J. Field Ornithol., 68(3):426–442

ESTIMATION OF ARTHROPODS AVAILABLE TO BIRDS: EFFECT OF TRAPPING TECHNIQUE, PREY DISTRIBUTION, AND BIRD DIET

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Abstract.—Few studies have attempted to measure food available to insectivorous birds. One reason for this is the difficulty of sampling potential prey adequately. In this paper, we present a simple mathematical approach to estimate seasonal availability of arthropods by considering both the differential probability of each taxon being sampled with a trapping technique and being preyed upon by a bird. Because our index is based on the summation of the percent abundance (relative to the whole sampling period) of each arthropod taxon in a sample, abundance of prey taxa collected with different trapping methods or even different food types (e.g., arthropods, seeds, fruits) can easily be combined. These values are further multiplied by the importance of each food taxon in the birds' diet, resulting in a weighted abundance index. Unlike other methods to estimate arthropod availability, this approach is readily applicable to community or long-term studies and offers flexibility in its use. We provide three applications of our index, each one in a different Neotropical habitat (thorn scrub, mangrove woodland, humid forest) where arthropod abundance and bird diet were monitored during a year. Regardless of the habitat type, the trapping technique used, and the bird species considered, our original data on arthropod numbers were importantly and unpredictably modified by our index. Using diet data to weight arthropod abundance had a strong impact on our estimates, suggesting that sampling of arthropods in the bird's foraging microhabitat might not be sufficient to assess food abundance to a particular species. Breeding of resident species as well as abundance pattern of migrant species at our study sites were better related to our weighted abundance index than to numbers of arthropods sampled with any trapping technique, suggesting that this method provides a reliable estimate of food availability. Selection of an appropriate trapping technique, level of prey identification, and biases associated with diet estimation from gut contents are also discussed.

ESTIMACIÓN DE ARTRÓPODOS DISPONIBLES PARA LAS AVES: EFECTOS DE LA TÉCNICA DE ATRAPARLOS, DISTRIBUCIÓN DE PRESA, Y DIETA DE LAS AVES

Sinopsis.—Pocos estudios han tratado de medir el alimento disponible a las aves insectívoras. Una razón para esto es la dificultad en muestrear adecuadamente las presas potenciales. Aquí presentamos una aproximación matemática sencilla para estimar la disponibilidad estacional de artrópodos al considerar tanto la probabilidad diferencial de cada taxón muestreado con una técnica particular y la de ser atrapado por un ave. Como nuestro índice se basa en la suma del porciento en abundancia (relativa al total del período de muestreo) de cada taxón artrópodo en una muestra, la abundancia de taxones de presa colectados con diferentes métodos o hasta de diferentes tipos de alimentos (e.g., artrópodos, semillas, frutas) se pueden combinar fácilmente. Estos valores son luego multiplicados por la importancia de cada taxón alimenticio en la dieta del ave, resultando en un índice cargado de abundancia. A diferencia de otros métodos para estimar la disponibilidad de artrópodos, este método es rápidamente utilizable para estudios comunitarios o de largo plazo y ofrece flexibilidad en el uso. Proveemos tres ejemplos del uso de nuestro índice, cada uno en un habitat neotropical diferente (bosque arbustivo espinoso, manglar, bosque húmedo) donde la abundancia de artrópodos y la dieta de las aves se monitoreó durante un año. Nuestros datos originales sobre los números de artrópodos fueron importantemente e impredeciblemente modificados

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por nuestro índice independientemente del tipo de hábitat, de la técnica de colección usada y de la especie de ave considerada. El uso de los datos de dieta para cargar la abundancía de artrópodos tuvo un fuerte impacto en nuestros estimados, sugiriendo que el muestreo de artrópodos en el microhabitat donde el ave se alimenta puede no ser suficiente para estimar la abundancia de alimento para una especie particular. La reproducción de especies residentes tanto como el patrón de abundancia de especies migratorias en nuestros lugares de estudio estaban mejor relacionados a nuestro índice cargado de abundancia que a números de artrópodos mestreados con cualquier técnica de muestreo, sugiriendo que este método provee un estimado confiable de disponibilidad de alimento. También se discuten la selección de una técnica apropiada de muestreo, del nivel de identificación de las presas, y vicios asociados con la estimación de la dieta de contenidos estomacales.

Food resources are crucial to many aspects of avian ecology (Wiens 1984). Yet, quantitative measures of food availability and food exploitation by birds are rarely attempted (Hutto 1990, Rosenberg and Cooper 1990). Sampling techniques to assess relative or absolute abundance of arthropods are numerous (Cooper and Whitmore 1990, Wolda 1990), but are often referred to as unreliable measures of food availability because of the conceptual problem of availability from the bird's perception (Hutto 1990, Wolda 1990). Reference to the bird's foraging activity (e.g., Lovette and Holmes 1995), to specific past weather conditions (e.g., Dunning and Brown 1982), or to calendar seasons (e.g., Marone 1992), is often considered more acceptable in estimating general food availability to birds than any attempt to measure directly food abundance.

Most studies dealing with food resources as explanatory factors of avian behaviors (e.g., breeding activity, bird abundance and movements, etc.) are interested in food level variation over time. In that situation, a trapping technique estimating relative abundance of arthropods is a suitable approach (Cooper and Whitmore 1990, Wolda 1990). However, the probability of each arthropod taxon to be sampled with a trapping technique does not necessarily reflect its probability of being taken by a bird. Prey size, life stage, palatability, nutritive value, coloration, activity patterns, and motility all affect the degree to which an arthropod is located, captured, and eaten (Cooper and Whitmore 1990). Therefore, using data on bird diets to correct for the frequency distribution of arthropods captured with an appropriate technique is probably the easiest and most reliable means to assess food available to an insectivore. Comparison of diets among coexisting species can further provide insight on how selective or opportunistic species are in their food choice.

In this paper we present a simple mathematical approach to estimate arthropod availability that includes both the differential probability of each taxon being sampled with a trapping technique and being preyed upon by a bird. We provide three applications of our model, each one in a different Neotropical habitat where bird abundance and breeding activities were monitored simultaneously to arthropod abundance and bird diet during at least a complete annual cycle. Because it is impossible to correlate our index with "real" food availability, timing of breeding and seasonal abundance of birds are used as indicators of food level over time. First, we use sweep-net, pitfall-trap, and light-trap data collected in a thorn scrub habitat where avian breeding is highly seasonal to estimate the effect of different trapping methods on our estimates of food abundance. Second, we contrast values of our index based on sweep-net data collected in two mangrove sites where abundance of migrant birds show an opposite seasonal pattern. Third, we use sweep-net data collected in a tropical humid forest site to estimate food abundance for two foliage-dwelling resident bird species which differ slightly in their respective periods of breeding activities.

STUDY AREAS AND METHODS

Thorn scrub site.—Located in northeastern Venezuela (10°39'N, 63°41'W), this study site experiences a severe dry season with annual rainfall of 430 mm (Poulin et al. 1992). Data on bird diet and arthropod abundance were collected twice monthly from September 1986–August 1987. Some 1178 birds were captured over the 24 netting periods (12 mist nets operated for 4 h after sunrise) and forced to regurgitate using the method of Poulin et al. (1994a). Arthropods were sampled with sweep net, pitfall trap, and light trap. Sweep-net samples were collected in late afternoon by sweeping the first 2 m of vegetation with a standard net for 15 min. Pitfall traps consisted of two receptacles 1-m long sunk into the ground with openings level with the ground. These traps were filled with a water-soap solution and operated for 24 h. Light traps were installed 1 m above ground and were activated 2 h after sunset for a 30-min period.

Mangrove sites.—Located on the Pacific (Juan Díaz- 9°00'N, 79°04'W) and the Caribbean (Galeta- 9°20'N, 79°09'W) coasts in central Panama, these study sites experience an average annual rainfall of 1786 mm and 3244 mm, and a mean tidal amplitude of 395 cm and 24 cm, respectively (Lefebvre and Poulin 1997). Data on bird diet were collected monthly, alternating the two sites, from November 1993 through May 1995. Some 1076 birds including 441 Nearctic-Neotropical migrants were captured during netting sessions (12 mist nets operated for 8 h after sunrise) and forced to regurgitate using the method of Poulin and Lefebvre (1995). The two migrant communities were composed of the same species, with a predominance of Prothonotary Warblers (*Protonotaria citrea*) and Northern Waterthrushes (*Seiurus noveboracensis*) (Lefebvre and Poulin 1996). Sweep-net samples were collected twice monthly from September 1993–August 1994. The first 2 m of vegetation were swept for 15 min in late morning. In this paper, we used only the data collected during the period when migrants were present (September–April).

Humid forest site.—This study site, located in Soberanía National Park in Central Panama (9°10'N, 79°07'W), experiences a moderately severe dry season with an average annual rainfall of 2133 mm. Data on bird diet and arthropod abundance were collected twice monthly from September 1993–November 1994. Because of low capture rates in this habitat, regurgitation sessions were carried out with 36 mist nets operated for three consecutive days from sunrise until early afternoon. We selected two insectivorous species from the Formicariidae, the Slaty Antshrike (*Tham-*

nophilus punctatus) and the Checker-throated Antwren (*Myrmotherula fulviventris*), which forage mostly by gleaning the understorey vegetation (Stiles and Skutch 1989). Some 103 and 62 regurgitation samples were collected, respectively, for the two species. Arthropod samples were collected by sweeping the first 2 m of vegetation for a 20-min period in late morning.

Sampling of arthropods vs regurgitations.—Most regurgitations were collected in early morning when bird foraging activities are expected to be highest. Arthropods were sampled at the same sites and periods as the birds' diet using a constant sampling effort throughout the study to allow comparison of samples. To maximize capture efficiency, we avoided sweep netting in early morning when the vegetation was still wet and in midday when flying arthropods become active and leave the vegetation (Hutto 1981). Pitfall traps, which sample mostly ground-welling arthropods, were operated for a 24-h period because of their low capture rates relative to other trapping methods. Although no insectivore passerine forages at night, light traps were used to estimate relative abundance of nocturnal flying arthropods preyed upon during daytime while they were inactive. Only sweep net was used in the mangrove and humid forests, because most bird species considered were primarily foliage-gleaners and that sweep net samples a great diversity of invertebrate taxa (Poulin et al. 1992).

Sorting and identification of arthropods.—Arthropods were preserved in 70% ethanol and sorted using a dissecting scope. The same taxonomic level and size approximation were used for arthropods sampled in traps and those found in regurgitations. Because most items regurgitated were highly fragmented and digested, arthropods were generally identified to order, and their body length measured (or extrapolated) to the nearest 5 mm. Among the Hymenoptera, we made distinction between ants, flying ants, and wasps. Early stages of insects were clumped in eggs and larvae, without taxonomic distinction except for Lepidoptera larvae. Each arthropod taxonomic group was further divided into small (0–5 mm) or large (>5 mm).

Estimation of food availability.—Regardless of the trapping method used, capture efficiencies are likely to vary from one arthropod taxon to another (Wolda 1990). However, these differences are generally constant, and variation in numbers of arthropods captured over time should provide a good estimate of the seasonal abundance of any taxon (Cooper and Whitmore 1990). Therefore, to illustrate seasonal variation in arthropod abundance, each sample collected at a specific time should be expressed as the summation of the relative abundance (in relation to the whole sampling period) of each arthropod taxon captured with:

$$\text{Abundance index} = \sum_{i=1}^{n} \frac{x_{ij}}{y_i} \qquad (1)$$

where x_{ij} is the number of arthropods from group i (taxon and size) sampled with a trapping method during the date j, and y_i is the number of arthropods from group i collected during the whole sampling period. Because arthropod groups that are rarely sampled have a major impact on the trend observed, we excluded those represented by five items or fewer. This index reaches a high value when several arthropod groups are simultaneously abundant.

Bird predation rates on arthropods vary from one taxon to another (Sherry 1984, Poulin et al. 1994b, Poulin and Lefebvre 1996). Therefore, food abundance can be weighted by multiplying each arthropod group by its relative importance in the birds' diet with:

$$\text{Weighed abundance index} = \sum_{i=1}^{n} p_i \frac{x_{ij}}{y_i} \qquad (2)$$

where p_i is the proportion of arthropods from group i in the birds' diet. This index reaches a high value when several arthropod groups extensively taken by the birds are abundant.

Statistical analyses.—Monthly values of the number of arthropods captured and both abundance indices were transformed into a similarity matrix based on Euclidean distance and submitted to an agglomerative chronological cluster analysis (Legendre et al. 1984). This clustering analysis identifies discontinuities along a temporal axis and was used to interpret seasonal trends. All groups were obtained at a similarity level of 20% and their significance was tested using ANOVA followed by a Duncan multiple comparisons procedure (when more than two groups), *t*-test (when only two groups) or Mann-Whitney U-test (when unequal variances among groups). Any two consecutive groups were significantly different from each other at $P < 0.05$, except when otherwise stated.

RESULTS

Thorn Scrub Site

A total of 2286, 25, 914, and 1502 arthropods distributed in 19, 15, and 24 groups was sampled with pitfall trap, light trap, and sweep net, respectively (Table 1). Each trapping method sampled a different fraction of the arthropod community and frequency of each taxon varied accordingly. However, some taxa found on a wide variety of substrates, such as beetles, ants, flies, and spiders, were commonly sampled with two of the three trapping techniques (Table 1). Some 3613 arthropods distributed in 29 groups were identified from the birds' regurgitation samples (Table 1). Ants, beetles, and insect larvae were the most common taxa in the birds' diet.

To allow comparisons of arthropod abundance among traps, which differed in their respective capture rates, monthly numbers of arthropods were divided by the total number of captures × 100.

Pitfall trap.—Numbers of arthropods captured with pitfall traps were low from October through January and high from February through September, with a peak in May (Fig. 1a). The index of abundance showed

TABLE 1. Proportion of each arthropod group sampled with the three trapping methods and found in the birds' regurgitations for the thorn scrub habitat.

Taxa	Size[a]	Pitfall trap $n = 2286$	Light trap $n = 25{,}914$	Sweep net $n = 1502$	Bird diet $n = 3613$
Gastropoda (snails)[b]	small	1.44		1.40	0.06
Gastropoda (snails)[b]	large	0.66			
Acari (mites, ticks)	small	1.05		1.53	0.03
Scorpionida	large	0.22			0.03
Pseudoscorpionida	small	0.70			
Araneida (spiders)	small	6.17		14.98	1.74
Araneida (spiders)	large	2.71		3.79	0.11
Isopoda	small	0.48			
Isopoda	large	0.17			
Diplopoda (millipedes)	large	0.48			0.11
Chilopoda (centipedes)	large	0.31			0.11
Ephemeroptera	large				0.03
Orthoptera	small	1.53		4.33	0.03
Orthoptera	large	2.97	0.05	2.46	0.06
Isoptera (termites)	small		0.72		
Psocoptera (psocids)	small			1.13	0.03
Heteroptera (true bugs)	small		0.51	1.07	0.64
Heteroptera (true bugs)	large		0.19	0.73	0.91
Homoptera (plant bugs)	small		1.98	4.39	1.58
Homoptera (plant bugs)	large		0.49	0.93	0.22
Neuroptera	large		0.10		
Coleoptera (beetles)	small	6.34	4.64	16.58	27.18
Coleoptera (beetles)	large	2.97	11.37	2.13	3.24
Lepidoptera (adults)	small		8.43	1.13	
Lepidoptera (adults)	large		9.12	0.67	0.14
Diptera (flies)	small		10.34	16.78	3.54
Diptera (flies)	large		0.20	0.13	0.28
Hymenoptera (ants)	small	42.48		14.31	28.01
Hymenoptera (ants)	large	24.54		4.13	8.39
Hymenoptera (alate ants)	large			0.13	5.26
Hymenoptera (wasps)	small		46.50	1.93	3.21
Hymenoptera (wasps)	large		5.37	1.33	0.83
Insect eggs	small				0.66
Insect eggs	large				0.19
Insect larvae[c]	small	2.19		2.46	5.12
Insect larvae[c]	large	2.58		1.53	8.28

[a] Small: ≤5 mm; large: >5 mm.

[b] Mollusca.

[c] Mostly Lepidoptera larvae.

no seasonal pattern, however, suggesting that the previous peak was related to only a few arthropod groups extensively sampled with this trap (Fig. 1b). This lack of seasonality is due to the fact that the different arthropod groups peaked at different times of the year. With the weighted abundance index, values are significantly higher in May–August than in September–April (Fig. 1c). The reappearance of the peak in May indicates that those arthropod groups more likely to be sampled with this trap (ants) were also the ones most frequently taken by the birds.

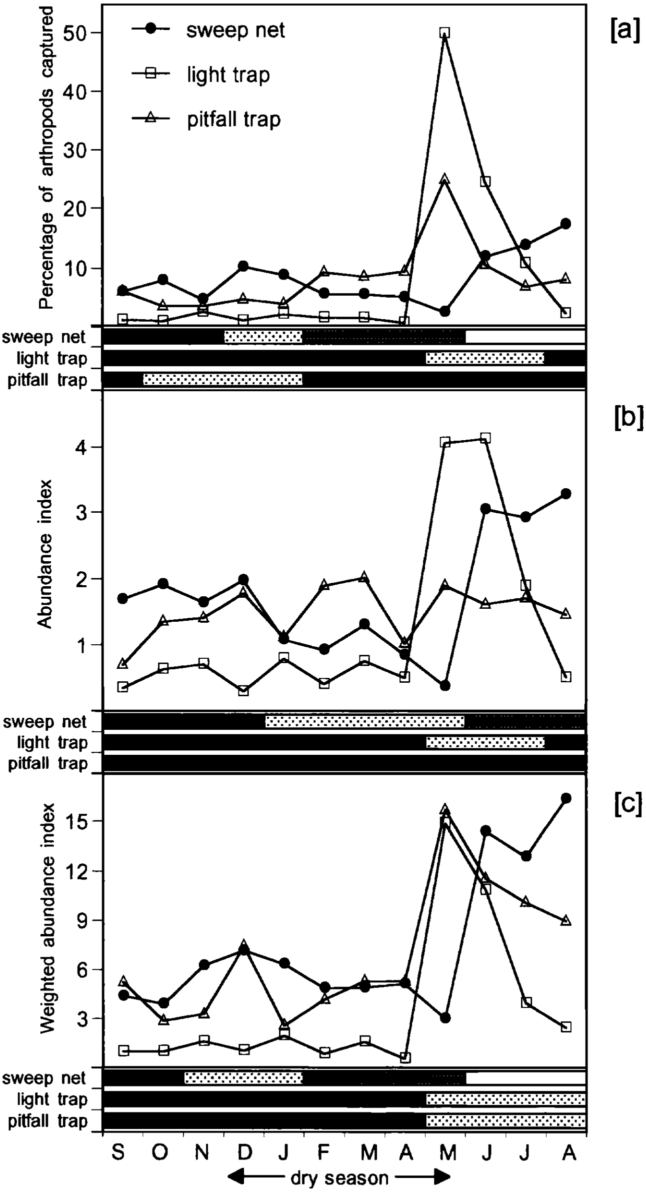

FIGURE 1. Monthly variation in (a) percentage of arthropods captured, (b) index of arthropod abundance, and (c) index of weighted arthropod abundance for each trapping technique at the thorn scrub site. Horizontal bars represent periods of seasonal homogeneity as identified by the chronological clustering analysis.

Light trap.—Numbers of arthropods captured with light trap were low from August through April and high from May through July (Fig. 1a). That seasonal pattern is unchanged with the abundance index, but the single peak previously observed in May is extended to May–June (Fig. 1b). With the weighted abundance index, the period of high abundance is prolonged to May–August (Fig. 1c).

Sweep-net.—Variation in numbers of arthropods captured with sweep net showed two periods of low abundance, September–November and February–May, and two periods of high abundance, December–January and June–August (Fig. 1a). With the abundance index, a minor peak is observed in September–December, followed by a low in January–May, and a major peak in June–August (Fig. 1b). The weighted abundance index showed a similar pattern to the one observed with numbers of sweep-netted arthropods, except that the peak in June–August is of higher amplitude (Fig. 1c). This indicates that the numerous arthropod groups abundant in the early wet season are especially important to the birds as a food source.

Bird breeding activities vs. food availability.—Although the different trapping methods sample arthropods from different substrates, the index of weighted arthropod abundance reaches maximal values in the first part of the wet season with all trapping techniques. The one month delay with sweep-net data (June–August) compared to light-trap and pitfall-trap data (May–August) is probably related to the fact that foliage-dwelling arthropods are more directly affected by vegetative growth (Janzen 1980), which was highest in June (Guevara de Lampe 1986), than by the onset of rainfall in May. Our index enhances the importance of those arthropods that are numerous in the first part of the wet season, which are certainly the most critical ones to the birds which breeding cycles were restricted to the June–August period (Poulin et al. 1992).

Mangrove Sites

A total of 4815 and 3607 arthropods distributed in 35 and 32 groups was sampled with sweep net at Juan Díaz and Galeta, respectively (Table 2). Flies, plant bugs, and spiders were the most commonly sampled taxa at both sites. Some 2189 and 1500 arthropod items distributed in 31 and 28 groups were identified in the regurgitations collected from migrant birds at Juan Díaz and Galeta, respectively (Table 2). Beetles and ants were important in the migrants' diet at both sites, whereas snails were commonly taken at Juan Díaz only, and insect larvae at Galeta only.

Juan Díaz.—Numbers of arthropod sampled at Juan Díaz were low in September–October, high in November–January, and low in February–April (Fig. 2a). With the abundance index, the November–January peak is delayed to the early dry season (January), indicating that few arthropod groups were responsible for the increase in the late wet season (Fig. 2b). With the weighted abundance index, values are constant for the first four months of sampling, followed by a peak in January and a sharp decrease in February–April (Fig. 2c).

TABLE 2. Proportion of each arthropod group sampled with sweep net and found in the birds' regurgitations at the two mangrove sites.

		Sweep net		Bird diet	
Taxa	Size[a]	Juan Díaz $n = 4815$	Galeta $n = 3607$	Juan Díaz $n = 2189$	Galeta $n = 1500$
Gastropoda (snails)[b]	small	3.90	0.36	49.75	4.33
Gastropoda (snails)[b]	large	0.08			0.07
Acari (mites, ticks)	small			0.05	
Pseudoscorpionida	small	0.12	0.06	0.23	0.67
Araneida (spiders)	small	13.69	18.77	1.87	8.47
Araneida (spiders)	large	0.62	1.52	0.41	3.53
Isopoda	small	0.87	0.08	0.59	0.07
Amphipoda	small	0.04			
Amphipoda	large	0.12			
Decapoda (crabs, shrimps)	small			0.09	0.33
Decapoda (crabs, shrimps)	large			0.18	0.20
Chilopoda (centipedes)	large		0.08	0.05	
Thysanura (bristletails)	large			0.05	
Odonata	large	0.06	0.30		0.47
Orthoptera	small	7.00	1.91	0.18	0.33
Orthoptera	large	2.39	1.14	0.32	0.93
Dermaptera (earwigs)	large			0.05	
Isoptera (termites)	small	0.06	0.33		
Psocoptera (psocids)	small	0.48	0.91		
Thysanoptera (thrips)	small	0.06			
Thysanoptera (thrips)	large	0.02			
Heteroptera (true bugs)	small	1.72	0.19	0.41	1.00
Heteroptera (true bugs)	large	0.77	0.39	0.05	0.53
Homoptera (plant bugs)	small	20.93	12.28	4.02	0.27
Homoptera (plant bugs)	large	2.64	1.83	0.18	0.13
Neuroptera	large	0.10	0.08		
Coleoptera (beetles)	small	4.92	3.44	17.59	23.40
Coleoptera (beetles)	large	1.54	1.28	0.41	0.87
Lepidoptera (adults)	small	0.10	0.58	0.05	
Lepidoptera (caterpillars)	small	0.04	0.22		
Lepidoptera (caterpillars)	large	0.12	0.53		
Diptera (flies)	small	23.72	25.20	0.69	0.80
Diptera (flies)	large	0.35	1.44	0.09	0.07
Hymenoptera (ants)	small	6.17	17.63	14.66	19.60
Hymenoptera (ants)	large	0.89	1.77	0.78	1.27
Hymenoptera (alate ants)	small	0.04	0.17	0.05	
Hymenoptera (wasps)	small	3.61	2.77	3.47	5.80
Hymenoptera (wasps)	large	0.35	1.16	0.09	1.20
Insect eggs	small	0.93	1.41	2.70	4.93
Insect eggs	large		0.03		
Insect larvae	small	1.35	1.33	0.59	2.80
Insect larvae	large	0.15	0.78	0.32	17.53
Fishes[c]	large				0.33
Frogs[c]	large			0.05	
Lizards[c]	large				0.07

[a] Small; ≤5 mm, large: >5 mm.

[b] Mollusca.

[c] Vertebrate-prey.

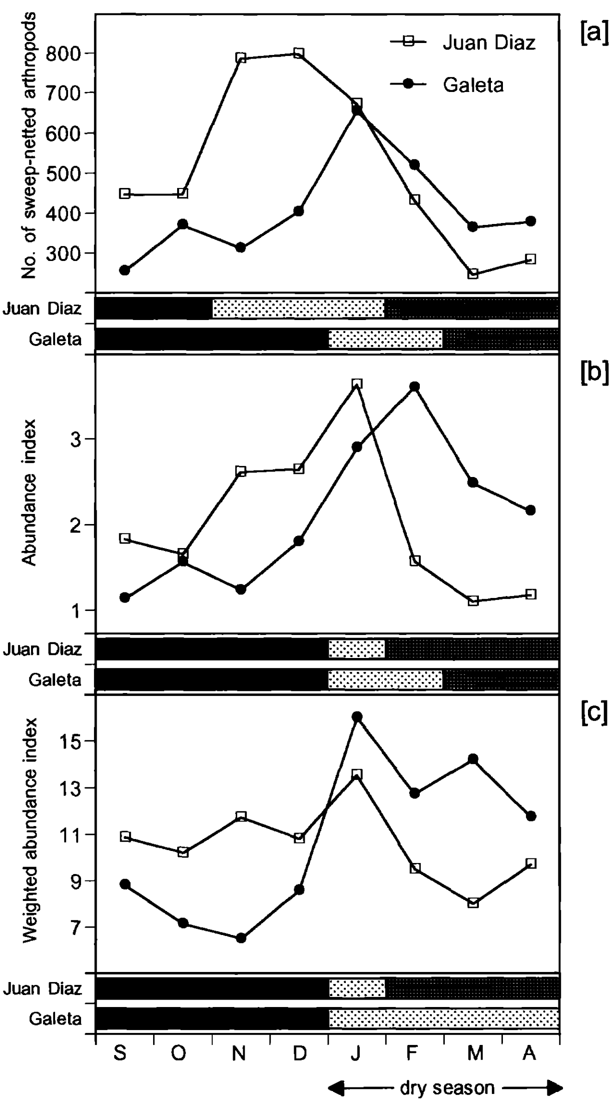

FIGURE 2. Monthly variation in (a) numbers of sweep-netted arthropods, (b) index of arthropod abundance, and (c) index of weighted arthropod abundance at each mangrove site. Horizontal bars represent periods of seasonal homogeneity as identified by the chronological clustering analysis.

Galeta.—Numbers of arthropods sampled at Galeta were low in the late wet season (September–December), reached a peak in the early dry season (January–February), and decreased afterwards (Fig. 2a). The abundance index showed a similar seasonal pattern, suggesting that the low abundance observed in the wet season is characteristic of several arthropod groups (Fig. 2b). The peak previously observed in the dry season, however, is delayed by a month and subsequent values are higher than before, indicating that several groups of arthropods, which are not predominant in sweep-net samples, are abundant during the dry season. The weighted abundance index is low during the wet season and high during the dry season (Fig. 2c). The higher values observed during the dry season compared to the previous data set indicate that birds feed more extensively on those arthropod groups that are especially abundant during the drought period.

Migrant abundance vs. food availability.—Originally, the two sites differed only during the late wet season, with arthropod numbers increasing two months earlier in Juan Díaz than in Galeta. With the index of weighted abundance, arthropods appeared to be more abundant in Juan Díaz than in Galeta during the wet season, and more abundant in Galeta than in Juan Díaz during the dry season. While the sweep-net data failed to explain why numbers of migrants were decreasing in Juan Díaz and increasing in Galeta in December–January, concurrent changes in our index and in migrant numbers were significantly correlated between the two sites (Lefebvre and Poulin 1996).

Humid Forest Site

A total of 8071 arthropods distributed in 43 groups was sampled with sweep net (Table 3). Ants, spiders, flies, and plant bugs were the most commonly sampled taxa. Some 516 and 426 arthropods (22 and 19 groups) were identified from the regurgitations of the Slaty Antshrike and the Checker-throated Antwren, respectively (Table 3). The antshrike fed mostly on insect eggs, and large true bugs and orthopterans, whereas the antwren showed a preference for wasps and large spiders.

Sweep-netted arthropods showed a minimal abundance during the late wet season (October–December), remained stable throughout the dry season (January–April), reached a peak in the early wet season (May–June), and decreased afterwards (Fig. 3a).

This seasonal pattern remains unchanged with the abundance index (Fig. 3b). However, arthropod abundance is lower during the dry season, suggesting that only a few taxa, extensively sampled with sweep net, are abundant at that period.

For the Slaty Antshrike, the weighted abundance index is low in October–November of both years, moderate in December–March, and high in April–September (Fig. 3c). No significant differences were found between the latter two periods (Duncan multiple comparisons, $P > 0.05$), suggesting that the lean season is restricted to October–November for that species. For the Checker-throated Antwren, the weighted abundance index peaks in April–September (Fig. 3c), whereas the periods of October 1995–March and October 1996–November were not significantly different from each other. Accordingly, each species differed in its respective period of high food availability, which appeared to be much longer than

TABLE 3. Proportion of each arthropod group sampled with sweep-net and found in the regurgitations of the Slaty Antshrike and the Checker-throated Antwren at the humid forest site.

Taxa	Size[a]	Sweep net $n = 8071$	Antshrike $n = 516$	Antwren $n = 426$
Gastropoda (snails)[b]	small	1.49	0.78	
Gastropoda (snails)[b]	large	0.02		
Acari (mites, ticks)	small	3.20	0.19	
Scorpionida	large			0.47
Pseudoscorpionida	small	0.04		
Araneida (spiders)	small	15.10	1.16	7.51
Araneida (spiders)	large	2.13	6.40	15.26
Isopoda	small	2.80		
Isopoda	large	0.06		
Diplopoda (millipedes)	large	0.24	0.39	
Chilopoda (centipedes)	large	0.01		
Thysanura (bristletails)	small	0.04		
Thysanura (bristletails)	large	0.15		
Odonata	large	0.02	0.39	
Orthoptera	small	1.29		0.23
Orthoptera	large	1.77	10.47	10.56
Isoptera (termites)	small	0.30		
Psocoptera (psocids)	small	0.77		
Thysanoptera (thrips)	small	0.10		
Thysanoptera (thrips)	large	0.01		
Heteroptera (true bugs)	small	1.14	0.19	0.70
Heteroptera (true bugs)	large	1.50	15.31	0.94
Homoptera (plant bugs)	small	10.38	0.58	
Homoptera (plant bugs)	large	5.04	2.13	0.47
Neuroptera	large	0.30		
Coleoptera (beetles)	small	6.90	7.95	9.15
Coleoptera (beetles)	large	2.34	7.56	3.05
Lepidoptera (adults)	small	0.33		
Lepidoptera (adults)	large	0.82		
Lepidoptera (caterpillars)	small	0.64		
Lepidoptera (caterpillars)	large	1.16	7.36	0.47
Diptera (flies)	small	12.25		
Diptera (flies)	large	1.77		
Hymenoptera (ants)	small	16.88	1.16	0.70
Hymenoptera (ants)	large	1.78	0.97	1.88
Hymenoptera (alate ants)	small	0.04		
Hymenoptera (alate ants)	large	0.07	0.97	0.23
Hymenoptera (wasps)	small	3.49		34.04
Hymenoptera (wasps)	large	0.64	0.19	
Insect eggs	small	1.14	18.02	7.98
Insect eggs	large		13.18	4.69
Insect larvae	small	1.20		
Insect larvae	large	0.41	2.71	0.23
Frogs[c]	large	0.11		1.41
Lizards[c]	large	0.10	1.94	

[a] Small: ≤5 mm; large: >5 mm.

[b] Mollusca.

[c] Vertebrate-prey.

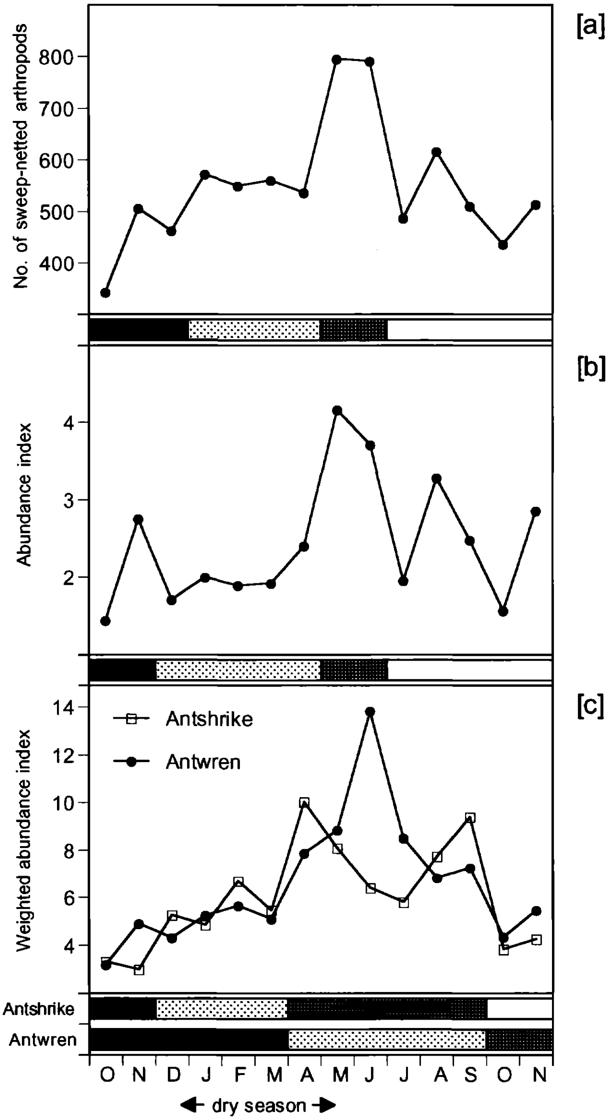

FIGURE 3. Monthly variation in (a) numbers of sweep-netted arthropods, (b) index of arthropod abundance, and (c) index of weighted arthropod abundance for the Slaty Antshrike and the Checker-throated Antwren at the humid forest site. Horizontal bars represent periods of seasonal homogeneity as identified by the chronological clustering analysis.

suggested by the sweep-net data. The new increase observed in April indicates that the few arthropod groups abundant at this period are commonly taken by both species.

Bird breeding activity vs. food availability.—The Slaty Antshrike and the Checker-throated Antwren are both insectivores that glean the understory vegetation (Stiles and Skutch 1989), and frequently forage together in mixed-species flocks (Ridgely and Gwynne 1989). Examination of active brood patch (B. Poulin, unpubl. data) suggests that the Slaty Antshrike has a breeding season extending from April through September, whereas data from the Checker-throated Antwren suggest a more restricted breeding period with highest activity in June. Throughout several habitats of Costa Rica, the Slaty Antshrike is reported to breed from January through September and the Checker-throated Antwren from March to August (Stiles and Skutch 1989), which confirm the trend observed at our study site and coincide with the respective periods of higher food availability for these two species.

DISCUSSION

Information on food availability and exploitation is of increasing importance as we progress in our understanding of bird community ecology and organization. Different approaches have been suggested to estimate arthropod availability. Wolda (1990) proposed to monitor absolute abundance of insects identified to the morpho-species in the birds' foraging microhabitat. Hutto (1990) used quantitative measures of foraging behavior, such as the bird's temporal and spatial attack rate, its mean stop-to-stop movement length, and the proportion of its daily time foraging, as indirect measurements of food level. Both methods, however, require extensive field work and become too laborious in studies involving several bird species, habitats, or sampling periods. Our index of weighted arthropod abundance is more readily applicable to community or long-term studies and offers flexibility in its application. The only requisite is that arthropods be sampled with an appropriate trapping method and that some information on diet of the bird species under study be available. Although this latter information can be drawn from the literature, collecting data on diet and arthropod abundance simultaneously at the same site is preferable. Taxonomic level for identifying arthropods is at the user's discretion, but if a lower taxonomic level is used, arthropod sampling effort has to be proportionally higher so that each taxon is still represented in sufficient numbers to accurately estimate their temporal variations.

Selection of a trapping technique.—Data from the thorn scrub showed that seasonal variations in the weighted abundance index differ little from one trapping method to another. This suggests that within a taxonomic order, seasonal abundance of arthropods is similar regardless of the dwelling substrates used. However, these results are from an extremely dry seasonal habitat, and more differences among arthropod dwelling-groups are to be expected in less seasonal environments (Janzen and Schoener

1968). Therefore, a trapping technique should be selected in order to best sample the birds' foraging microhabitat. An extensive review of trapping methods and their limitations are provided in Cooper and Whitmore (1990) and Wolda (1990). On the other hand, many bird species use various foraging sites and maneuvers, and if different kinds of arthropods are preyed upon, an adequate sampling of all arthropod groups might require the use of several techniques. A problem with methods providing indices of relative abundance is that their units are not comparable and their results cannot be combined (Cooper and Whitmore 1990). Because our index of arthropod abundance is based on the summation of the percent abundance (relative to the whole sampling period) of each arthropod taxon in a sample, abundance of prey taxa collected with different trapping methods or even different food types (e.g., arthropods, seeds, fruits) can easily be combined. A second criteria to consider in selection of a trapping technique is the diversity of arthropods sampled. If only one sampling method is to be used, it should be selected in order to maximise the number of potential prey taxa collected.

Determination of arthropod groups.—A lower taxonomic level than the one we used to identify arthropods would certainly provide more accurate results, especially when there is considerable variability in prey preference within a taxonomic order. These variations, however, are not necessarily related to taxonomical affinities, and often reflect differences in prey foraging substrate, colonial habits, motility, and nutritive value. For instance, insect larval and pupal forms, as well as alates of ants and termites have a much higher fat content than sedentary adults (Bell 1990, Redford and Dorea 1984), and several bird species feed opportunistically on them (Dial and Vaughan 1987, Holmes 1988, Poulin et al. 1994b). Size is also an important factor in prey selection by insectivorous birds (Hespenheide 1971, Hespenheide 1975, Rotenberry 1980, Poulin and Lefebvre 1996). Accordingly, segregation of arthropod groups should be based on size classes and developmental stages, in addition to taxonomy and ecological affinity.

Diet estimation.—The use of diet data to weight arthropod abundance had a strong impact on our estimates of food level in all three applications. These results suggest that sampling of arthropods in the bird's foraging microhabitat might not be sufficient to assess food available to a particular species. Even the Slaty Antshrike and the Checker-throated Antwren, which frequently forage together, differed importantly in their prey selection. It is therefore necessary to accurately determine the diet of the bird species under study. While the sacrifice of a large number of birds is neither practical nor ethical to many scientists, several non-destructive methods have been developed to collect diet samples (Rosenberg and Cooper 1990). Differential rate of digestibility among prey is often referred to as a major bias in diet estimation from gut contents (Custer and Pitelka 1975, Major 1990, Rosenberg and Cooper 1990). If soft-bodied arthropods were consistently underestimated in diet samples, our index would be biased towards the hard-bodied prey. However, most soft-bodied prey contain hard body parts (e.g., mandibles of orthopterans, termites, and caterpillars, chelicerae and legs of spiders, etc.), which are likely to persist as long as hard-bodied arthropod in the digestive tract (Chapman and Rosenberg 1991, Major 1990). Therefore, knowledge of the particular fragments which are most characteristic of any partially digested arthropod allows to substantially reduce biases associated with differential digestion rates of prey.

Regardless of the habitat type, the trapping technique used, and the bird species considered, our original data on arthropod numbers were importantly and unpredictably modified by our indices which correct for the differential probability of each taxon to be sampled with a trapping technique and preyed upon by birds. Breeding of resident species in thorn scrub and humid forest habitats, as well as abundance pattern of migrant species in mangrove forests, were better related to our weighted abundance index than to numbers of arthropods sampled with any trapping technique, suggesting that this method provides a reliable estimate of food availability.

ACKNOWLEDGMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC). We thank Richard Hutto for reviewing this manuscript. We are also grateful to the Smithsonian Tropical Research Institute for providing logistical support and to INRENARE for issuing the research permits to work in Soberanía National Park and the mangrove sites.

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Received 1 Jul. 1996; accepted 29 Oct. 1996.