecture and adaptive radiation. *Journal of Avian Biology*, **37**, 260–272, doi:10.1111/j.2006.0908-8857.03612.x.
- James, H. F. 2004. The osteology and phylogeny of the Hawaiian finch radiation (Fringillidae: Drepanidini), including extinct taxa. *Zoological Journal of the Linnean Society*, **141**, 207–255, doi:10.1111/j.1096-3642.2004.00117.x.
- Jönsson, K. A. & Fjeldsa, J. 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). *Zoologica Scripta*, **35**, 149–186, doi:10.1111/j.1463-6409.2006.00221.x.
- Jullien, M. & Thiollay, J.-M. 1998. Multi-species territoriality and dynamic of neotropical understory bird flocks. *Journal of Animal Ecology*, **67**, 227–252, doi:10.1046/j.1365-2656.1998.00171.x.
- Jullien, M. & Clobert, J. 2000. The survival value of flocking in neotropical birds: reality or fiction? *Ecology*, **81**, 3416–3430, doi:10.1890/0012-9658(2000)081[3416:TSVOFI]2.0.CO;2.
- Koenig, W. D. & Dickinson, J. L. 2004. *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge: Cambridge University Press.
- Kotagama, S. W. & Goodale, E. 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. *Forktail*, **20**, 63–70.
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.
- Krebs, J. R. 1973. Social learning and the adaptive significance of mixed-species flocks of chickadees. *Canadian Journal of Zoology*, **51**, 1275–1288.
- Latta, S. C. & Wunderle, J. M. 1996a. The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. *Condor*, **98**, 595–607.
- Latta, S. C. & Wunderle, J. M. 1996b. Ecological relationships of two todies in Hispaniola: effects of habitat and flocking. *Condor*, **98**, 769–779.
- Lea, A. J., Barrera, J. P., Tom, L. M. & Blumstein, D. T. 2008. Heterospecific eavesdropping in a nonglocal species. *Behavioral Ecology*, **19**, 1041–1046, doi:10.1093/beheco/arn064.
- Lee, T. M., Soh, M. C. K., Sodhi, N., Koh, L. P. & Lim, S. L. H. 2005. Effects of habitat disturbance on mixed-species bird flocks in a tropical sub-montane rainforest. *Biological Conservation*, **122**, 193–204, doi:10.1016/j.biocon.2004.07.005.
- Lovette, I. J. & Bermingham, E. 1999. Explosive speciation in the New World *Dendroica* warblers. *Proceedings of the Royal Society B*, **266**, 1629–1636, doi:10.1098/rspb.1999.0825.
- Lovette, I. J. & Bermingham, E. 2002. What is a wood-warbler? Molecular characterization of a monophyletic parulidae. *Auk*, **119**, 695–714.
- Lukoschek, V. & McCormick, M. I. 2002. A review of multi-species foraging associations in fishes and their ecological significance. In: *Proceeding of the Ninth International Coral Reef Symposium, Bali, Indonesia, 23–27 October 2000*, Vol. 1, pp. 467–474.
- Macdonald, D. W. & Henderson, D. G. 1977. Aspects of the behaviour and ecology of mixed species bird flocks in Kashmir. *Ibis*, **119**, 489–493, doi:10.1111/j.1474-919X.1977.tb02055.x.
- Maddison, W. P. 2000. Testing character correlation using pairwise comparisons on a phylogeny. *Journal of Theoretical Biology*, **202**, 195–204, doi:10.1006/jtbi.1999.1050.
- Maldonado-Coelho, M. & Marini, M. A. 2000. Effects of forest fragment size and successional stage on mixed-species bird flocks in southeastern Brazil. *Condor*, **102**, 585–594.
- Millikan, G. C., Gaddis, P. & Pulliam, H. R. 1985. Interspecific dominance and the foraging behaviour of juncos. *Animal Behaviour*, **33**, 428–435, doi:10.1016/S0003-3472(85)80067-1.
- Møller, A. P. & Birkhead, T. R. 1992. A pairwise comparative method as illustrated by copulation frequency in birds. *American Naturalist*, **139**, 644–656.
- Monkkonen, M., Forsman, J. T. & Helle, P. 1996. Mixed-species foraging aggregations and heterospecific attraction in boreal bird communities. *Oikos*, **77**, 127–136.
- Moriarty, D. J. 1977. Flocking and foraging in the scarlet-rumped tanager. *Wilson Bulletin*, **89**, 151–153.
- Morrison, M. L., With, K. A., Timossi, I. C. & Milne, K. A. 1987. Composition and temporal variation in flocks in the Sierra Nevada. *Condor*, **89**, 739–745.
- Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecological Monographs*, **40**, 119–168, doi:10.2307/1942443.
- Morse, D. H. 1977. Feeding behaviour and predator avoidance in heterospecific groups. *Bioscience*, **27**, 332–339.
- Moynihán, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. *Smithsonian Miscellaneous Collections*, **143**, 1–140.
- Munn, C. A. & Terborgh, J. W. 1979. Multi-species territoriality in neotropical foraging flocks. *Condor*, **81**, 338–347.
- Neill, S. R. S. J. & Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. *Journal of Zoology*, **172**, 549–569.
- Nicholls, J. A., Double, M. C., Rowell, D. M. & Magrath, R. D. 2000. The evolution of cooperative and pair breeding in thornbills *Acanthiza* (Pardalotidae). *Journal of Avian Biology*, **31**, 165–176, doi:10.1034/j.1600-048X.2000.310208.x.
- Ohlson, J., Fjeldsa, J. & Ericson, P. G. P. 2008. Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of Tyrannidae (Aves, Passeriformes). *Zoologica Scripta*, **37**, 315–335, doi:10.1111/j.1463-6409.2008.00325.x.
- Olsson, U., Alstrom, P., Ericson, P. G. P. & Sundberg, P. 2005. Non-monophyletic taxa and cryptic species: evidence from a molecular phylogeny of leaf-warblers (*Phylloscopus*, Aves). *Molecular Phylogenetics and Evolution*, **36**, 261–276, doi:10.1016/j.ympev.2005.01.012.
- Partridge, L. & Ashcroft, R. 1976. Mixed-species flocks of birds in hill forest in Ceylon. *Condor*, **78**, 449–453.
- Pasquet, E., Cibois, A., Baillon, F. & Erard, C. 2002. What are African monarchs (Aves, Passeriformes)? A phylogenetic analysis of mitochondrial genes. *Comptes Rendus Biologies*, **325**, 107–118, doi:10.1016/S1631-0691(02)01409-9.
- Pearson, D. L. 1971. Vertical stratification of birds in tropical dry forest. *Condor*, **73**, 46–55.
- Pomara, L. Y., Cooper, R. J. & Petit, L. J. 2003. Mixed-species flocking and foraging behavior of four Neotropical warblers in Panamanian shade coffee fields and forests. *Auk*, **120**, 1000–1012.
- Pomara, L. Y., Cooper, R. J. & Petit, L. J. 2007. Modeling the flocking propensity of passerine birds in two neotropical habitats. *Oecologia*, **153**, 121–133, doi:10.1007/s00442-007-0701-7.
- Popp, J. W. 1988. Scanning behaviour of finches in mixed-species groups. *Condor*, **90**, 510–512.
- Powell, G. V. N. 1985. Sociobiology and the adaptive significance of interspecific flocks in the Neotropics. *Ornithological Monographs*, **36**, 713–732.
- Pravosudov, V. V. & Grubb, T. C. 1999. Effects of dominance on vigilance in avian social groups. *Auk*, **116**, 241–246.
- Pulliam, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology*, **38**, 419–422.
- Ragusa-Netto, J. 2000. Raptors and 'Campo-Cerrado' bird mixed-flock led by *Cypsnagra hirundinacea* (Emberizidae: Thraupinae). *Revista Brasileira de Biologia*, **60**, 461–467.
- 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, doi:10.1076/snfe.37.3.219.8573.
- Rosenberg, M. S., Adams, D. C. & Gurevitch, J. 2000. *MetaWin: Statistical Software for Meta-Analysis. Version 2*. Sunderland, Massachusetts: Sinauer.
- Sasvari, L. 1992. Great tits benefit from feeding in mixed-species flocks: a field experiment. *Animal Behaviour*, **43**, 289–296, doi:10.1016/S0003-3472(05)80224-6.
- Satischandra, S. H. K., Kudavidanage, E. P., Kotagama, S. W. & Goodale, E. 2007. The benefits of joining mixed-species flocks for greater racket-tailed drongos *Dicrurus paradiseus*. *Forktail*, **23**, 145–148.
- Stensland, E., Angerbjörn, A. & Berggren, P. 2003. Mixed species groups in mammals. *Mammal Review*, **33**, 205–223, doi:10.1046/j.1365-2907.2003.00022.x.
- Styring, A. R. & Ickes, K. 2001. Woodpecker participation in mixed species flocks in peninsular Malaysia. *Wilson Bulletin*, **113**, 342–345.
- Suhonen, J. 1993. Risk of predation and foraging sites of individuals in mixed-species tit flocks. *Animal Behaviour*, **45**, 1193–1198, doi:10.1006/anbe.1993.1141.
- Sullivan, K. A. 1984. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, **91**, 294–311, doi:10.1163/156853984X00128.
- Szekely, T., Szep, T. & Juhasz, T. 1989. Mixed species flocking of tits (*Parus* spp.): a field experiment. *Oecologia*, **78**, 490–495, doi:10.1007/BF00378739.
- 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, doi:10.1002/ajp.1350210203.
- Thiollay, J.-M. 1999. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *Journal of Avian Biology*, **30**, 282–294.
- Thiollay, J.-M. & Jullien, M. 1998. Flocking behaviour of foraging birds in a neotropical rain forest and the antipredator defence hypothesis. *Ibis*, **140**, 382–394, doi:10.1111/j.1474-919X.1998.tb04599.x.
- Thomson, R. L. & Ferguson, J. W. H. 2007. Composition and foraging behaviour of mixed-species flocks in two adjacent African woodland habitats: a spatial and temporal perspective. *Ostrich*, **78**, 65–73, doi:10.2989/OSTRICH.2007.78.1.10.54.
- Veena, T. & Lokesh, R. 1993. Association of drongos with myna flocks: are drongos benefited? *Journal of Biosciences*, **18**, 111–119.
- Vuilleumier, F. 1967. Mixed-species flocks in Patagonian forests with remarks on interspecies flock formation. *Condor*, **69**, 400–404.
- Waite, T. A. & Grubb, T. C. 1988. Copying of foraging location in mixed-species flocks of temperate-deciduous woodland birds: an experimental study. *Condor*, **90**, 132–140.
- Warkentin, I. G. & Morton, E. S. 2000. Flocking and foraging behavior of wintering prothonotary warblers. *Wilson Bulletin*, **112**, 88–98, doi:10.1676/0043-5643(2000)112[0088:FAFBOW]2.0.CO;2.
- Winterbottom, J. M. 1943. On woodland bird parties in northern Rhodesia. *Ibis*, **84**, 437–442.
- Yuri, T. & Mindell, D. P. 2002. Molecular phylogenetic analysis of Fringillidae, 'New World nine-primaried oscines' (Aves: Passeriformes). *Molecular Phylogenetics and Evolution*, **23**, 229–243, doi:10.1016/S1055-7903(02)00012-X.
- Zamora, R., Hodar, J. A. & Gomez, J. M. 1992. Dartford warblers follow stonechats while foraging. *Ornis Scandinavica*, **23**, 167–174.

APPENDIX

Table A1

Pairs of closely related species that are both found in the same site and differ in flocking propensity by at least 20 percentage points

Pair code	Genus	Species	Family	Source
1*	<i>Cacomantis</i>	<i>flabelliformis</i>	Cuculidae	Bell 1980; Hughes 2000
	<i>Chrysococcyx</i>	<i>lucidus</i>		
2*	<i>Melithreptus</i>	<i>lunatus</i>	Meliphagidae	Bell 1980
		<i>brevirostris</i>		
3*	<i>Pachycephala</i>	<i>pectoralis</i>	Pachycephalidae	Bell 1980
		<i>rufiventris</i>		
4*	<i>Pardalotus</i>	<i>striatus</i>	Pardalotidae	Bell 1980
		<i>punctatus</i>		
5*	<i>Smicromnis</i>	<i>brevirostris</i>	Acanthizidae	Bell 1980
	<i>Pyrrholaemus</i>	<i>sagittatus</i>		
6*	<i>Petroica</i>	<i>phoenicea</i>	Petroicidae	Bell 1980
		<i>multicolor</i>		
7*	<i>Coracina</i>	<i>boyeri</i>	Campephagidae	Bell 1983
		<i>melas</i>		
8*	<i>Monarcha</i>	<i>chrysomela</i>	Monarchidae	Bell 1983
		<i>guttula</i>		
9*	<i>Rhipidura</i>	<i>maculipectus</i>	Rhipiduridae	Bell 1983; Pasquet et al. 2002
		<i>hyperythra</i>		
10*	<i>Rhipidura</i>	<i>threothorax</i>	Rhipiduridae	Bell 1983
		<i>rufiventris</i>		
11*	<i>Seiurus</i>	<i>noveboracensis</i>	Parulidae	Ewert & Askins 1991; Lovette & Bermingham 2002
	<i>Mniotilta</i>	<i>varia</i>		
12*	<i>Seiurus</i>	<i>aurocapillus</i>	Parulidae	Ewert & Askins 1991; Lovette & Bermingham 2002
	<i>Setophaga</i>	<i>ruticilla</i>		
13*	<i>Muscicapa</i>	<i>muttui</i>	Muscicapidae	E. Goodale, unpublished data
	<i>Cyornis</i>	<i>tickelliae</i>		
14*	<i>Gracula</i>	<i>ptilogenys</i>	Sturnidae	E. Goodale, unpublished data
	<i>Sturnus</i>	<i>albofrontatus</i>		
15*	<i>Phylloscopus</i>	<i>trochiloides</i>	Sylviidae	E. Goodale, unpublished data; Olsson et al. 2005
		<i>magnirostris</i>		
16*	<i>Rhopocichla</i>	<i>atriceps</i>	Timaliidae	E. Goodale, unpublished data; Cibois 2003
	<i>Garrulax</i>	<i>cinereifrons</i>		
17*	<i>Hemignathus</i>	<i>virens</i>	Fringillidae	Hart & Freed 2003; James 2004
		<i>munroi</i>		
18*	<i>Coua</i>	<i>coquereli</i>	Cuculidae	Hughes 2000; Hino 2002
		<i>cristata</i>		
19	<i>Xenopirostris</i>	<i>damii</i>	Vangidae	Hino 2002
	<i>Cyanolanius</i>	<i>madagascarinus</i>		
20	<i>Cacicus</i>	<i>melanicterus</i>	Icteridae	Hutto 1994
	<i>Icterus</i>	<i>pustulatus</i>		
21*	<i>Wilsonia</i>	<i>pusilla</i>	Parulidae	Hutto 1994; Lovette & Bermingham 2002
	<i>Dendroica</i>	<i>nigrescens</i>		
22	<i>Empidonax</i>	<i>difficilis</i>	Tyrannidae	Hutto 1994; Ohlson et al. 2008
	<i>Camptostoma</i>	<i>imberbe</i>		
23*	<i>Dendroica</i>	<i>tigrina</i>	Parulidae	Latta & Wunderle 1996a; Lovette & Bermingham 1999
		<i>discolor</i>		
24*	<i>Geothlypis</i>	<i>trichas</i>	Parulidae	Latta & Wunderle 1996a; Lovette & Bermingham 2002
	<i>Mniotilta</i>	<i>varia</i>		
25*	<i>Seiurus</i>	<i>aurocapilla</i>	Parulidae	Latta & Wunderle 1996a; Lovette & Bermingham 1999
	<i>Dendroica</i>	<i>dominica</i>		
26	<i>Microligea</i>	<i>palustris</i>	Parulidae	Latta & Wunderle 1996a; Lovette & Bermingham 2002
	<i>Setophaga</i>	<i>ruticilla</i>		
27*	<i>Pteruthius</i>	<i>flaviscapis</i>	Timaliidae	Lee et al. 2005; Cibois 2003
		<i>melanotis</i>		
28*	<i>Pyrrhula</i>	<i>pyrrhula</i>	Fringillidae	Monkkonen et al. 1996; Yuri & Mindell 2002
	<i>Carduelis</i>	<i>pinus</i>		
29*	<i>Phylloscopus</i>	<i>collybita</i>	Sylviidae	Monkkonen et al. 1996; Olsson et al. 2005
		<i>trochilus</i>		
30	<i>Turdus</i>	<i>migratorius</i>	Turdidae	Morrison et al. 1987
	<i>Ixoreus</i>	<i>naevius</i>		
31*	<i>Dryocopus</i>	<i>pileatus</i>	Picidae	Morrison et al. 1987; Benz et al. 2006
	<i>Picoides</i>	<i>albolavatus</i>		
32*	<i>Picoides</i>	<i>villosus</i>	Picidae	Morse 1970; Benz et al. 2006
		<i>pubescens</i>		
33*	<i>Lipaugus</i>	<i>vociferans</i>	Cotingidae	Pearson 1971
	<i>Tityra</i>	<i>semifasciata</i>		
34*	<i>Piaya</i>	<i>melanogaster</i>	Cuculidae	Pearson 1971; Hughes 2000
		<i>cayana</i>		
35*	<i>Wilsonia</i>	<i>pusilla</i>	Parulidae	Lovette & Bermingham 2002; Pomara et al. 2007
	<i>Mniotilta</i>	<i>varia</i>		
36*	<i>Meiglyptes</i>	<i>tukki</i>	Picidae	Styring & Ickes 2001; Benz et al. 2006
	<i>Picus</i>	<i>mentalis</i>		

Table A1 (continued)

Pair code	Genus	Species	Family	Source
37*	<i>Bucco</i>	<i>capensis</i>	Bucconidae	Thiollay & Jullien 1998
	<i>Monasa</i>	<i>atra</i>		
38*	<i>Cyanocompsa</i>	<i>cyanooides</i>	Cardinalidae	Thiollay & Jullien 1998
	<i>Caryothraustes</i>	<i>canadensis</i>		
39*	<i>Querula</i>	<i>purpurata</i>	Cotingidae	Thiollay & Jullien 1998
	<i>Pachyramphus</i>	<i>minor</i>		
40*	<i>Xiphorhynchus</i>	<i>obsoletus</i>	Dendrocolaptidae	Thiollay & Jullien 1998; Irestedt et al. 2004a
	<i>Xiphorhynchus</i>	<i>pardolatus</i>		
41*	<i>Dendrocolaptes</i>	<i>picumnus</i>	Dendrocolaptidae	Thiollay & Jullien 1998; Irestedt et al. 2004a
	<i>Campylorhamphus</i>	<i>procurvoides</i>		
42*	<i>Automolus</i>	<i>rubiginosus</i>	Furnariidae	Thiollay & Jullien 1998; Irestedt et al. 2006
		<i>infuscatus</i>		
43*	<i>Philydor</i>	<i>pyrrhodes</i>	Furnariidae	Thiollay & Jullien 1998; Irestedt et al. 2006
		<i>erythrocercum</i>		
44*	<i>Galbula</i>	<i>albirostris</i>	Galbulidae	Thiollay & Jullien 1998
		<i>dea</i>		
45*	<i>Piculus</i>	<i>chrysochloros</i>	Picidae	Thiollay & Jullien 1998; Benz et al. 2006
		<i>flavigula</i>		
46*	<i>Campephilus</i>	<i>rubricollis</i>	Picidae	Thiollay & Jullien 1998; Benz et al. 2006
	<i>Picumnus</i>	<i>exilis</i>		
47*	<i>Microbatas</i>	<i>collaris</i>	Poliopitilidae	Thiollay & Jullien 1998
	<i>Poliopitila</i>	sp.		
48	<i>Herpsilochmus</i>	<i>sticturus</i>	Thamnophilidae	Thiollay & Jullien 1998; Irestedt et al. 2004b
		<i>stictocephalus</i>		
49*	<i>Myrmotherula</i>	<i>guttata</i>	Thamnophilidae	Thiollay & Jullien 1998; Irestedt et al. 2004b
		sp.		
50*	<i>Thamnophilus</i>	<i>punctatus</i>	Thamnophilidae	Thiollay & Jullien 1998; Irestedt et al. 2004b
		<i>amazonicus</i>		
51*	<i>Schistocichla</i>	<i>leucostigma</i>	Thamnophilidae	Thiollay & Jullien 1998; Irestedt et al. 2004b
	<i>Terenura</i>	<i>spodiopitila</i>		
52*	<i>Tachyphonus</i>	<i>surinamus</i>	Thraupidae	Burns 1997; Thiollay & Jullien 1998
		<i>cristatus</i>		
53	<i>Lamprospiza</i>	<i>melanoleuca</i>	Thraupidae	Burns 1997; Thiollay & Jullien 1998
	<i>Hemithraupis</i>	sp.		
54	<i>Contopus</i>	<i>albogularis</i>	Tyrannidae	Thiollay & Jullien 1998; Ohlson et al. 2008
	<i>Myiobius</i>	<i>barbatus</i>		
55	<i>Hylophilus</i>	sp.	Vireonidae	Thiollay & Jullien 1998; Cicero & Johnson 2001
		<i>ochraceiceps</i>		
56	<i>Vireo</i>	<i>olivaceus</i>	Vireonidae	Thiollay & Jullien 1998; Cicero & Johnson 2001
	<i>Vireolanius</i>	<i>leucotis</i>		
57	<i>Hylexastes</i>	<i>perrotii</i>	Dendrocolaptidae	Thiollay & Jullien 1998; Irestedt et al. 2004a
	<i>Glyphorhynchus</i>	<i>spirurus</i>		
58*	<i>Sclerurus</i>	sp.	Furnariidae	Thiollay & Jullien 1998; Benz et al. 2006
	<i>Xenops</i>	<i>minutus</i>		
59	<i>Myrmotherula</i>	<i>brachyura</i>	Thamnophilidae	Thiollay & Jullien 1998; Irestedt et al. 2004b
		<i>gutturialis</i>		
60	<i>Myrmeciza</i>	<i>atrothorax</i>	Thamnophilidae	Thiollay & Jullien 1998; Irestedt et al. 2004b
	<i>Myrmotherula</i>	<i>axillaris</i>		
61*	<i>Hemitriccus</i>	<i>zosterops</i>	Tyrannidae	Thiollay & Jullien 1998; Ohlson et al. 2008
	<i>Myiornis</i>	<i>ecaudatus</i>		
62*	<i>Corythopsis</i>	<i>torquata</i>	Tyrannidae	Thiollay & Jullien 1998; Ohlson et al. 2008
	<i>Myiopagis</i>	<i>gaimardii</i>		
63	<i>Ramphotrigon</i>	<i>ruficauda</i>	Tyrannidae	Thiollay & Jullien 1998; Ohlson et al. 2008
	<i>Todirostrum</i>	<i>pictum</i>		
64*	<i>Pericocotus</i>	<i>cinnamomeus</i>	Campephagidae	P. Trivedi & V. C. Soni, unpublished data
		<i>flammeus</i>		
65*	<i>Corvus</i>	<i>macrorhynchos</i>	Corvidae	P. Trivedi & V. C. Soni, unpublished data
	<i>Dendrocitta</i>	<i>vagabunda</i>		
66	<i>Chrysocolaptes</i>	<i>festivus</i>	Picidae	P. Trivedi & V. C. Soni, unpublished data; Benz et al. 2006
	<i>Dinopium</i>	<i>benghalense</i>		

* Pairs used in the phylogenetically corrected analysis. For each pair, the first species listed represents the species with the lower flocking frequency.

Table A2

Pairs of closely related species that are both found in the same site in which one is known to lead flocks and the other is not

Pair code	Genus	Species	Family	Source
1*	<i>Gymnorhinus</i>	<i>cyanocephalus</i>	Corvidae	Balda et al. 1972
	<i>Cyanocitta</i>	<i>stelleri</i>		
2*	<i>Acanthiza</i>	<i>reguloides</i>	Acanthizidae	Bell 1980; Nicholls et al. 2000
		<i>pusilla</i>		
3*	<i>Pomatostomus</i>	<i>isidorei</i>	Pomatostomidae	Bell 1983
	<i>Melanocharis</i>	<i>nigra</i>	Melanocharidae	
4*	<i>Gerygone</i>	<i>chrysoaster</i>	Acanthizidae	Bell 1983; Nicholls et al. 2000
		<i>magnirostris</i>		
5*	<i>Alcippe</i>	<i>morrisonia</i>	Timaliidae	Chen & Hsieh 2002; Cibois 2003
		<i>brunnea</i>		
6*	<i>Dicrurus</i>	<i>aeneus</i>	Dicruridae	Croxall 1976
	<i>Rhipidura</i>	<i>perlata</i>	Rhipiduridae	
7	<i>Thamnomanes</i>	<i>caesius</i>	Thamnophilidae	Develey & Stouffer 2001; Brumfield et al. 2007
	<i>Myrmotherula</i>	<i>gutturialis</i>		
8*	<i>Myrmotherula</i>	<i>fulviventris</i>	Thamnophilidae	Gradwohl & Greenberg 1980; Brumfield et al. 2007
		<i>axillaris</i>		
9	<i>Parus</i>	<i>leucomelas</i>	Paridae	Greig-Smith 1978
	<i>Remiz</i>	<i>parvulus</i>	Remizidae	
10*	<i>Schetba</i>	<i>rufa</i>	Vangidae	Hino 2002
	<i>Cyanolanius</i>	<i>madagascarinus</i>		
11*	<i>Lanio</i>	<i>fulvus</i>	Thraupidae	Burns 1997; Jullien & Clobert 1998
	<i>Tachyphonus</i>	<i>cristatus</i>		
12*	<i>Turdoides</i>	<i>rufescens</i>	Timaliidae	Cibois 2003; Kotagama & Goodale 2004
	<i>Garrulax</i>	<i>cinereifrons</i>		
13	<i>Alcippe</i>	<i>peracensis</i>	Timaliidae	Lee et al. 2005; Cibois 2003; T. M. Lee personal communication
	<i>Cutia</i>	<i>nipalensis</i>		
14*	<i>Phylloscopus</i>	<i>occipitalis</i>	Phylloscopidae	Macdonald & Henderson 1977
		<i>trochiloides</i>		
15	<i>Trichothraupis</i>	<i>melanops</i>	Thraupidae	Maldonado-Coelho & Marini 2000
	<i>Tachyphonus</i>	<i>coronatus</i>		
16*	<i>Tangara</i>	<i>inornata</i>	Thraupidae	Moynihan 1962; Burns & Naoki 2004
		<i>larvata</i>		
17*	<i>Chlorospingus</i>	<i>ophthalmicus</i>	Thraupidae–Emberizidae	Moynihan 1962; Burns 1997
		<i>pileatus</i>		
18*	<i>Thamnomanes</i>	<i>schistogynus</i>	Thamnophilidae	Munn & Terborgh 1979; Brumfield et al. 2007
	<i>Cymbilaimus</i>	<i>lineatus</i>		
19	<i>Culicicapa</i>	<i>ceylonensis</i>	Stenostiridae	Partridge & Ashcroft 1976
	<i>Parus</i>	<i>major</i>	Paridae	
20	<i>Cypsnagra</i>	<i>hirundinacea</i>	Thraupidae	Ragusa-Netto 2000
	<i>Emberizoides</i>	<i>herbicola</i>		
21*	<i>Parus</i>	<i>niger</i>	Paridae	Jönsson & Fjeldså 2006; Thomson & Ferguson 2007
		<i>cinerascens</i>		
22	<i>Turdoides</i>	<i>striata</i>	Timaliidae	P. Trivedi & V. C. Soni unpublished data; Cibois 2003
	<i>Alcippe</i>	<i>poioicephala</i>		
23*	<i>Aphrastura</i>	<i>spinicauda</i>	Furnariidae	Vuilleumier 1967; Irestedt et al. 2006
	<i>Pygarrhichas</i>	<i>albogularis</i>		
24*	<i>Saxicola</i>	<i>torquatus</i>	Muscicapidae	Zamora et al. 1992
	<i>Oenanthe</i>	<i>leucura</i>		

* Pairs included in the phylogenetically corrected analysis. For each pair, the first species listed leads flocks more than the second species.

Table A3

List of species included in the meta-analysis of influence of social context (solitary/intraspecific group versus mixed-species flock) on foraging rates

Genus	Species	Family	Type of participant	Source
<i>Turdus</i>	<i>pilaris</i>	Turdidae	Follower	Barnard & Stephens 1983
<i>Turdus</i>	<i>iliacus</i>	Turdidae	Leader	
<i>Dicrurus</i>	<i>forficatus</i>	Dicruridae	Follower	
<i>Newtonia</i>	<i>brunneicauda</i>	Vangidae	Leader	
<i>Terpsiphone</i>	<i>mutata</i>	Monarchidae	Follower	
<i>Shetba</i>	<i>rufa</i>	Vangidae	Leader	Hino 1998
<i>Cyanolanius</i>	<i>madagascariensis</i>	Vangidae	Follower	
<i>Phyllastrephus</i>	<i>madagascariensis</i>	Bernieriidae	Follower	
<i>Coracina</i>	<i>cinerea</i>	Campephagidae	Follower	
<i>Todus</i>	<i>subulatus</i>	Todidae	Follower	Latta & Wunderle 1996b
<i>Todus</i>	<i>angustirostris</i>	Todidae	Follower	
<i>Contopus</i>	<i>caribaeus</i>	Tyrannidae	Leader	Latta & Wunderle 1996a
<i>Dendroica</i>	<i>caerulescens</i>	Parulidae	Follower	
<i>Junco</i>	<i>hyemalis</i>	Emberizidae	Follower	Millikan et al. 1985
<i>Junco</i>	<i>caniceps</i>	Emberizidae	Follower	
<i>Ramphocelus</i>	<i>passerini</i>	Thraupidae	Follower	Moriarty 1977

Table A3 (continued)

Genus	Species	Family	Type of participant	Source
<i>Basileuterus</i>	<i>culicivorus</i>	Parulidae	Leader	Pomara et al. 2003
<i>Mniotilta</i>	<i>varia</i>	Parulidae	Follower	
<i>Myioborus</i>	<i>miniatus</i>	Parulidae	Follower	
<i>Wilsonia</i>	<i>pusilla</i>	Parulidae	Follower	
<i>Parus</i>	<i>major</i>	Paridae	Follower	Sasvari 1992
<i>Dicrurus</i>	<i>paradiseus</i>	Dicruridae	Follower	Satischandra et al. 2007
<i>Picoides</i>	<i>pubescens</i>	Picidae	Follower	Sullivan 1984
<i>Dicrurus</i>	<i>adsimilis</i>	Dicruridae	Follower	Veena & Lokesha 1993
<i>Protonotaria</i>	<i>citrea</i>	Parulidae	Follower	Warkentin & Morton 2000
<i>Saxicola</i>	<i>torquata</i>	Muscicapidae	Leader	Zamora et al. 1992

Table A4

List of species included in the meta-analysis of influence of social context (solitary/intraspecific group versus mixed-species flock) on foraging rates

Genus	Species	Family	Source
<i>Neothraupis</i>	<i>fasciata</i>	Thraupidae	Alves & Cavalcanti 1996
<i>Picoides</i>	<i>pubescens</i>	Picidae	Dolby & Grubb 1998
<i>Sitta</i>	<i>carolinensis</i>	Sittidae	
<i>Loxops</i>	<i>coccineus</i>	Fringillidae	Hart & Freed 2005
<i>Carduelis</i>	<i>tristis</i>	Fringillidae	Popp 1988
<i>Carduelis</i>	<i>pinus</i>	Fringillidae	
<i>Carpodacus</i>	<i>purpureus</i>	Fringillidae	
<i>Poecile</i>	<i>carolinensis</i>	Paridae	Pravosudov & Grubb 1999
<i>Baeolophus</i>	<i>bicolor</i>	Paridae	
<i>Picoides</i>	<i>pubescens</i>	Picidae	Sullivan 1984
<i>Protonotaria</i>	<i>citrea</i>	Parulidae	Warkentin & Morton 2000