ORNITOLOGÍA NEOTROPICAL
(2018) 29: 289–296
ORIGINAL ARTICLE

# ON THE ADAPTIVE CHARACTERISTICS OF BIRD FLOCKS: SMALL BIRDS FORM MIXED FLOCKS

**Cristina Sainz-Borgo[1] · Sheina Koffler[2] · Klaus Jaffé[1]**

[1] Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado Postal 89.000, Caracas, Venezuela.
[2] Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Brazil.
E-mail: Cristina Sainz-Borgo · cristinasainzb@usb.ve

**Abstract** · Mixed bird flocks are very diverse in size, number of species, habitats, and interactions between members, however there are few reports about which morphological characteristics of species lead to flocking behavior. We conducted a literature search in order to test the effect of body weight on flocking behavior, and performed an ordinal regression with flocking category as the dependent variable. Data from 1289 species belonging to 116 families from 17 orders were evaluated. A strong correlation was found between species' total length and body mass with the types of flocks that they form: species forming mixed flocks tended to be smaller than species that foraged solitarily, in pairs or in monospecific flocks. The best predictors for flocking behavior were mass and habitat, we found no significant effect of region or migratory behavior. This result is congruent with an adaptive role of flocks balancing inter-specific competition and anti-predator protection. These findings add to reports on similarities in foraging behavior and in alarm calls among birds in a flock, suggesting co-evolutionary dynamics acting on species of mixed flocks.

**Resumen · El valor adaptativo de las bandadas mixtas: aves pequeñas se agrupan en bandadas mixtas**
Las bandadas mixtas son muy diversas en tamaño, número de especies, hábitats e interacciones entre los miembros, sin embargo, existen pocos reportes de correlaciones morfológicas entre los mismos. Se realizó una búsqueda en la literatura para determinar el efecto de la masa corporal en el comportamiento de formación de bandadas, realizándose con dichos datos una regresión ordinal con la categoría bandada como variable dependiente. Se recolectó información de 1289 especies, pertenecientes a 116 familias y 17 órdenes. Se encontró una fuerte correlación entre la masa corporal de las especies dependiendo del tipo de bandada que conformaban; las especies que realizaban bandadas mixtas tendían a pesar menos que las especies que forrajeaban solas, en pareja o en bandadas monoespecíficas. El mejor predictor para el comportamiento de bandada fue la masa y el hábitat, mientras que no se encontró efecto de la región, hábitos migratorios o acuáticos. Este resultado es congruente con el rol adaptativo de las bandadas, donde se encuentran involucrados la competencia interespecífica y las ventajas antidepredadoras. Estos resultados junto con registros similares en hábitos de forrajeo y llamadas de alarma entre los miembros de una bandada, sugieren una dinámica coevolutiva que actúa sobre las especies que conforman bandadas mixtas.

**Key words**: Antipredator strategies · Body mass · Mixed flocks · Monospecific flocks

## INTRODUCTION

Bird foraging groups can be divided into flocks and aggregations. Aggregation members remain together due to incidental factors such as food, or other key resource; while flocks are groups whose cohesion depends on the social interactions of its members (Powell 1974). Hutto (1994) define flock as a group of two or more individuals, of the same or different species found in a range of 20–30 m that move together.

Individuals participating in flocks balance costs and benefits. Benefits are mainly two: a reduction of the probability of suffering predation and a higher foraging efficiency. The first may be achieved due to a dilution effect (Krebs 1977, Dehn 1990, Bednekoff & Lima 1998), confusion effect (Hamilton 1971, Jeskche & Tollrian 2007, Ioannou et al. 2008), a higher probability of detection of the predator due to higher surveillance rates (Lack 1954, 1968, 1970, Caraco 1980, Glück 1987, Goss-Custard & Durell 1988, Popp 1988), and the coordinated response of individuals that reduce the vulnerability to predators (Morse 1970). The second benefit, higher foraging efficiency (Powell 1985, Beauchamp 2006, Morand-Ferron & Quinn 2011), may be due to cross communication of newly discovered food sources or lower rate of vigilance per individual. However, flocking in birds also generates disadvantages: increased competition and aggression that decrease feeding efficiency, and greater attraction of predators (Hutto 1988, Terborgh 1990).

Flocks may be monospecific or mixed, mixed flocks being composed by individuals of different species. Mixed-species flocks are a common phenomenon in many habitats (Jullien & Clobert 2000, Sridhar et al. 2009), and vary in size, permanence of the individuals, and composition and interactions between species (Munn 1985, Greenberg 2000). The high frequency of mixed flock in birds is considered an optimal trade-off between predator protection and feeding efficiency (Terborgh 1990).

Receipt 8 March 2018 · First decision 22 May 2018 · Acceptance 30 October 2018 · Online publication 5 November 2018
Communicated by Kaspar Delhey 

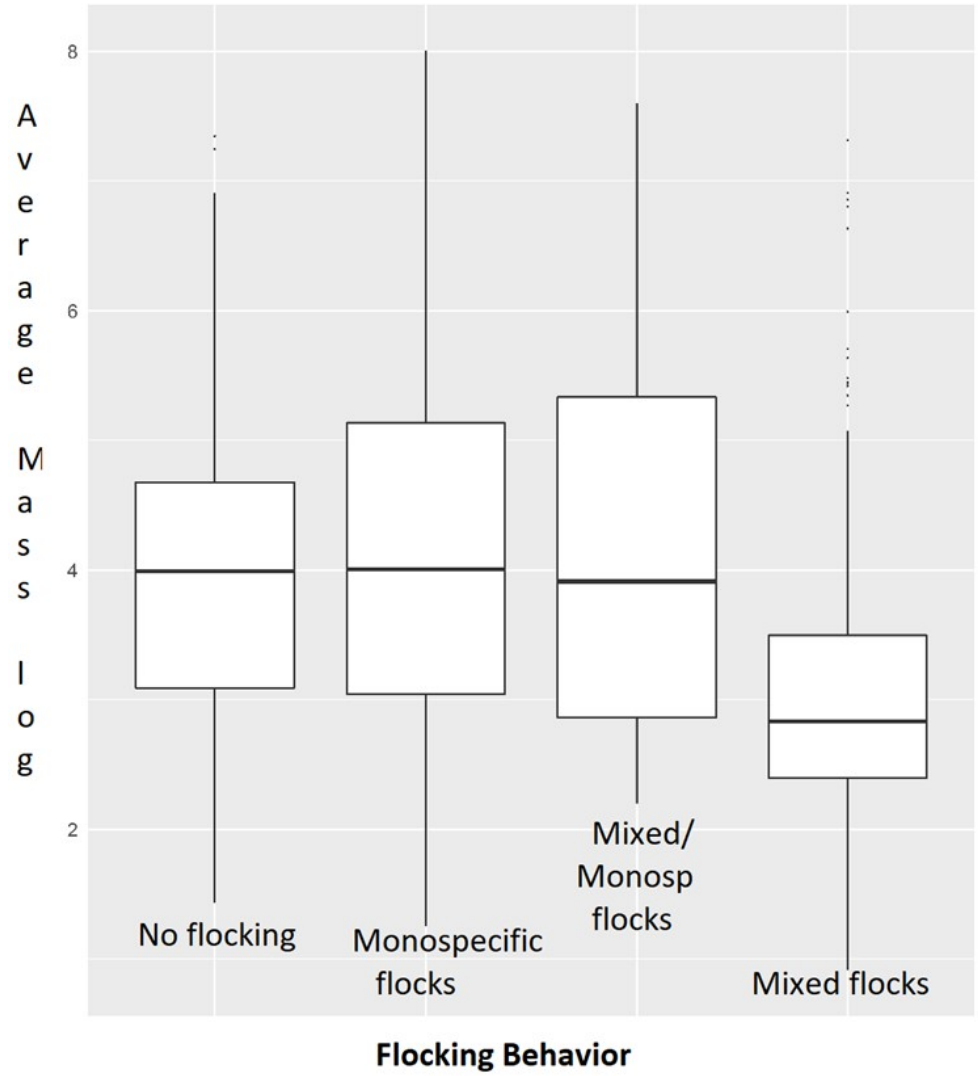


**Figure 1.** Boxplots depicting variation in average body mass (g, ln transformed) of bird species across the different flocking categories.

In our study, we became interest in exploring the possible relationship between flocking behavior and bird size because there is evidence that individuals of small-sized species are preferred by predators (Fitzgibbon, 1990, Cooper & Stankowich 2010). Are there advantages of joining a mixed flock over a monospecific flock? Is it an opportunistic strategy? In birds, small species are often at a greater risk of predation (Buskirk 1976, Thiollay & Jullien 1998); therefore, they might obtain greater benefits of joining a flock than individuals of larger species. Under the assumption that mixed flocks provide better protection from predators, we would predict that individuals of the species that form mixed flocks have a smaller size than those species that form monospecific flocks or that forage alone. The aim of this study was to review the literature to determine quantitatively the possible relationship between body mass and the likelihood of birds to participate in mixed or single species flocks.

## MATERIALS AND METHODS

We conducted a literature search using the Web search engine Google Scholar, and field guides (Hilty 2003, Phelps & Meyer de Schaueense 1994). This was done to obtain information on bird species regarding three kinds of social behavior: 1) foraging in monospecific flocks, 2) foraging in mixed flocks, and 3) foraging solitary or in pairs. For each species we also retrieved information on: average body mass (g), main region of distribution (Africa, Asia, Australia, Neartic, Neotropical, Paleartic), habitat (forest, grassland, sea, or wetland), migratory habits (migratory or resident), and if it is an aquatic or terrestrial species.

In order to test the effect of average body mass on flocking behavior, we performed an ordinal regression with flocking category as the dependent variable. Four categories were employed to discriminate behaviors (in increasing complexity order): (a) no flocking or pairs, (b) monospecific flocks, (c) mixed or monospecific flocks (facultative behavior), and (d) mixed flocks. Species exhibiting both solitary and flocking behavior were included in the flocking category. A full model was constructed including body mass, region, habitat, migratory habits, and aquatic habits as independent variables, allowing to test the effect of body mass while controlling for the other effects. We log-transformed average body mass to account for the positive skew of this trait, and family nested in taxonomic order were included as random factors, to account for phylogenetic effects. The full model was compared to reduced models excluding each of the predictors, using likelihood ratio tests ($\alpha = 0.05$). This procedure was performed until a best model was found, where the exclusion if any predictor significantly decreased the model's log-likelihood (Zuur et al. 2009). Significance of the phylogenetic effects was tested contrasting the full model with random

**Table 1.** Average body mass by occurrence/flock type in relation to the geographical area occupied by birds and their migratory or aquatic habits. Number of species in parenthesis), W = average mass (g). Body masses and values of social behavior were obtained from: Vuilleumier (1967), Greig-Smith (1978), Leck (1972), Morton (1979), Gochfeld & Burger (1981), Székely (1984), Sullivan (1984), Pearson 1989, Székely et al. (1989), With et al. (1990), Mahon et al. (1992), Hutto (1994), Gochfeld & Burger (1981), Metcalfe (1984), Hino (2000), Ragusa-Netto (2000), Ramos (2000), Kubota & Nakamura (2000), Nakamura & Shindo (2001), Hilty (2003), Bohórquez (2003), Remsen (2003 a,b), Remsen & Kirwan (2003) Marantz et al. (2003), Fitzpatrick et al. (2004), Mobley (2004), Snow (2004), Farnsworth & Lebbin (2004a,b), Kroodsma & Brewer (2005), Collar (2005), Hunt et al. (2005), Monticelli et al. (2006), Moeliker (2006), Gosler & Clement (2007), Canales-Delgadillo et al. (2008), Craig & Feare (2009), Arbelaez-Cortez et al. (2011), Hilty (2011 a,b,c), Brewer (2010), Brewer (2010), Rising (2011), Gochfeld et al. 2013, Jolles et al. (2013), Pizo (2013), Christie & de Juana (2014), Collar & Christie (2014), Donald & de Juana (2014), Farnsworth et al. (2014), Fitzpatrick et al. (2014), Remsen & Bonan (2014), Remsen & Kirwan (2014), Rising & Christie (2014), Hilty & de Juana (2015), Rao et al. (2015), Remsen & Kirwan (2015), Payne & Kirwan (2015), Winker et al. (2015).

| Bioregion | Solitary | Monospecific | Mixed | $W_{Mixed}/W_{Mono}$ |
|---|---|---|---|---|
| Neotropic | 61 (193) | 249 (168) | 29 (404) | 0.12 |
| Africa | 86 (17) | 45 (8) | 30 (41) | 0.67 |
| Asia | 78 (40) | 35 (26) | 23 (65) | 0.66 |
| Nearctic | 90 (17) | 235 (38) | 51 (82) | 0.22 |
| Palearctic | 62 (38) | 38 (33) | 101 (52) | 2.66 |
| Australia | 164 (37) | 88 (7) | 21 (37) | 0.24 |
| Aquatic | 385 (9) | 397 (35) | 593 (7) | 1.49 |
| Migratory | 410 (12) | 219 (22) | 17 (35) | 0.08 |

effects to a model without random effects, using likelihood ratio tests. All analyses were performed in R, using the R package ordinal (Christensen 2015).

## RESULTS

Of the 1154 species assessed, we recorded 616 that form mixed flocks, 55 facultative behavior, 267 monospecific flocks, and 351 that forage solitarily or in pairs (Table 1S, Supplementary Material online). The data belong to 116 families from the orders: Anseriformes, Galliformes, Suliformes, Pelecaniformes, Accipitriformes, Charadriiformes, Columbiformes, Cuculiformes, Apodiformes, Coliiformes, Trogoniformes, Bucerotiformes, Coraciiformes, Galbuliformes, Piciformes, Psittaciformes, and Passeriformes. The families with more species were Tyrannidae with 110 (77 species forming mixed flocks), Furnariidae with 86 species (54 forming mixed flocks), Parulidae with 55 (all forming mixed flocks), and Thraupidae with 40 species (36 forming mixed flock).

More than half of all Neotropical species examined participate in mixed-species flocks (55%, 403 species). A smaller number formed monospecific groups (23%, 168 species) or forage solitarily (26%, 193 species). For Palearctic birds, 42% (52 species) conform mixed flocks, 27% (33) conform monospecific flocks, and 31% are solitary birds (28). For the Nearctic region, 70% (82 species) conform mixed flock, 32% (38) monospecific flocks, and 14% (17) forage solitarily. For Asia, Africa, and Australia, we analyzed 305 species, of which 50% (151 species) conform mixed flocks and 19% (58) monospecific flocks while 31% (95) are solitary.

**Table 2.** Full model with all tested predictors describing flocking behavior and best selected model across 1289 bird species. Likelihood-ratio tests (LRT) were employed to compare a full model with reduced models and p-values were obtained using a $\chi^2$ distribution.

| Model | Predictor | Degrees of freedom | LRT ($\chi^2$) | *p* |
|---|---|---|---|---|
| Full model | Average mass | 1 | 40.47 | < 0.001 |
| | Region | 6 | 6.87 | 0.33 |
| | Habitat | 3 | 33.14 | < 0.001 |
| | Aquatic habit | 1 | 1.64 | 0.20 |
| | Migratory habit | 1 | 0.62 | 0.43 |
| Best model | Average mass | 1 | 37.65 | < 0.001 |
| | Habitat | 3 | 31.77 | < 0.001 |

Birds that form mixed flocks were significantly smaller than birds that forage in monospecific flocks (Figure 1, Table 1). In addition, the ratio between the average mass of species that form mixed and monospecific flocks by families shows, except for Palearctic and Aquatic species in which mixed flock are formed by individuals of smaller size (Table 1).

The best predictors for flocking behavior were average mass and habitat (Table 2), thus we found no significant effect of region, migratory, or aquatic habits. Smaller species participated mostly in mixed flocks (Table 3). Regarding species habitat, forest and sea species tend to participate more often in mixed flocks, while grassland and wetland species tend to exhibit mostly monospecific flocks or solitary behavior (Table 3). Phylogenetic effects were significant ($p < 0.001$), since removing the random effects decreased the model's log-likelihood. Taxonomic family nested in order exhibited a variance of 3.37, while taxonomic order exhibited a variance of 1.32.

## DISCUSSION

We found that species forming mixed flocks were smaller than those forming monospecific flocks or that forage alone, suggesting the existence of benefits for individuals of smaller size species to engage in mixed flocks.

Although our analyses were not designed to explore the possible cause of this relationship, we explore some possible explanations. The literature on bird aggregations is very abundant, but is focussed mainly on the description and analyses of insectivorous mixed-species flocks, formed mostly by Passeriformes (Powell 1984, Terborgh 1990, Jullien & Clobert 2000, Coelho & Marini 2004); without focusing on the physical variables of the species involved. Some previous studies hinted on the similarity in size of the members of flocks, like species of tanagers in Neotropical mixed flocks that are small and similar in size (Hutto 1994). The same phenomenon has been observed in mixed flocks of Sanderlings (*Calidris alba*) (Silliman et al. 1977, Stawarczyk 1984) and gulls (Barnard et al. 1982, Chilton & Sealy 1987). However, there are exceptions to the trend of similar sized species forming mixed flocks: some reports show birds of different sizes flocking together. For example, in Neotropical mixed flocks the presence of larger birds, such as trogons or Squir-

**Table 3.** Parameter estimates for the best model describing flocking behavior. P-values were calculated using Wald's tests. Estimates for each habitat type are given with forest habitat as comparison base.

| Predictor | | Estimate | SE | *p* |
|---|---|---|---|---|
| Average mass (g) | | -0.56 | 0.09 | < 0.001 |
| Habitat | Grassland | -1.15 | 0.25 | < 0.001 |
| | Sea | 2.88 | 1.65 | 0.08 |
| | Wetland | -2.01 | 0.62 | 0.001 |

rel Cuckoos (*Piaya cayana*), can provide benefits by sharing information increasing the detectability of food (Develey & Peres 2000).

Predation risk has been an important factor that affects the size of individuals, but the relationship is unclear and experimental evidence is contradictory. Some research indicates that heavier individuals have higher predation risk due to reduced flight performance and maneuverability (i.e., Starlings *Sturnus vulgaris*, Witter et al. 1994; Zebra Finches *Taeniopygia guttata*,Metcalfe & Ure 1995; Blackcaps *Sylvia atricapilla*, Kullberg et al. 1996, and Brown-headed Cowbirds *Molothrus ater*, Walters et al. 2017). In contrast with this, Sridhar et al. (2009) and Thiollay & Jullien (1998), among others, argue that a small size increases vulnerability to predation in insectivorous mixed flock. Both observations indicate that size is related to predation risks, which supports our findings that lower mass is associated with mixed-flock species.

Our results also indicate that an additional predictor of mixed-flock membership is habitat, suggesting a trend for seabirds and forest species to form mixed flocks at a higher rate. The evidence of the influence of habitat on the formation of flocks is abundant. For example, in gulls and lapwings it has been suggested that flock size increased foraging efficiency in mixed flocks (Barnard et al. 1982), as it occurs in many terrestrial species. In addition, the "information centers" in seabirds suggest that the main advantage of flock formation is that individuals can follow others to rich food source (Götmark et al. 1986). Ducks inhabit marshes that are unstable and have ephemeral resources. Here, individuals that feed in flocks have higher rates of food intake than solitary birds (Hepp 1989, Fox et al. 1994). Thiollay (1999) found in terrestrial birds that when the habitat is more open, the tendency to form mixed flocks will increase. The same applies to aquatic species, where open habitat allow a predator to locate potential prey. Marbled Murrelets (*Brachyramphus marmoratus*) are almost always found in pairs or monospecific flocks when foraging in exposed waters, while in protected waters, they are frequently conforming mixed flocks (Hunt et al. 1985). Studies in tropical forests show that in areas more vulnerable to predators the propensity to group in flocks is higher (Thiollay & Julliem 1998), while in areas with low predation, like islands, it is lower (Beauchamp 2004). However, our results also indicate that in grasslands and wetlands, generally open areas, species tend to behave solitarily and form monospecific flocks. Belonging to certain foraging guilds may also affect this pattern, since grasslands are often used by granivorous birds (Whittingham & Evans 2004) while in forests, mixed flocks are predominantly formed by insectivorous species.

No effect was found between the region of occurrence and flocking behavior. Even though several studies on birds show that temperate climates favor larger body size as a way to optimize body heat (Meiri & Dayan 2003), here we show that flocking behavior is affected by species mass, regardless of region. Concerning migratory species, we observed no differences between migratory status and the trend to form mixed flocks. This might be related to the heterogeneity of guilds and families evaluated, which included disparate species, such as osprey, herons, plovers, flycatchers, and parulid warblers.

Our results indicate that in the complex adaptive landscape of bird-flocking, the species that conform mixed flocks tend to be smaller than species foraging solitarily or forming monospecific flocks. The most likely adaptive force explaining this result is that small birds are more vulnerable to predation. This adaptive force seems to have the strongest impact among a complex diversity of interactions between the species that conform flocks.

## ACKNOWLEDGMENTS

We thank the editor and two anonymous referees for their suggestions, Carlos Bosque, Miguel Lentino, Luis Gonzalo Morales, and Adriana Rodríguez-Ferraro for their very helpful comments on the manuscript, and Luis Miguel Montilla for his help in the statistical analyses.

## REFERENCES

Arbeláez-Cortés, E, HA Rodríguez-Correa & M Restrepo-Chica (2011) Mixed bird flocks: patterns of activity and species composition in a region of the Central Andes of Colombia. *Revista Mexicana de Biodiversidad* 82: 639–651.

Austin, GT & EL Smith (1972) Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. *The Condor* 74: 17–24.

Barnard, CJ, DBA Thompson & H Stephens (1982) Time budgets, feeding efficiency and flock dynamics in mixed species flocks of lapwings, golden plovers and gulls. *Behavior* 80: 44–69.

Beauchamp, G (2002) Higher-level evolution of intraspecific flock-feeding in birds. *Behavioral Ecology and Sociobiology* 51: 480–487.

Beauchamp, G (2004) Reduced flocking by birds on islands with relaxed predation. *Proceedings of Royal Society of London B* 271: 1039–1042.

Beauchamp, G & E Goodale (2011) Plumage mimicry in avian mixed species flocks: more or less than meets the eye? *The Auk* 128: 487–496.

Beauchamp, G (2013) Is the magnitude of the group-size effect on vigilance underestimated? *Animal Behaviour* 85: 281–285.

Benkman, CW (1988) Flock size, food dispersion, and the feeding behavior of crossbills. *Behavioral Ecology and Sociobiology* 23: 167–175.

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

Blackburn, TM, KJ Gaston & N Loder (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* 5: 165–174.

Bohórquez, CI (2003) Mixed-species bird flocks in a montane cloud forest of Colombia. *Ornitologia Neotropical* 14: 67–78.

Brewer, D (2010) Red-eyed Vireo (*Vireo olivaceus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61266 [Accessed 13 March 2015].

Brewer, D (2010) Black-billed Peppershrike (*Cyclarhis nigrirostris*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61235 [Accessed 14 March 2015].

Brumfield, RT, JG Tello, ZA Cheviron, MD Carling, N Crochet & KV Rosenberg (2007) Phylogenetic conservatism and antiquity of a tropical specialization: army-ant-following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics and Evolution* 45: 1–13.

Buskirk, WH (1976) Social systems in a tropical forest avifauna. *American Naturalist* 110: 293–310.

Canales-Delgadillo, JC, LM Scott-Morales, M Cotera Correa & M Pando Moreno (2008) Observations on flocking behavior of Worthen's Sparrows (*Spizella wortheni*) and occurrence in mixed-species flocks. *Wilson Journal of Ornithology* 120: 569–574.

Caraco, T (1980) Stochastic dynamics of avian foraging flocks. *American Naturalist* 115: 262–275.

Chilton, G, & SG Sealy (1987) Species roles in mixed-species feeding flocks of seabirds. *Journal of Field Ornithology* 58: 456–463.

Christensen, RHB (2015) Ordinal-regression models for ordinal data. R package version 2015.6-28. Available at http://www.cran.r-project.org/package=ordinal.

Collar, N (2005) Great Thrush (*Turdus fuscater*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/58311 [Accessed 14 March 2015].

Collar, N & DA Christie (2014) Western Bluebird (*Sialia mexicana*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx EdicionsEdicions, Barcelona, Spain. Available at http://www.hbw.com/node/58230 [Accessed 11 March 2015].

Colorado, GJ & AD Rodewald. (2015) Assembly patterns of mixed-species avian flocks in the Andes. *Journal of Animal Ecology* 84: 386–395.

Cooper Jr, WE & T Stankowich (2010) Prey or predator? Body size of an approaching animal affects decisions to attack or escape. *Behavioral Ecology* 21: 1278–1284.

Craig, A & C Feare (2009) Common Starling (*Sturnus vulgaris*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx EdicionsEdicions, Barcelona, Spain. Available at http://www.hbw.com/node/60851 [Accessed 11 March 2015].

Develey, PF & CA Peres (2000) Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. *Journal of Tropical Ecology* 16: 33–53.

Donald, P & E de Juana (2014) Horned Lark (*Eremophila alpestris*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/57664 [Accessed 11 March 2015].

dos Anjos, L & A Bonan (2016) Crows (*Corvidae*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/52369 [Accessed 11 December 2016].

Eguchi, K, S Yamagishi & V Randrianasolo (1993) The composition and foraging behavior of mixed-species flocks of forest-living birds in Madagascar. *Ibis* 135: 91–96.

Elgar, MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* 64: 13–33.

Ellington, CP (1991) Limitations on animal flight performance. *Journal of Experimental Biology* 160: 71–91.

Farnsworth, A & D Lebbin (2004a) Smoke-coloured Pewee (*Contopus fumigatus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx EdicionsEdicions, Barcelona, Spain. Available at http://www.hbw.com/node/57367. [Accessed 14 March 2015].

Farnsworth, A & D Lebbin (2004b) Cinnamon Flycatcher (*Pyrrhomyias cinnamomeus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/57340. [Accessed 14 March 2015].

Farnsworth, A, G Langham & E de Juana (2014) Fire-eyed Diucon (*Xolmis pyrope*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx EdicionsEdicions, Barcelona, Spain. Available at http://www.hbw.com/node/57424 [Accessed 11 March 2015].

Fitzpatrick, J (2004) Rufous-breasted Flycatcher (*Leptopogon rufipectus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/57238 [Accessed 13 March 2015].

Fitzgibbon, CD (1990) Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour* 39: 1116–1126.

Fox, AD, AJ Green, B Hughes & G Hilton (1994) Rafting as an antipredator response of wintering White-headed duck *Oxyura leucocephala. Wildfowl* 45: 232–241.

Gillooly, JF, JH Brown, GB West, VM Savage & EL Charnov (2001) Effects of size and temperature on metabolic rate. *Science* 293: 2248–2251.

Glück, E (1987) Benefits and costs of social foraging and optimal flock size in goldfinches (*Carduelis carduelis*). *Ethology* 74: 65–79.

Götmark, F, DW Winkler & M Andersson (1986) Flock-feeding on fish schools increases individual success in gulls. *Nature* 319: 589–591.

Goodale, E & G Beauchamp (2010) The relationship between leadership and gregariousness in mixed-species bird flocks. *Journal of Avian Biology* 41: 99–103.

Gochfeld, M & J Burger (1981) Age-related differences in piracy of frigatebirds from Laughing Gulls. *The Condor* 83: 79–82.

Gochfeld, M & J Burger (1996) Roseate Tern (*Sterna dougallii*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/54021 [Accessed 10 March 2015].

Gochfeld, M, J Burger & DA Christie (2013). Common White Tern (*Gigys alba*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/54054 [Accessed 11 March 2015].

Gosler, A & P Clement (2007) Oak Titmouse (*Baeolophus inornatus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/59881 [Accessed 15 March 2015].

Goss-Custard, JD & SL Durell (1988) The effect of dominance and feeding method on the intake rates of oystercatchers, *Haematopus ostralegus*, feeding on mussels. *Journal of Animal Ecology* 57: 827–844.

Greig-Smith, PW (1978) The formation, structure and function of mixed-species insectivorous bird flocks in West African savanna woodland. *Ibis* 120: 284–297.

Harrison NM & MJ Whitehouse (2011) Mixed-species flocks: an example of niche construction? *Animal Behavior* 81: 675–682.

Hepp, GR (1989) Benefits, costs, and determinants of dominance in American black ducks. *Behaviour* 109: 222–234.

Hilty, S (1994) *Birds of Tropical America.* A watcher's introduction to behavior, breeding, and diversity. Texas Univ. Press, Austin, Texas, USA.

Hilty, S (2003) *Birds of Venezuela*. Princeton Univ.Univ. Press, Princeton, New Jersey, USA.

Hilty, S (2011a) Multicolored Tanager (*Chlorochrysa nitidissima*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Hand-*

*book of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61673 [Accessed 13 March 2015].

Hilty, S (2011b) Rufous-crested Tanager (*Creurgops verticalis*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61582 [Accessed 14 March 2015].

Hilty, S (2011c) Saffron-crowned Tanager (*Tangara xanthocephala*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61689 [Accessed 13 March 2015].

Hilty, S & E de Juana (2015) Fawn-breasted Tanager (*Pipraeidea melanonota*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61670 [Accessed 14 March 2015].

Hino, T (2000) Intraspecific differences in benefits from feeding in mixed-species flocks. *Journal of Avian Biology* 31: 441–446.

Hunt, J (1995) Monospecific and mixed species foraging associations of Marbled Murrelets. Ralph, C, G Hunt, M Raphael & J Piatt (eds). *Ecology and conservation of the Marbled Murrelet.* General Technical Report PSW-GTR-152: 255–256. Pacific Southwest Research Station, Point Reyes, California, USA.

Hutto, RL (1987) A description of mixed-species insectivorous bird flocks in western Mexico. *The Condor* 89: 282–292.

Hutto, RL (1988) Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks. *Oikos* 51: 79–83.

Hutto, RL (1994) The composition and social organization of mixed-species flocks in a tropical deciduous forest in Western Mexico. *The Condor* 96: 105–118.

Ioannou, CC, CR Tosh, L Neville & J Krause (2008) The confusion effect-from neural networks to reduced predation risk. *Behavioral Ecology* 19: 126–130.

Jaffe, K, A Rios & A Florez (2013) Statistics shows that economic prosperity needs both high scientific productivity and complex technological knowledge, but in different ways. *Interciencia* 38: 150–156.

Jolles, JW, AJ King, A Manica & A Thornton (2013) Heterogeneous structure in mixed-species corvid flocks in flight. *Animal Behavior* 85: 743 –750.

Jullien, M & J Clobert (2000) The survival value of flocking in Neotropical birds: Reality or fiction? *Ecology* 81*:* 3416–3430.

Karr, JR (1971) Structure of avian communities in selected Panama and Illinois habitats. *Ecological Monographs* 41: 207–233.

Kersten, M, Britton, R, & P Dugan (1991) Flock feeding and food intake in little egrets: the effects of prey distribution and behaviour. *Journal of Animal Ecology* 60(1): 241**–**252.

Krause, J & GD Ruxton (2002) *Living in groups.* Oxford Univ. Press, New York, USA.

Krebs, JR (1977) Colonial nesting and social feeding strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). *Behaviour* 51: 99–134.

Krebs, JR & NB Davies (1993) *An introduction to behavioral ecology.* 3r ed. Blackwell Scientific Publications, Oxford, UK.

Kronauer, DJ (2009) Recent advances in army ant biology (Hymenoptera: Formicidae). *Myrmecological News* 12: 51–65.

Kroodsma, D & D Brewer (2005) Mountain Wren (*Troglodytes solstitialis*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/58158 [Accessed 14 March 2015].

Kubota, H, & M Nakamura (2000) Effects of supplemental food on intra- and inter-specific behaviour of the Varied Tit *Parus varius*. *Ibis* 142: 312–319.

Kullberg, C, T Fransson & S Jakobsson (1996) Impaired predator evasion in fat Blackcaps (*Sylvia atricapilla*). *Proceedings of the Royal Society of London B*, *263*(1377): 1671–1675.

Lack, D (1954) *The natural regulation of animal numbers*. The Clarendon Press, Oxford, UK.

Langley, W (2001) Competition between American crows and red-tailed hawks for a carcass: flock advantage. *Transactions of the Kansas Academy of Science* 104: 28–30.

Leck, CF (1972) The impact of some North American migrants at fruiting trees in Panama. *The Auk* 89: 842–850.

Lloyd, P, F Abadi, R Altwegg & TE Martin (2014) South temperate birds have higher apparent adult survival than tropical birds in Africa. *Journal of Avian Biology* 45: 493–500.

Marantz, CA, A Aleixo, LR Bevier & MA Patten (2003) Brown-billed Scythebill (*Campylorhamphus pusillus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56645 [Accessed 14 March 2015].

MacArthur, RH (1958) Population ecology of some warblers of north-eastern coniferous forests. *Ecology* 39: 599–619.

Martin, TE (2004) Avian life-history evolution has an eminent past: does it have a bright future? *The Auk* 121: 289–301.

Martin, TE, JC Oteyza, AE Mitchell, AL Potticary & P Lloyd (2015) Postnatal growth rates covary weakly with embryonic development rates and do not explain adult mortality probability among songbirds on four continents. *American Naturalist* 185: 380–389.

Meiri, S & T Dayan (2003) On the validity of Bergmann's rule. *Journal of Biogeography* 30: 331–351.

McNab, BK (1971) On the ecological significance of Bergmann's rule. *Ecology* 52: 845–854.

Metcalfe, NB (1984) The effects of mixed-species flocking on the vigilance of shorebirds: who do they trust? *Animal Behaviour* 32: 986–993.

Metcalfe, NB & SE Ure (1995) Diurnal variation in flight performance and hence potential predation risk in small birds. *Proceedings of Royal Society of London B* 261: 395–400.

Mobley, J (2004) Barred Becard (*Pachyramphus versicolor*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/57536 [Accessed 16 March 2015].

Moeliker, K (2006) Madagascar Paradise-flycatcher (*Terpsiphone mutata*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/59200 [Accessed 16 March 2015].

Monticelli, D, JA Ramos & J Pereira (2006) Habitat use and foraging success of roseate and common terns feeding in flocks in the Azores. *Ardeola* 53: 293–306.

Morand-Ferron, J & JL Quinn (2011) Larger groups of passerines are more efficient problem solvers in the wild. *Proceedings of the National Academy of Sciences of the USA.* 108: 15898–15903.

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

Morton, ES (1979) Effective pollination of *Erythrina fusca* by the Orchard Oriole (*Icterus spurius*): coevolved behavioral manipulation? *Annals of the Missouri Botanical Garden* 66: 482–489

Moynihan, M (1962) The organization and probable evolution of some mixed species flocks of Neotropical birds. *Smithsonian Miscellaneous Collections* 143: 1–14.

Myers, N, RA Mittermeier, CG Mittermeier, GA Da Fonseca & J Kent (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Nakamura, M & N Shindo (2001) Effects of snow cover on the social and foraging behavior of the great tit *Parus major*. *Ecological Research* 16: 301–308.

O'Donnell, S, CJ Logan & NS Clayton (2012) Specializations of birds that attend army ant raids: an ecological approach to cognitive and behavioral studies. *Behavioural Processes* 91: 267–274.

Pausas, JG & M Verdu (2010) The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience* 60: 614–625.

Payne, R & GM Kirwan (2015) Common Squirrel-cuckoo (*Piaya cayana*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/57536 [Accessed 14 March 2015].

Pearson, SM (1989) Food patches and foraging group size in granivorous birds. *Animal Behaviour* 38: 665–674.

Phelps, WH (Jr) & R Meyer de Schauensee (1994) *Una guía de las aves de Venezuela*. Editorial Ex Libris, Caracas, Venezuela.

Pizo, MA (2013) Feeding ecology of two *Cacicus* species (Emberezidae, Icterinae). *Revista Brasileira de Ornitologia* 4: 87–92.

Porter, W & M Kearney (2009) Size, shape and the thermal niche of endotherms. *Proceedings of the National Academy* of *Sciences U.S.A*. 106: 19666–19672.

Poulsen, BO (1996) Relationships between frequency of mixed-species flocks, weather and insect activity in a montane cloud forest in Ecuador. *Ibis* 138: 466–470.

Powell, GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour* 22: 501–505.

Powell, GVN (1985) Sociobiology and adaptative significance of heterospecific foraging flocks in the Neotropics. *Ornithological Monographs* 36: 713–732.

Ragusa-Netto, J (2000) Raptors and "campo-cerrado" bird mixed flock led by *Cypsnagra hirundinacea* (Emberizidae: Thraupinae). *Revista Brasileira de Biologia* 60: 461–467.

Ramos, JA (2000) Characteristics of foraging habitats and chick food provisioning by tropical Roseate Terns. *The Condor* 102: 795–803.

Rao, GB, AJ Patil, B Shirke, G Quadros & S Babu (2015) *Flock structure and composition of mixed species flocks of gulls in the Sindhudurg District, Maharashtra. Wetlands: present status, ecology and conservation*. UGC Sponsored National Conference on Wetlands: present status, ecology and conservation. Maharshi Dayanand College, Mumbai, India.

Remsen JV Jr (2003a) Pearled Treerunner (*Margarornis squamiger*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56532 [Accessed 14 March 2015].

Remsen, JV Jr (2003b) White-throated Treerunner (*Pygarrhichas albogularis*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56593 [Accessed 14 March 2015].

Remsen, JV Jr & GM Kirwan (2003) Lineated Foliage-gleaner (*Syndactyla subalaris*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56544 [Accessed 14 March 2015].

Remsen, JV Jr & A Bonan (2014) Thorn-tailed Rayadito (*Aphrastura spinicauda*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56401 [Accessed 14 March 2015].

Remsen, JV Jr & GM Kirwan (2014) Striped Treehunter (*Thripadectes holostictus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56567 [Accessed 14 March 2015].

Remsen, JV Jr & GM Kirwan (2015) Spotted Barbtail (*Premnoplex brunnescens*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56526 [Accessed 13 March 2015].

Rising, J (2011) Black-throated Sparrow (*Amphispiza bilineata*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61941 [Accessed 11 March 2015].

Rising, J & DA Christie (2014) Vesper Sparrow (*Pooecetes gramineus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/61938 [Accessed 11 March 2015].

Rolando, A, P Laiolo & M Formica (1997) The influence of flocking on the foraging behaviour of the Chough (*Pyrrhocorax pyrrhocorax*) and the Alpine Chough (*P. graculus*) coexisting in the Alps*. Journal of Zoology* 242: 299–308.

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

Silliman, J, GS Mills & S Alden (1977) Effect of flock size on foraging activity in wintering Sanderlings. *Wilson Bulletin* 89: 434–438.

Short, LL & GM Kirwan (2014) Emerald Toucanet (*Aulacorhynchus prasinus*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56070 [Accessed 15 March 2015].

Snow, D (2004) Green-and-black Fruiteater (*Pipreola riefferii*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/57004 [Accessed 15 March 2015].

Snow, DW & A Lill (1974) Longevity records for some Neotropical land birds. *The Condor* 76: 262–267.

Sirot, E (2006) Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour* 72: 373–382.

Sridhar, H, G Beauchamp & K Shanker (2009) Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour* 78: 337–347.

Sridhar, H & K Shanker (2014) Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. *Behavioral Ecology and Sociobiology* 68: 185–196.

Sridhar, H, U Srinivasan, RA Askins, JC Canales-Delgadillo, CC Chen, DN Ewert, GA Gale, E Goodale, WK Gram, PJ Hart, KA Hobson, RL Hutto, SW Kotagama, JL Knowlton, T Ming Lee, CA Munn, S Nimnuan, BZ Nizam, G Péron, VV Robin, AD Rodewald, PG Rodewald, RL Thomson, P Trivedi, SL Van Wilgenburg & K Shanker (2012) Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. *American Naturalist* 180: 777–790.

Stawarczyk, T (1984) Aggression and its suppression in mixed-species wader flocks. *Ornis Scandinavia* 15: 23–37.

Sullivan, KA (1984) Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour* 91: 294–311.

Székely, T, T Szep & T Juhasz (1989) Mixed species flocking of tits (*Parus* spp.): a field experiment. *Oecologia* 78: 490–495.

Thiollay, J (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 (1998) Flocking behaviour of foraging birds in a Neotropical rain forest and the antipredator defence hypothesis. *Ibis* 140: 382–394.

Tellerıa, JL, E Virgós, R Carbonell, J Pérez-Tris & T Santos (2001) Behavioural responses to changing landscapes: flock structure and antipredator strategies of tits wintering in fragmented forests. *Oikos* 95: 253–264.

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.

Vuilleumier, F (1967) Mixed species flocks in Patagonian forests, with remarks on interspecies flock formation. *The Condor* 69: 400–404.

Walters, BT, TNN Cheng, J Doyle, CG Guglielmo, M Clinchy & LY Zanette (2017) Too important to tamper with: predation risk affects body mass and escape behaviour but not escape ability. *Functional Ecology* 31(7): 1405-1417.

Webster, S & L Lefebvre (2001) Problem-solving and neophobia in a passeriform–columbiform assemblage in Barbados. *Animal Behav-*

*iour* 62: 23–32.

Winkler, H, DA Christie & A Bonan (2015) Crimson-mantled Woodpecker (*Colaptes rivolii*). *In*: del Hoyo, J, A Elliott, J Sargatal, DA Christie & E de Juana (eds). *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona, Spain. Available at http://www.hbw.com/node/56264 [Accessed 15 March 2015].

With, K.A & ML Morrison (1990) Flock formation of two parids in relation to cyclical seed production in a pinyon-juniper woodland. *The Auk* 107: 522–532.

Whittingham, MJ & KL Evans (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* 146: 210–220.

Winterbottom, JM (1943) On woodland bird parties in northern Rhodesia. *Ibis* 84: 437–442.

Witter, MS, IC Cuthill & RH Bonser (1994) Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. *Animal Behaviour 48*: 201–222.

Young, KA, MJ Genner, DA Joyc & MP Haesler (2009) Hotshots, hot spots, and female preference: exploring lek formation models with a bower-building cichlid fish. *Behavioral Ecology* 20: 609–615.

Zuur, AF, EN Ieno, NJ Walker, AA Saveliev & GM Smith (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.