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Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil

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ABSTRACT. Multi-species bird flocks in tropical forests are maintained throughout the annual cycle despite seasonal differences in resource availability, and the reproductive schedules and ecological requirements of individual species. This study examines the relationship between seasonal variation in flock structure and the availability of fruits and arthropods over a 12-mo period at a coastal Atlantic forest within the Juréia–Itatins Ecological Station, São Paulo, Brazil. Fruit abundance was estimated by a phenological survey of both canopy and understorey trees, whereas arthropod abundance was quantified monthly on the basis of a nocturnal visual census technique. The seasonal variation in flock structure and composition was affected by both the breeding seasons of different core and attendant species, and the availability of food resources. The number of bird species attending flocks was greater during the dry season, declining thereafter during the breeding season. Understorey fruit availability exhibited a marked seasonal fluctuation with the lowest levels between the late dry and early wet season. Seasonal variation in canopy fruit availability, on the other hand, was far less demarcated than that of understorey plants. Arthropod abundance was greatest during the wettest months of the year, which apparently determined the timing of the main breeding season. Bird species richness attending flocks was, therefore, significantly correlated with the availability of understorey arthropods, but not with that of either understorey and canopy fruits. Arthropod abundance thus appears to affect profoundly the reproductive schedules of the understorey avifauna, which in turn influences the seasonal variation of flock size and composition.

RESUMO. Nas florestas tropicais a formação de bandos mistos de aves ocorre ao longo de todo o ano, porém existem variações sazonais na composição e estrutura destes bandos. Tais variações estão ligadas ao período reprodutivo das aves, à disponibilidade de recursos alimentares e a requisitos ecológicos inerentes a cada espécie. Este trabalho analisou a dinâmica sazonal destes bandos durante um ano,

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relacionando estes dados com a disponibilidade de recursos alimentares em uma área de Mata Atlântica na Estação Ecológica Juréia–Itatins. A disponibilidade de frutos foi estimada através de acompanhamento fenológico de espécies de dossel e de sub-bosque, enquanto a abundância de artrópodos foi feita através de censos noturnos mensais. A variação sazonal na estrutura e composição dos bandos foi afetada pela atividade reprodutiva das espécies mais freqüentes e pela disponibilidade de recursos alimentares. Nos meses mais secos ocorreu um aumento do número de espécies nos bandos, ocorrendo um declínio durante o período de reprodução das aves. A quantidade de frutos de sub-bosque apresentou maior escassez entre o final do período seco e o início do período chuvoso, variando de maneira muito mais drástica quando comparada aos frutos de dossel. A abundância de artrópodos foi maior durante os meses mais chuvosos do ano, coincidindo com a época reprodutiva das aves. A riqueza das espécies de aves associadas a bandos mistos foi significativamente correlacionada com a abundância de artrópodos, mas não com a disponibilidade de frutos de dossel e sub-bosque. A abundância de artrópodos deve ter influenciado o início das atividades reprodutivas das aves, que por sua vez, causou as variações sazonais na composição e tamanho dos bandos.

KEY WORDS: arthropod abundance, Atlantic forest, Brazil, breeding season, fruit availability, insect availability, mixed species flocks, plant phenology, seasonality

INTRODUCTION

Mixed species foraging flocks of avian insectivores are a consistent and worldwide phenomenon in forest habitats. The spatial cohesion of these flocks depends on the network of interactions between different species, and the net benefits derived from flock membership associated with increased predator avoidance and foraging efficiency (see reviews in Barnard & Thompson 1985, Morse 1970, Moynihan 1962). In temperate regions, mixed species flocks are primarily a winter phenomenon restricted to the non-reproductive season, when the so-called winter flocks are formed (Morse 1970, Thiollay 1988). In contrast, such foraging associations persist throughout the year in tropical forests (Greenberg in press, Jullien & Thiollay 1998, Munn 1985; Powell 1979, 1985; Terborgh 1990), although flock size and composition may change on a seasonal basis. Seasonal changes in flock size and species composition could be explained by seasonal differences in the availability of food resources and breeding cycles (Alves & Cavalcanti 1996, Davis 1946, Machado 1991, Powell 1985). Few studies, however, have examined the relationship between fruit and arthropod abundance and the seasonal variation in mixed species flock structure. Poulsen (1996) documented a negative correlation between insect availability and flocking activity, suggesting that flock formation appears to be affected by the annual period of food shortage. Processes such as mate selection, seasonal changes in habitat requirements, and physiological constraints of attendant species are also critical in understanding the mechanics of flock formation and stability through time (Morrison *et al.* 1987). Moreover, the influx of migratory species across different habitats, elevation zones, and latitudinal bands may also contribute to seasonal pulses in flock size and species richness (Hutto 1994, Machado 1991).

That the seasonal variation in flocking activity and food availability remains poorly investigated in tropical forests could be largely attributed to difficulties in quantifying the abundance of food items harvested by birds. The seasonal variation in arthropod and fruit abundance within a given site may be closely tied, however, as both are affected by similar abiotic variables such as rainfall and solar radiation (Foster 1982, Janzen & Schoener 1968, Levings & Windsor 1982, Morellato 1992, Wolda 1978a). In addition, arthropod abundance may be directly affected by seasonal changes in forest productivity of vegetative and reproductive plant parts, including young leaves, flowers and fruits, because of trophic rather than climatic reasons. Indeed, long-term studies in tropical forests have clearly demonstrated that arthropod populations exhibit pronounced seasonal fluctuations (Janzen & Schoener 1968, Levings & Windsor 1982; Wolda 1978a, b; Wolda & Wong 1988). The diurnal and seasonal variation in rainfall, wind, temperature, humidity and insulation clearly affects arthropod availability, which in turn influences the foraging behaviour of avian insectivores in both the canopy and the understorey (Munn & Loiselle 1995). Likewise, tropical plant communities display a marked seasonal variation in the presence of new leaves, flowers and fruits (see review in van Schaik *et al.* 1993), all of which may affect the foraging behaviour and the local and between-habitat movements of frugivorous birds (Levey 1988). If participation in mixed species flocks confers advantages in terms of increased foraging efficiency for either fruits or arthropods, an increment in flock size and species richness might be expected during periods of low food availability. Alternatively, interspecific competition may be more severe during periods of resource scarcity, determining an upper threshold on flock size and composition. In this paper we present data from a lowland Atlantic forest of south-eastern Brazil on the relationship between seasonal variation in flock structure and the availability of fruits and arthropods, which were concurrently sampled over a 1-y period.

STUDY AREA

The study area was located just within the subtropics in a coastal undisturbed forest encompassed by the Juréia–Itatins Ecological Station (24° 27′S, 47°15′W) in the State of São Paulo, Brazil. This 80 000-ha strictly protected forest reserve represents one of the few large Atlantic forest remnants and protects a large elevational gradient of primary forest that extends from sea-level to the top of the Serra do Mar mountain range over 1300 m above sea level. The climate is considered to be wet tropical without a pronounced dry season. Annual rainfall in the study area during this study was 1796 and 2120 mm in 1994 and 1995 (Figure 1), respectively (range over a 10-y period = 1401–3154 mm: DAEE 1991). Annual minimum and maximum temperatures averaged 19.9 °C and 25.0 °C, respectively. The 32-ha study plot (elevation = 20–250 m asl) consisted

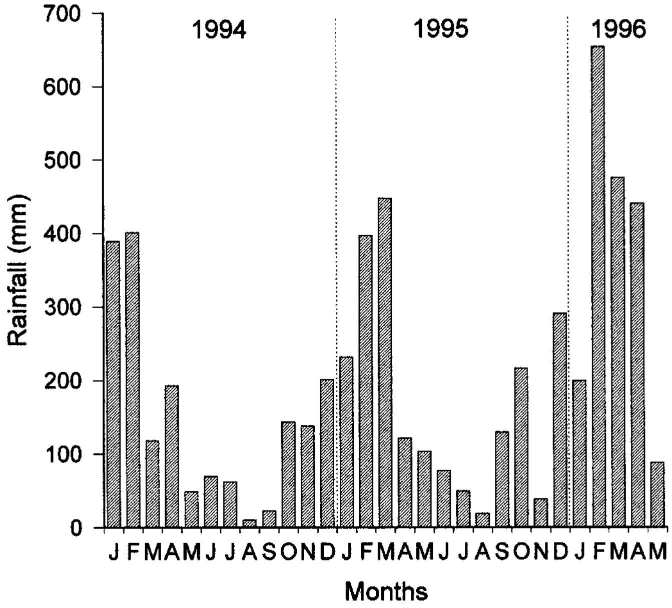

Figure 1. Monthly rainfall at the Juréia–Itatins Ecological Station, São Paulo, Brazil between January 1994 and May 1996.

of primary coastal lowland Atlantic forest where canopy height ranged from 20 to 30 m. Dominant tree species in this forest belong primarily to the families Myrtaceae, Moraceae, Lauraceae, Palmae and Myristicaceae. Canopy trees were covered with epiphytes (Orchidaceae, Bromeliaceae and Araceae) and climbing vines such as several Cyclanthaceae. Small understorey trees were primarily representatives of the Rubiaceae and Myrtaceae.

METHODS

Mixed species flocks

Fieldwork was conducted from May 1995 until May 1996 after a trail system had been cut and mapped in order to facilitate observations of the avifauna. Prior to this period, a total of four mixed species understorey flocks had been mist-netted (2.5-m × 12.8-m, 32-mm mesh; total 1435 net-hours) and uniquely colour-banded for individual identification. These flocks were systematically followed and observed on a monthly basis, and their location and species composition were recorded at 15-min intervals for 320 h over 13 mo. Most observations presented here refer to understorey flocks, as observations of flocks in the forest canopy were usually difficult. Mixed species flocks are defined as associations of two or more species in close proximity, moving in the same direction for at least 5 min with no external resource concentration (cf. Stotz 1993). A detailed description of structure, composition and territoriality of these flocks is presented elsewhere (Develey 1997).

Fruit phenology

Although most understorey bird species in neotropical forest are often described as largely or entirely insectivorous, we made no a priori assumptions on the importance (or lack thereof) of fruits to the mixed species flocks when designing the resource sampling protocol. We therefore chose to monitor the fruit production in the understorey and canopy because they could be potentially important to flock participants.

Canopy

A fruiting phenology survey was conducted on a monthly basis between April 1995 and March 1996. Fruit patches (presence of fruit on the ground) produced by trees ≥10 cm in diameter at breast height (DBH) were carefully searched along a 1 m wide linear transect of 2.2 km in length. For each fruit patch detected, the fruiting tree was located and its DBH was recorded in order to calculate the tree basal area (BA). A voucher specimen of the fruits and vegetative material were also obtained. The quantity of ripe and immature fruits was ranked based on a fruit abundance score (F) defined by a five-graded scale ranging from the total absence (0) to the full crown capacity (4) of fruits (Fournier 1974). We then followed Peres (1994) in calculating a monthly index of fruit availability based on the sum of the basal area of all fruiting trees found in any given month times their fruit abundance scores (as a proportion of four: 0.0, 0.25, 0.5, 0.75 or 1.0) as in Σ (BA * F/4).

Understorey trees

This survey was conducted concurrently with the canopy fruiting phenology and along the same transect by searching for all understorey trees (<10 cm DBH) bearing ripe fruits within 2.5 m on either side of transect. Ripe fruits were then counted for each fruiting tree detected, and a voucher specimen was collected (cf. Gentry & Emmons 1987; Peres 1994). An index of understorey fruit availability was then calculated simply on the basis of the sum of all mature fruits produced by all fruiting individuals. Vouchers of both understorey and canopy species were identified by the herbarium staff at the São Paulo Botany Institute, São Paulo, Brazil.

Arthropod availability

Arthropod abundance was sampled using a nocturnal line-transect census technique conducted over 13 consecutive months (May 1995–May 1996) along six random transects of 100 m which intersected different portions of the study area. Following initial experimental trials of nocturnal surveys targeted to forest arthropods at Juréia, which proved to work well for several taxa of prey items consumed by birds joining mixed species flocks (P. Develey, *pers. obs.*), we decided to adopt it as a standard arthropod abundance census technique. These visual censuses attempted to mimic the search methods of foliage-gleaning birds, and were conducted from 19 to 21 h during two nights in each month of the study (three transects per night). Transects were walked very slowly (150 m h^{-1}), and all understorey arthropods encountered on all exposed surfaces – including the upper and undersides of leaves and stems, leaf bracts, shallow holes and crevices in woody surfaces of the vegetation – were recorded and visually classified to order (and sometimes to family) without disturbing the surrounding foliage. All arthropods were recorded along a rectangular 'tunnel' of vegetation within 1 m on either side of the transects and up to 2 m in height. We excluded ants from our censuses, however, because adult Formicidae are rarely consumed by understorey birds typically found in Amazonian and Atlantic forest flocks (C. Peres & P. Develey, *pers. obs.*). Rainy nights were avoided in order to minimize potential bias due to weather conditions.

Several techniques for sampling insects and other prey items have been used by avian ecologists, each of which has its own set of advantages and disadvantages (Cooper & Whitmore 1990, Karr & Brawn 1990, Winnet-Murray 1986). Admittedly, the arthropod census technique used in this study is effectively biased towards only a fraction of the total arthropod fauna. Small-bodied species and those restricted to either the leaf litter or the canopy were clearly underestimated. In addition, not all arthropods detected were potential prey items for birds as some may have been unpalatable or require excessive amounts of foraging time and energy (Wolda 1990). We are confident, however, that the arthropod taxa of most importance to avian understorey insectivores were adequately sampled. Finally, such sampling biases were homogeneous throughout the study and across different transects, providing a reasonably good measure of the seasonal variation in arthropod abundance which was relevant to our mixed species flocks.

Statistical analyses

A repeated-measures ANOVA was used to examine differences in the mean flock size (number of species) during the 13 mo of study, following square-root transformations of the number of bird species recorded in each flock. A Kruskal–Wallis one-way ANOVA was used to test for differences in arthropod abundance over the same period because normality and homoscedasticity could not be corrected for using data transformations. Spearman's rank correlations (two-tailed in all cases) were used to examine the relationship between seasonal variance in flock structure and food availability. All statistical analyses were carried out using STATISTICA (v. 5.1), following Zar (1996).

RESULTS

Flock size

The mean number of flock observations recorded during each month was 40.2 ± 2.3, resulting in a total of 523 flock observations over the entire study. A total of 72 bird species were recorded within mixed species flocks (see Appendix 1) over the entire study. The mean number of species joining flocks at any one time was 6.6 ± 0.1 SE (range = 2–16 species, n = 523), and flock size was significantly different during different months of the year (F = 2.16, df = 12, P = 0.03).

Breeding seasons and flock membership

During October and November, a small group of red-crowned ant-tanagers (*Habia rubica*) (1 male and 2 females) was observed building a nest and caring for nestlings. A disproportionate amount of time was, therefore, spent in the vicinity of their nest at this time of the year. Several bird species assiduously joining flocks were observed in close association with *H. rubica* even when this species was actively attending nests. This is almost certainly because of the importance of *H. rubica* in maintaining the cohesion and stability of mixed species flocks in the southern Atlantic forests. Although nests of other core species frequently joining flocks were not found, immature individuals of *Myrmotherula minor*, *Philydor atricapillus* and *Lepidocolaptes fuscus* were recorded attending flocks with their parents in December and January. The number of species attending flocks was lowest during the main breeding season (October–January), when flocks were consistently formed by roughly six species (Figure 2). As we shall see, this breeding period was largely synchronized with the months of greatest arthropod abundance, presumably to maximize fledgling survival and minimize prey-capture efforts at a time of heavy foraging demands imposed on parents.

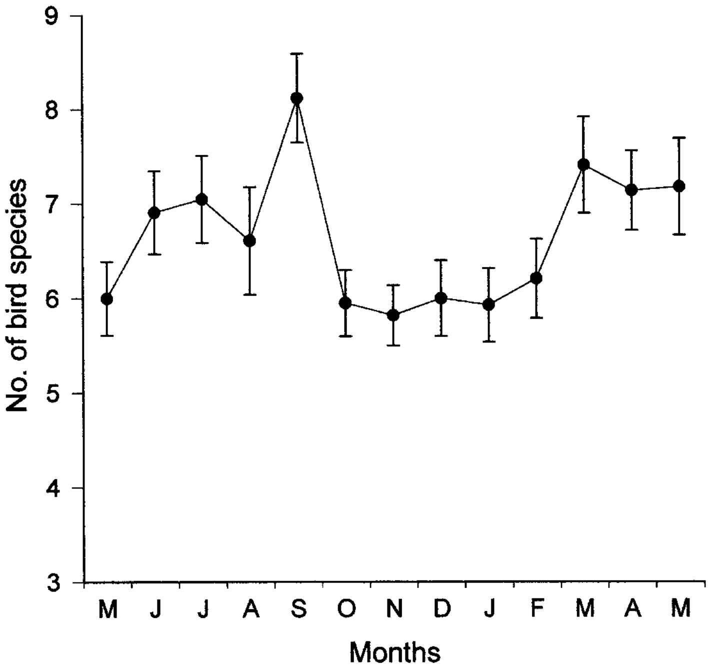

Figure 2. Seasonal variation in flock species richness (mean ± SE) at the Juréia–Itatins Reserve between May 1995 and May 1996. Sample size is four flocks, each measured approximately 10 times per month.

Table 1. Mean arthropod number sampled during 13 mo along six transects of 100 m by nocturnal census at Juréia–Itatins forest. Total of 3953 individuals.

Arthropod taxa	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Hemiptera	0.5	0	0.5	0	0.2	0.2	0	0.3	0	0.5	0.5	0	0
Hymenoptera	0	3.8	1.3	1	0.8	0.3	3	1.7	6	5	2.3	0.7	0.8
Diptera	1	1	2.3	2	3.3	2.7	3	1.7	3.2	4.3	4.3	2.7	2.2
Coleoptera	0.5	1.8	2.3	0.5	2.3	3.5	5.7	7	6.2	3.8	1	0.8	0.2
Lepidoptera	3	2.2	4	3.33	2.3	4.5	5.5	2.5	3.7	3.2	6.3	7.2	2.8
Blattodea	1	7.3	4.7	8.2	6.7	6.7	13.2	15.5	9.5	13.7	2.7	8	8.5
Orthoptera	7.2	9.7	9.3	12	10.3	6	8.5	12.5	8.7	5	5.8	6.8	10.7
Arachnida	17.3	17.3	16	21.3	11.8	23.5	21	28.3	27	24.2	18.8	18.5	18.7
Others	1	1.5	1	1.7	1.7	1.2	1.2	1.8	2	2.8	2	1.7	2.3
Total number	229	258	249	299	239	304	367	427	395	375	256	278	277
Mean ± SE	38.2 ± 2.3	43.2 ± 6.3	41.5 ± 7.1	49.8 ± 3.8	39.8 ± 3.2	50.7 ± 4.9	61.2 ± 5.5	71.2 ± 6.8	65.8 ± 8.4	62.5 ± 8.5	42.7 ± 3.6	46.3 ± 6.2	46.2 ± 6.0

Arthropod availability

A total of 3953 insects and arachnids were sampled using our nocturnal line-transect census method (Table 1). There was significant monthly variation in arthropod abundance (K = 29.2, df = 12, P < 0.01), which increased primarily during the wet season (Figure 3). Considering the entire sampling period of 13 mo, arachnids (spiders and whipscorpions) were the most representative group accounting for 40% of all arthropods detected. These were followed by orthopterans (e.g. katydids and crickets) and blattodeans (forest cockroaches) which together accounted for 34% of the entire sample.

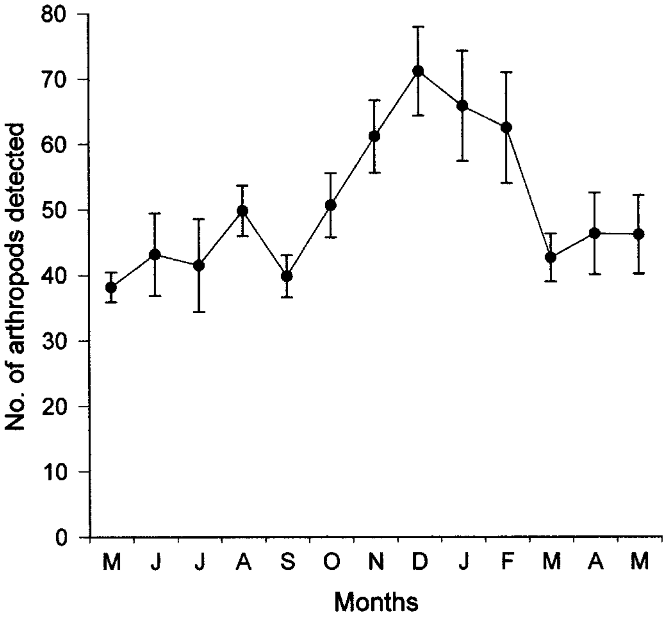

Figure 3. Seasonal variation in arthropod abundance (mean ± SE) based on a nocturnal line-transect census conducted over a 13-mo period.

Not surprisingly, the main breeding period of forest birds joining mixed species flocks took place at the time of greatest arthropod abundance. Bird species richness attending mixed species flocks was, therefore, clearly negatively correlated with arthropod abundance ($r_s = -0.66$, n = 13, P = 0.01). The greater availability of protein-rich food at that time is presumably critical to egg formation and offspring growth. In contrast, the seasonal variation in flock species richness was poorly correlated with fruit production by either canopy trees ($r_s = 0.18$, n = 11, P = 0.58) or understorey trees ($r_s = 0.23$, n = 11, P =0.49).

Fruit availability

A total of 40 canopy species belonging to 22 families was observed fruiting during the 12-mo sampling period (Appendix 2). Canopy fruit production fluctuated during the annual cycle with a moderate increase in the dry season between April and August (Figure 4). Such greater levels of fruit production may reflect a response to rainfall in the previous 3 mo, from January to March. In the understorey, a total of 32 species belonging to 15 families were recorded

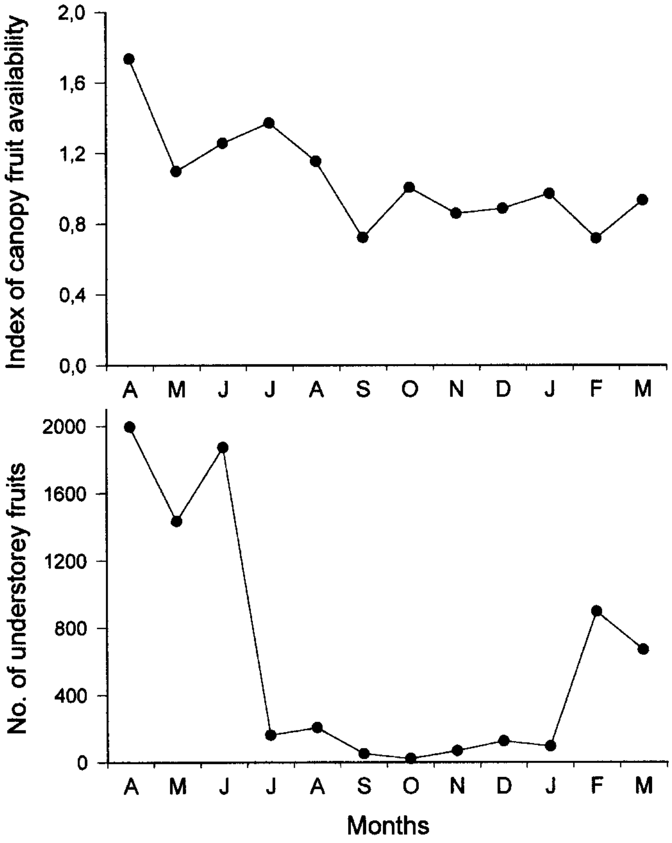

Figure 4. Fruit availability in the forest canopy (above) and understorey (below) over a 12-mo sampling period along a 2.2-km transect (see text for details on fruit availability indices).

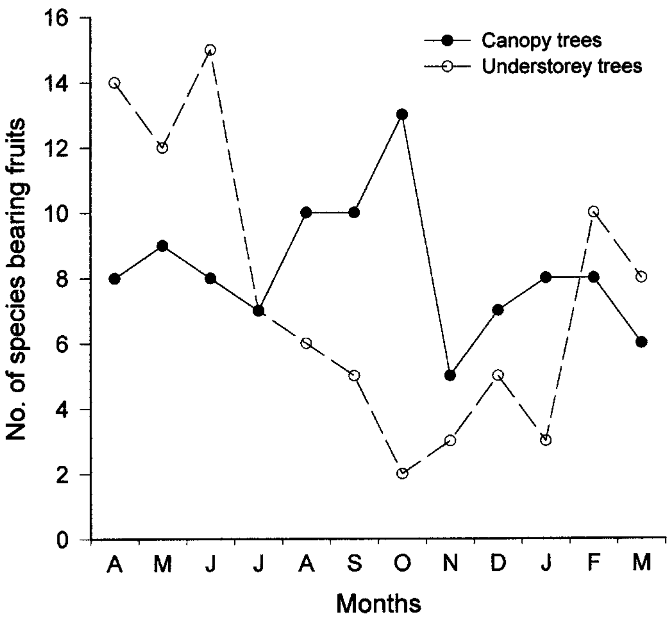

Figure 5. Number of tree species bearing fruits in the forest canopy and understorey between April 1995 and March 1996.

producing ripe fruits (Appendix 3). Similar to the pattern shown by canopy species, understorey fruit production increased during the wet season and was greatest during the early dry season. Unlike canopy trees, however, understorey trees showed a strongly demarcated seasonal variation in fruit production, with a prolonged period of scarcity between July and January (Figure 4). The two peaks of fruit production by small trees coincided with the fruiting periods of eight species of *Psychotria* (Rubiaceae), which combined with two *Geonoma* palms, were the most important species determining the overall pattern of fruit production in the forest understorey.

The monthly variation in the number of species bearing fruits in the forest canopy and the understorey was clearly out of phase but not necessarily inversely correlated with one another ($r_s = -0.08$, $n = 12$, $P = 0.79$; Figure 5). Because the quantity of fruits produced in the canopy was highly variable between individual trees throughout the year, the number of canopy species bearing fruits was poorly correlated with the index of canopy fruit availability which was a better measure of fruit patch size ($r_s = 0.189$, $n = 12$, $P = 0.56$). On the other hand, the number of fruiting species in the understorey was highly correlated with the number of fruits produced ($r_s = 0.954$, $n = 12$, $P < 0.001$).

DISCUSSION

Fruiting seasonality

Understorey plant species presented a marked fruiting peak between the middle of the wet season and the onset of the dry season. Both abiotic and biotic factors may account for this interspecific synchrony. Plants are expected to invest in flowering and fruiting when rainfall, temperature, and light conditions are most favourable, thus increasing the community-wide overlap in fruiting phenology. The low levels of understorey fruit production between the early dry and the mid-wet season has also been documented in the highland semi-deciduous forest (800–1100 m) of Serra do Japi, São Paulo (Morellato & Leitão-Filho 1992), and may simply reflect unfavourably cold conditions at this time of year at these relatively high latitudes and elevations. In contrast, understorey fruit abundance at several forest sites in Costa Rica (Frankie *et al*. 1974, Levey 1988, Opler *et al*. 1980) and central Amazonia (Peres 1994) did not show a marked fluctuation throughout the year. The strong in seasonality rainfall at the Juréia–Itatins coastal forest may also partly account for these differences.

In contrast with other neotropical forests where canopy fruiting peaks coincide primarily with the early wet season (e.g. Foster 1982, Frankie *et al*. 1974, Peres 1994), most canopy trees at the Juréia–Itatins lowland forest produced fruits between the dry season and the onset of the rainy season. However, fruit production by different species of canopy and emergent trees could be observed throughout the year (cf. Morellato & Leitão-Filho 1992). In staggering their fruit crops over time, these species appeared to minimize temporal overlap with one another, thus potentially avoiding competition for seed-dispersal services and attracting a larger number of frugivores (van Schaik *et al.* 1993). The weak correlation between the number of fruiting species and the overall fruit availability index in the canopy largely reflected the fact that a small number of large-crowned fruiting species disproportionately increased the overall fruit abundance in the study area. Moreover, because most strictly frugivorous birds (e.g. toucans, cotingas, guans) in this coastal Atlantic forest were restricted to the canopy, they cannot represent a strong selective pressure against fruiting synchrony in the understorey.

Arthropod seasonality

Our visual censuses indicate that the seasonal variation in arthropod abundance is directly or indirectly affected by rainfall. Even small fluctuations in rainfall have been shown to have an effect on food availability for some groups of insects (Fogden 1972, Wolda 1978b). In the lowland forest of Juréia–Itatins, arthropods were most abundant during the rainy season, a pattern documented in several other neotropical forests (Davis 1945, Gradwohl & Greenberg 1982, Karr & Brawn 1990). In the semi-deciduous forest of Serra do Japi, the main emergence period for lepidopteran larvae, which were often captured by flock attendants, takes place during the onset of the rainy season (Brown 1992). It remains unclear, however, whether these patterns are directly caused by moisture gradients or are related to forest primary productivity such as the availability of new leaves. In other tropical forests the highest level of young leaf production takes place during the wet season for both understorey (Fogden

1972) and canopy species (Peres 1994). This pattern could also prove to be the case at Juréia–Itatins so that the increase in herbivorous arthropod numbers may well be a direct response to high food availability (cf. Karr & Brawn 1990). This effect may be extended to invertebrate predators, the numbers of which may be indirectly boosted by an increase in the abundance of herbivorous insects (Wolda 1978b).

On the basis of a diurnal visual sampling method, Robinson *et al.* (1990) estimated that the Orthoptera and Blattodea accounted for almost half of the arthropod biomass available in the understorey of a western Amazonia forest, whereas Diptera was the order with the greatest number of individuals sampled. In this study, orthopterans and blattodeans combined were the second most commonly detected arthropods, while Diptera was hardly ever represented. These differences appear to be related to the time of day at which sampling was carried out. A large portion of the neotropical forest invertebrate fauna is strictly nocturnal probably because of the strong selective pressure against a diurnal activity pattern generated by predators operating by day (Elton 1973). Nocturnal sampling was, therefore, thought to be most appropriate for the purpose of this study, since morphological and behavioural adaptations allow diurnal insectivorous birds to exploit inactive arthropods exposed on the foliage or embedded within daytime shelters.

Orthopterans and spiders were the most abundant prey items in dead leaves and in the stomach contents of dead-leaf specialist birds of western Amazonia (Rosenberg 1990). These groups of arthropods were also the most commonly captured by antwrens (*Myrmotherula* spp.) on live foliage when feeding nestlings in Barro Colorado Island, Panama (Gradwohl & Greenberg 1982). These studies suggest that orthopterans and arachnids – the most commonly detected arthropods at Juréia–Itatins – are the arthropod taxa most frequently preyed upon by foliage-gleaning insectivorous birds in neotropical forests.

Flock size and composition

Tropical forests, particularly in humid lowland sites, may boast as many as 50–100 bird species participating in a given flock at one time (e.g. Jullien & Thiollay 1998, Munn & Terborgh 1979, Munn 1985). In contrast, the equivalent number for temperate flocks is more like 10–15 species (Greenberg in press). Yet the number of species simultaneously attending one of our four systematically observed flocks was as few as two and at most 16. The species richness of avian flocks at our southern Atlantic forest site thus fell within the range of those typically found in temperate woodlands rather than other neotropical forests studied to date. Since the Juréia Reserve is located just below the Tropic of Capricorn (24.5 °S), we can only surmise that there appears to be a previously overlooked latitudinal gradient in flock species richness in the New World tropics. This is relevant because decades of research on mixed species flocks in neotropical forests within 10° of the equator (Gradwohl & Greenberg 1980, Jullien & Thiollay 1998, Munn & Terborgh 1979, Munn 1985, Powell 1979, Wiley 1980) generally portray the image of relatively species-rich flocks enjoying a relatively stable core membership. Flocks in the southern Atlantic forest are thus relatively impoverished and, in the absence of nuclear species such as *Thamnomanes* antshrikes, which are so critical to the coalescence of the more complex flocks of Amazonia and the Guianan Shield (Jullien & Thiollay 1998, Munn & Terborgh 1979), are enormously influenced by less specialized substitutes such as red-crowned ant-tanagers, *Habia rubica* (Develey 1997).

In montane Atlantic forests, the highest number of species following mixed species flocks was recorded during the summer from January to March (Davis 1946, Machado 1991). An influx of summer migrants such as *Vireo olivaceus*, *Pachyramphus polychopterus* and *Myiarchus swainsoni* was recorded following flocks at that time of year (Machado 1991), thus increasing their size and species richness. In the lowland forest of Juréia–Itatins, mixed species flocks consisted mainly of year-round resident species, so that the presence of either latitudinal or altitudinal migrants had little influence on flock size. Indeed mixed species flocks at our site were reasonably stable despite the pronounced seasonal variation in resource availability.

Seasonal variation in flock size

This study strongly suggests that flock attendants were able to track the temporal variation in arthropod abundance. The seasonal variation in flock size appears to be a response to the bird breeding period and temporal distribution of food resources. The smallest flocks were recorded between October and January, when arthropod availability was steadily increasing. In south-eastern Brazil, the breeding season of forest birds is largely confined to these months of the year (Davis 1945), when most species allocate a disproportionate amount of time to different stages of the breeding cycle. The reproductive activities severely restrict the foraging behaviour of breeding birds to the vicinity of the nest, thus precluding flock attendance (Moynihan 1962, Powell 1985). However, in southern Peru (Munn & Terborgh 1979), Panama (Gradwohl & Greenberg 1980), and French Guiana (Jullien & Thiollay 1998), members of the nuclear species often remained with the flock even when they were breeding. More reminiscent of this study, Powell (1979) found that mixed flocks in a Costa Rican highland forest are almost completely dissolved during the breeding season of the nuclear species (*Basileuterus*). The lower frequency of birds participating in flocks during the breeding season was also reported in the Brazilian *cerrado* scrublands (Alves & Cavalcanti 1996). These results strongly suggest an influence of reproductive activities on seasonal fluctuations in flock size at least in open habitats and high-elevation and high-latitude forests.

The lack of any obvious relationship between canopy and understorey fruit availability and the number of species attending flocks could be attributed to the fact that the study flocks consisted primarily of insectivorous species confined to the understorey. Frugivorous birds of the Atlantic forest rarely follow mixed species flocks typically foraging in the forest canopy, and even the tanager species commonly seen in canopy flocks include insects as a critical component of their diet (Rodrigues 1995).

Flocking appears to increase food availability by flushing prey that are otherwise inaccessible or undetectable (Leck 1971). The presence of a nuclear species may also provide vigilance services which enhance foraging efficiency, since attendant species can allocate more time to food searches without being as concerned about predators (Morse 1977, Powell 1985). The most common species attending the Juréia–Itatins mixed flocks were specialized in capturing insects on tree trunks, live foliage, and dead leaves suspended above ground in the forest understorey (Develey 1997). Dead leaves often shelter spiders and orthopterans, representing a predictable and renewable foraging microhabitat. In south-eastern Peru, dead-leaf specialists even recognize particular leaves within their territories which they return to and inspect repeatedly (Rosenberg 1990). Other species may follow these specialists, presumably to learn the location of potential food sources. This strategy could be more important when arthropod availability is at low levels or during the breeding period, when more prey items are required.

Birds in mixed species flocks present a higher arthropod capture rate than that of species searching for prey solitarily (Thiollay 1988). The frequency and number of species following mixed flocks can be inversely related to the number and biomass of insects (Poulsen 1996). These studies suggest that food availability is an important aspect of the dynamics of mixed species flock formation. Arthropod availability is also critical to flock structure in the lowland Atlantic forest of Juréia–Itatins, leading to more favourable breeding conditions which translate into fewer flock participants.

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Appendix 1. Bird species recorded in four mixed-species flocks in a lowland forest at Juréia–Itatins, São Paulo, Brazil, from a total of 523 flock observations. Species are ranked from the most to the least assiduous according to the number of flocks (n) in which they were recorded.

Species	n	Species	n
Habia rubica	475	*Pitylus fuliginosus*	11
Lepidocolaptes fuscus	342	*Pynglena leucoptera*	10
Philydor atricapillus	329	*Hemitriccus orbitatus*	10
Myrmotherula unicolor	305	*Myrmotherula gularis*	9
Basileuterus culicivorus	251	*Hypoedaleus guttatus*	8
Automolus leucophthalmus	245	*Xiphocolaptes albicollis*	7
Myrmotherula minor	234	*Trogon surrucura*	5
Dysithamnus mentalis	144	*Baryphtengus ruficapillus*	5
Terenura maculata	143	*Schiffornis virescens*	5
Picumnus temminckii	121	*Coereba flaveola*	5
Herpsilochmus rufimarginatus	109	*Cacicus haemorrhous*	5
Dendrocincla turdina	106	*Trogon rufus*	4
Sittasomus griseicapillus	96	*Melanerpes flavifrons*	4
Drymophila squamata	92	*Dendrocolaptes platyrostris*	4
Leptopogon amaurocephalus	89	*Platycichla flavipes*	4
Phylloscartes paulistus	84	*Piaya cayana*	3
Xenops minutus	73	*Selenidera maculirostris*	3
Ramphocaenus melanurus	60	*Sclerurus scansor*	3
Myiobius barbatus	57	*Myiornis auricularis*	3
Piculus flavigula	51	*Oxyrunchus cristatus*	3
Mionectes rufiventris	51	*Thryotorus longirostris*	3
Euphonia pectoralis	33	*Trichothraupis melanops*	3
Veniliornis spilogaster	30	*Thalurania glaucopis*	2
Turdus albicollis	29	*Conopophaga melanops*	2
Tachyphonus cristatus	29	*Rhytipterna simplex*	2
Dysithamnus stictothorax	28	*Parula pitiayumi*	2
Tolmomyias sulphurescens	24	*Orthogonys chloricterus*	2
Hemithraupis ruficapilla	24	*Rhamphodon naevius*	1
Tangara seledon	20	*Amazilia versicolor*	1
Euphonia violacea	19	*Platyrinchus mystaceus*	1
Tachyphonus coronatus	17	*Lathrotriccus euleri*	1
Tangara cyanocephala	16	*Contopus cinereus*	1
Trogon viridis	13	*Sirystes sibilator*	1
Celeus flavescens	13	*Tityra cayana*	1
Pachyramphus marginatus	13	*Chlorophanes spiza*	
Myrmeciza squamosa	11		

Appendix 2. Monthly indices of fruit availability for canopy tree species observed fruiting.

Family Species	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Annonaceae												
Xylopia brasiliensis	0	0	0	0	0	0	0.019	0	0	0	0	0
Araliaceae												
Didymopanax calvum	0	0	0	0	0	0	0	0	0.153	0.33	0.171	0.08
Bombacaceae												
Eriotheca penthaphilla	0	0	0	0	0	0	0.248	0	0	0	0	0
Boraginaceae												
Cordia sellowiana	0	0	0	0	0	0	0.013	0	0	0	0	0
Burseraceae												
Protium widgrenii	0	0	0	0	0	0.285	0.194	0.11	0.045	0	0	0
Celastraceae												
Maytenus cf. robusta	0.367	0.183	0	0	0	0	0	0	0	0	0	0
Maytenus sp.	0.09	0.09	0.024	0	0	0	0	0	0	0	0	0
Chrysobalanaceae												
Licania hoehnei	0	0	0	0	0.143	0.057	0.028	0	0	0	0	0
Euphorbiaceae												
Actinostemon concolor	0	0	0	0	0.006	0	0	0	0	0	0	
Pera glabrata	0	0	0	0	0.026	0.026	0	0	0	0	0	0
Tetrorchidium rubrivenium	0	0	0	0	0	0	0.114	0.344	0.225	0.281	0.11	0
Guttiferae												
Rheedia gardneriana	0	0	0	0	0	0	0	0.061	0.039	0.023	0.022	0
Lacistemataceae												
Lacistema cf. pubescens	0	0	0	0	0	0	0.014	0	0	0	0	0
Lauraceae												
Cryptocarya moschata	0.2	0.18	0.096	0	0	0	0	0	0	0	0.26	0.155
Leguminosae												
Balizia pedicellaris	0	0.233	0.323	0	0	0	0.06	0	0	0	0	0
Copaifera trapezifolia	0	0.027	0.027	0	0	0	0	0	0	0	0	0
Inga marginata	0	0	0	0	0	0	0	0	0	0	0.019	0
Hymenea courbaril	0	0	0	0	0.06	0	0	0	0	0	0	0
Moraceae												
Ficus sp. 1	0.58	0	0	0	0	0	0	0	0	0	0	0
Ficus sp. 2	0	0	0	0	0.257	0	0	0	0	0	0	0
Ficus sp. 3	0	0	0	0	0	0	0	0	0.089	0.044	0	0
Myristicaceae												
Virola oleifera	0.202	0.202	0.507	0.742	0.202	0.095	0	0	0	0	0	0.4

Appendix 2. *cont.*

Family Species	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Myrtaceae												
Calycorectes acutatus	0	0	0	0	0	0	0	0	0.26	0.06	0	0
Campomanesia guaviroba	0.019	0.012	0	0	0	0	0	0	0	0.087	0	0
Campomanesia schlechtendaliana	0	0	0	0	0	0	0	0	0	0.057	0.05	0.03
Eugenia multicostata	0	0	0	0	0	0.002	0.004	0	0	0	0	0
Eugenia pruinosa	0	0	0	0	0	0	0	0	0	0	0	0.24
Eugenia sulcata	0	0	0	0	0	0.101	0	0	0	0	0	0
Myrcia pubipetala	0	0	0	0.067	0.05	0.025	0	0	0	0	0	0
Unidentified species	0.057	0.035	0	0	0	0	0	0	0	0	0	0
Palmae												
Euterpe edulis	0	0.095	0.061	0.023	0.004	0	0	0	0	0	0	0.027
Proteaceae												
Roupala sp.	0	0	0	0.06	0	0	0	0	0	0	0	0
Olacaceae												
Heisteria silvianii	0	0	0	0	0	0	0.118	0.291	0.075	0	0	0
Rubiaceae												
Alibertia sp.	0	0	0	0.128	0.072	0.06	0.022	0	0	0	0	0
Sapindaceae												
Cupanea oblongifolia	0	0	0	0	0	0	0	0.052	0	0	0	0
Sapotaceae												
Chrysophillum inornatum	0.22	0	0	0.22	0.275	0	0	0	0	0	0	0
Manilkara subsericea	0	0	0	0	0	0	0.091	0	0	0	0	0
Pouteria sp.	0	0	0.016	0	0	0	0	0	0	0	0	0
Tiliaceae												
Luehea divaricata	0	0	0.202	0.13	0.065	0.065	0.065	0	0	0	0.04	0
Unidentified species	0	0	0	0	0	0	0	0	0	0.085	0.045	0
Overall index	1.735	1.079	1.256	1.37	1.154	0.722	1.005	0.858	0.886	0.97	0.717	0.932
Number of species	8	9	8	7	10	10	13	5	7	8	8	6

Appendix 3. Fruiting tree species and total fruit counts sampled in the forest understorey.

Family Species	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Bombacaceae												
Quararibea turbinata	3	0	2	3	0	0	0	0	0	0	0	0
Euphorbiaceae												
Actinostemon concolor	0	0	0	0	0	2	0	0	0	0	0	0
Melastomataceae												
Miconia sp.	0	0	15	0	0	0	0	0	0	0	26	0
Meliaceae												
Trichilia silvatica	0	0	0	0	2	0	0	0	0	0	0	0
Moraceae												
Sorocea sp.	0	0	0	0	0	0	0	0	17	0	0	0
Myrsinaceae												
Stylogine ambigua	0	0	0	0	0	0	0	0	0	0	85	0
Myrtaceae												
Eugenia cuprea	0	0	0	0	0	0	0	0	0	0	1	0
Eugenia riedeliana	0	0	0	0	25	0	0	0	0	0	0	0
Gomidesia flagellaris	67	2	1	0	0	0	0	0	0	0	0	0
*Marlierea reitzi*i	0	0	0	0	0	0	0	0	0	0	48	5
Nyctaginaceae												
Guapira sp.	0	0	0	0	1	30	10	0	0	0	0	0
Ochnaceae												
Ouratea sp.	66	0	0	0	0	0	0	0	0	0	0	0
Palmae												
Geonoma sp. 1	453	316	183	37	0	9	12	4	4	0	18	100
Geonoma sp. 2	27	135	0	0	98	0	0	0	27	28	81	12

Appendix 3. *cont*

Family Species	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Piperaceae												
Piper sp.1	87	40	85	3	0	0	0	61	74	40	123	119
Piper sp. 2	0	0	15	0	0	0	0	0	0	0	18	13
Rubiaceae												
Alibertia sp.	0	0	0	100	70	0	0	0	0	0	0	0
Psychotria astrellantha	143	54	4	1	0	0	0	0	0	0	0	61
Psychotria barbiflora	0	650	1313	13	0	0	0	0	0	0	0	0
Psychotria brachypoda	23	15	0	0	0	0	0	0	0	0	0	0
Psychotria carthaginensis	550	41	67	0	0	0	0	0	0	0	0	0
Psychotria leiocarpa	0	59	43	0	0	1	0	0	0	0	26	0
Psychotria nuda	190	80	23	0	0	0	0	4	4	27	120	100
Psychotria sp.	118	20	1	0	0	0	0	0	0	0	0	0
Rudgea jasminoides	259	0	0	0	0	0	0	0	0	0	0	0
Rudgea recurva	1	0	0	5	10	6	0	0	0	0	0	0
Unidentified species	0	0	0	0	0	0	0	0	0	0	351	260
Sapindaceae												
Allophyllus petiolulatus	0	0	22	0	0	0	0	0	0	0	0	0
Cupanea sp.	9	22	0	0	0	0	0	0	0	0	0	0
Urticaceae												
Urera nitida	0	0	70	0	0	0	0	0	0	0	0	0
Unidentified species	0	0	30	0	0	0	0	0	0	0	0	0
Other unidentified species	0	0	0	0	0	1	0	0	0	0	0	0
Total fruit count	1996	1434	1874	162	206	51	22	69	126	95	897	670
Total number of species	14	12	15	7	6	5	2	3	5	3	10	8