



SHORT COMMUNICATIONS

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GIVING-UP DENSITIES AND HABITAT PREFERENCES OF EUROPEAN STARLINGS AND AMERICAN ROBINS

JOSEPH O. OYUGI^{1,2,3} AND JOEL S. BROWN¹

¹*Department of Biological Sciences, University of Illinois at Chicago, 845 West Taylor Street, Chicago, IL 60607*

²*National Museums of Kenya, Department of Ornithology, P.O. Box 40658, Nairobi, Kenya*

Abstract. In a field experiment, we measured the giving-up densities and activity of co-occurring American Robins (*Turdus migratorius*) and European Starlings (*Sturnus vulgaris*). Across six distances from cover, both species had lower giving-up densities near cover (safe) than away (risky). In terms of activity, both species were more active near than away from cover. Preference for cover was more pronounced for robins. Both species foraged more in the morning than in the afternoon. This pattern was more pronounced for starlings. Relative to the background environment (mowed grass), robins favored the food patches more than starlings. For starlings and robins, respectively, it took 72.6 m² and 382.3 m² of background environment to generate the same feeding activity in a 1-m² food patch filled with 210 mealworms (*Tenebrio molitor*). The greater degree of herbivory by starlings may explain the robins' greater affinity for food patches (invertebrates only) relative to the background environment (both invertebrates and plants).

Key words: *American Robin, European Starling, foraging theory, giving-up density, habitat preference, patch use, predation risk.*

Densidades de Abandono y Preferencias de Hábitat de *Turdus migratorius* y *Sturnus vulgaris*

Resumen. En un experimento de campo, medimos las densidades de abandono (i.e., "giving-up densities") y la actividad de individuos simpátricos de *Turdus migratorius* y *Sturnus vulgaris*. A través de seis distancias a sitios cubiertos, ambas especies presenta-

ron menores densidades de abandono cerca de sitios cubiertos (seguros) que lejos de éstos (riesgosos). En términos de actividad, ambas especies fueron más activas cerca que lejos de sitios cubiertos. La preferencia por sitios cubiertos fue más pronunciada en *T. migratorius*. Ambas especies forrajearon más en la mañana que en la tarde, siendo este patrón más pronunciado en *S. vulgaris*. Con relación al ambiente de fondo (pasto cortado), *T. migratorius* prefirió los parches de alimento más que *S. vulgaris*. Generar la misma actividad de alimentación en un parche de 1 m² con 210 gusanos de la harina (*Tenebrio molitor*), tomó 72.6 m² de ambiente de fondo para *T. migratorius* y 382.3 m² para *S. vulgaris*. El más alto grado de herbivoría de *S. vulgaris* podría explicar la mayor afinidad de *T. migratorius* hacia parches de alimento (sólo invertebrados) con relación al ambiente de fondo (invertebrados y plantas).

Optimal foraging theory (Stephens and Krebs 1986) can be used to investigate patch use by animals. Patch use can indicate habitat preference as influenced by predation risk and competition (Brown 1988). This indicator assumes that individuals make foraging decisions in ways that maximize their individual fitness. Assuming that a forager experiences no predation and has no alternative activities (such as territorial defense, mate finding, resting, or nest maintenance), the amount of time spent in a given patch is determined by the marginal value theorem (Charnov 1976). An individual should continue foraging in a depletable patch until its patch-specific harvest rate is equal to its average net harvest rate across all patches. Brown (1988) extended the marginal value theorem to include the effects of predation risk and alternative activities on patch use. A fitness-maximizing forager should cease harvesting a resource patch when the value of its harvest rate (H) no longer exceeds the sum of its energetic cost of foraging (C), predation risk (P), and the missed opportunity cost (MOC): $H = C + P + MOC$.

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³ Present address: Department of Biological Sciences, University of Illinois at Chicago, 845 West Taylor Street, Chicago, IL 60607. E-mail: joyugil@uic.edu

When harvest rates are related to the remaining abundance of food, the giving-up density (the amount of food remaining in an experimental food patch following use by one or several foragers) estimates the food density at which the animal has balanced costs and benefits. The forager reveals its preference and assessment of the environment when it stops feeding in the food patch. The temporal and spatial differences in giving-up density can give insights into species interactions, habitat preferences, patch use versus rejection, habitat quality, and species-specific foraging efficiencies (Brown 1988).

Giving-up densities have been used to assess habitat selection and community structure among desert rodents (Brown 1989, Brown et al. 1994, Kotler and Brown 1999). In seed-eating birds and small mammals, giving-up densities have been used to assess microhabitat preferences (Brown 1988, Hughes et al. 1994, Kohlmann and Risenhover 1996, Brown et al. 1997) and animals' assessment of habitat quality (Olsson et al. 1999, Morris and Davidson 2000). In this paper, we conducted foraging experiments on American Robins (*Turdus migratorius*) and European Starlings (*Sturnus vulgaris*) in depletable food patches to test for (1) the role of cover as safety in microhabitat preferences, (2) temporal habitat preferences, and (3) the habitat quality of mowed grass.

METHODS

We conducted experiments at the greenhouse compound of the University of Illinois at Chicago (41°50'N, 87°39'W). The habitat comprised clumps of shrubs and tall trees within open mowed lawn. We filled nursery trays (53 cm long × 27 cm wide × 6 cm deep) with 675 mL of vermiculate and 30 mealworms (*Tenebrio molitor*). We began with a 10-day training period during which birds learned about the trays and mealworms. During the training period, the trays were placed at random in the study area and observed at 2-hr intervals. We noted the number of robins and starlings and whether they were inside or outside the tray.

After the birds were trained, we established four transects, two in each of two habitats: shrub-covered lawn versus tree-canopy-covered lawn. Transects ran from the edge of cover (shrub or tree canopy) into open grass. Along each transect, we used string to mark the boundaries of six 2 × 10 m plots at 2-m intervals. These plots were adjacent to one another and ran parallel to either the shrub or tree-canopy habitats.

Within each plot, we placed one food tray. These trays offered a food patch in which the longer a forager spent the lower was the rate at which it found new worms (see Olsson et al. 2001 for similar food patches with starlings). Because the worms were buried in the substrate, the birds had to search for them. As the birds continued to exploit the food patch, their harvest rates eventually declined to a point at which they should seek another patch, or pursue other activities (Brown 1988, 1992). The number of mealworms left in the resource patch after the foragers have quit exploiting the patch (the giving-up density) provides a surrogate for their quitting harvest rate and estimates habitat-specific differences in foraging costs.

Food patches were provided for six days (23, 28, 29, 31 July and 5, 6 August 1999), between 08:30 and 14:30. At the end of each day, the remaining worms in the tray were counted to give the giving-up density. All of the plots and trays within the study plots were checked for birds at intervals of 1 hr. We grouped the hourly checks into AM and PM categories. The trays were numbered and the following notes were taken: time of day, species and number of individuals present, and whether each bird was inside the tray or on the ground within plots. We used activity in the trays (7 trays m⁻²) and in the surrounding 20 m² of mowed grass to determine an exchange rate between our food patches and the background environment for each species. Only robins and starlings were ever observed feeding from the trays.

Giving-up densities were square-root transformed for analyses to normalize the data and remove the tendency for the variance to increase with the mean. We used a partially hierarchical ANOVA to test for the effect of day, habitat (canopy vs. shrub), transect nested within habitat, and distance from cover (0, 2, 4, 6, 8, and 10 m from cover) on giving-up densities. We also used an ANOVA to analyze the hourly data on the numbers of birds active within the plots. The analysis tested for the effects of time of day (AM vs. PM), distance from cover (lumped into three distance categories of 0–4 m, 4–8 m and 8–12 m from cover), species (robin vs. starling), and choice of feeding location (food trays vs. adjacent lawn within plot). The numbers of birds for each combination of independent variables were calculated as the means from the six days of the experiment. These means were square root transformed for analyses. The means reported in the results have units of birds per hourly check per food patch (or per 2 × 10 m plot) and are reported ± SE. All statistical analyses were carried out using SYSTAT version 10.0 (SPSS Inc. 2000).

RESULTS

The giving-up densities tended to be lower for transects associated with shrub cover than for transects associated with canopy cover (although this effect was not significant, $P = 0.1$, probably due to too few transects; Table 1). Giving-up densities were lowest near cover (independent of cover type) and increased steadily with distance from cover (Fig. 1). There were no significant interaction effects among distance from cover, habitat (shrub vs. tree cover) and day.

There were two significant interaction effects on our hourly check data. While both species foraged more in the morning than afternoon, this effect was more pronounced for starlings than robins (Fig. 2A, Table 2). Relative to the background environment, robins used the experimental food patches (trays) far more than starlings (Fig. 2, Table 2). The main effect of species indicated more starling than robin activity ($n = 24$ patches each, 0.12 ± 0.03 vs. 0.06 ± 0.01 birds per check per patch), more activity in the morning than in the afternoon (0.14 ± 0.03 vs. 0.04 ± 0.01 ; Fig. 2A), and more activity near cover than away from cover (0–4 m: 0.15 ± 0.03 ; 4–8 m: 0.07 ± 0.02 ; 8–12 m: 0.04 ± 0.02 ; Fig. 2B).

TABLE 1. Effect of day, habitat, and distance from cover on giving-up densities of European Starlings and American Robins foraging on mealworms, as shown by partially hierarchical ANOVA.

Variable	df	Mean square	F
Day	5	8.4	13.3***
Habitat (shrub vs. canopy cover)	1	18.9	12.9+
Distance from cover	5	3.3	5.2***
Distance × Habitat	5	1.0	1.5
Habitat × Day	5	0.7	1.1
Distance × Day	25	0.4	0.7
Transect (nested within Habitat)	2	1.5	2.7*
Error	93	0.6	—

*** $P < 0.001$, * $P < 0.05$, + $P = 0.10$.

The food patches offered 210 mealworms m^{-2} , and of these the birds harvested about 131 mealworms m^{-2} day^{-1} . For starlings it took 72.6 m^2 of background environment to produce the same activity level as 1 m^2 of food patch (one food patch had 0.52 as much activity as one 20- m^2 area of grass). For robins, it took 382.3 m^2 of background environment to generate activity equal to 1 m^2 of food patch (1 food patch had 2.72 times as much activity as one 20 m^2 area of grass). Relative to background environment, robins found the food patches more valuable than did the starlings. We do not believe that this effect is due to in-

terference competition. If anything, the starlings appeared more able to displace robins from food patches than vice versa.

DISCUSSION

By using the giving-up densities as a measure of quitting harvest rate and foraging efficiencies (Brown 1988), robins and starlings revealed that microhabitats near cover provide safer feeding areas than those away from cover. Giving-up densities increased with distance from the edge of shrub or tree canopy. Although not statistically significant, there was a strong trend suggesting that shrub cover provides greater safety than tree canopies without understory vegetation. Giving-up densities were lower on the two transects associated with clumps of shrubs than the two associated with clumps of tall trees (oaks and maple). Total bird activity (in or out of the food patches) declined from morning to afternoon, with starlings showing a steeper decline than robins. Bird activity on lawns declined with distance from cover, with robins showing a steeper decline than starlings. In terms of use of the food patches relative to the background lawns, robins found the food patches roughly five times more valuable than starlings did. Both starlings and robins required large amounts of lawn to generate the same feeding activity as the food patches. During this study, predation threats to the birds, though rarely observed, included Peregrine Falcon (*Falco peregrinus*), feral cats (*Felis catus*), raccoons (*Procyon lotor*) and occasional human disturbances. Giving-up densities and activity data provided information about current habitat suitability.

The difference in the foraging behavior of robins and starlings may emerge, in part, from their social behavior. Starlings occurred in flocks ranging from 6 to over 50 individuals. As such they cover much larger feeding areas than solitary individuals or pairs of robins. The decline in starling feeding in the afternoons may reflect a shift in feeding location at scales larger than the greenhouse grounds. Furthermore, large flocks may promote a greater sense of safety through group vigilance. This may explain the starling's greater willingness to feed away from cover than the robins. The broader diet of the starling, which includes shoots, seeds, and seedlings in addition to vertebrates and in-

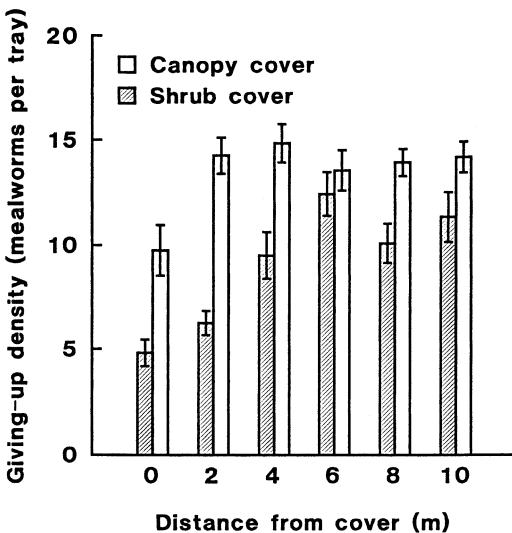


FIGURE 1. Mean \pm SE giving-up densities of American Robins and European Starlings foraging on mealworms increased with distance from cover. The type of cover also influenced patch use, with lower giving-up densities near dense shrubs than near tree-canopy cover. Giving-up density was measured as the number of mealworms remaining per tray at the end of each day of observation.

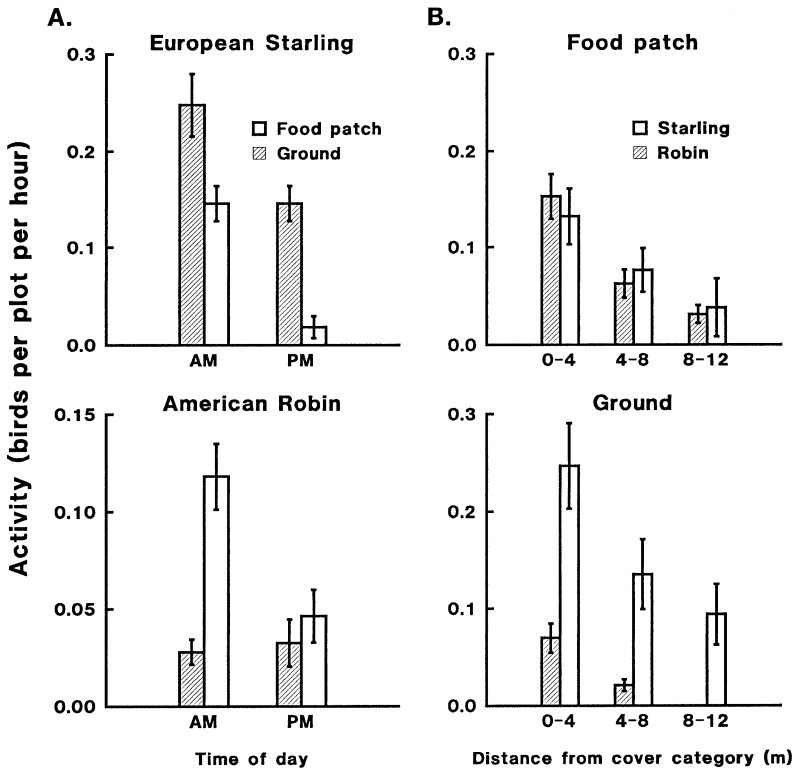


FIGURE 2. (A) European Starlings preferred to feed from mowed field (ground) over feeding from food patches containing mealworms; the reverse was true for American Robins. Both species sharply declined in activity from morning to afternoon in the food patches. Only starlings showed an activity decline from morning to afternoon on the ground. (B) Both bird species were more active near than away from cover. This effect of distance from cover was the same for food patches and background mowed field (ground). Starlings and robins were equally active in the food patches, whereas starling activity was substantially higher than robin activity on the ground.

TABLE 2. Results of ANOVA testing for the effects of species (American Robin vs. European Starling), time of day (morning vs. afternoon), distance from cover, and feeding location (ground vs. tray) on the number of birds counted during hourly checks of feeding trays and surrounding mowed lawn (ground).

Variable	df	Mean square	F-test
Species	1	7.5	7.2**
Time	1	26.5	25.5***
Distance from cover	2	15.1	14.5***
Feeding location	1	0.1	0.1
Species × Time	1	9.2	8.8**
Species × Distance	2	0.04	0.03
Species × Feeding location	1	11.3	10.8**
Time × Distance	2	0.2	0.2
Time × Feeding location	1	1.1	1.1
Distance × Feeding location	2	0.2	0.2
Error	33	1.0	—

*** $P < 0.001$, ** $P < 0.01$.

vertebrates (Feare 1984), may explain the two bird species' differing exchange rates for background lawn and food patch. The food patches offered only invertebrates while the lawn provided both invertebrates (favorable to starlings and robins) and plants (favorable to starlings).

Association of risk with closed versus open habitats, or with distance from cover, varies among bird species (Lima 1998). For example, Schneider (1984) provided *ad libitum* peanut hearts at wooden feeders to test whether the White-throated Sparrow (*Zonotrichia albicollis*) preferred feeding in sites close to cover. Under these conditions, it was not possible to measure quitting harvest rate. Regardless, out of 249 samples in which only one individual occupied the feeder, 199 times the bird occupied the square closest to cover, 44 times it was in the next most distant row, and 6 times it was farthest from cover. Grubb and Geenwald (1982) and Lima (1987) found that House Sparrows (*Passer domesticus*) favored food patches closer to the protection of cover. Similarly, Willow Tits (*Parus montanus*) preferred to feed in patches close to cover (Hogstad 1988). When food patches provided identical net energy returns, birds selected sites with greater protection from predators.

In contrast to these results, Lima et al. (1987) found that Dark-eyed Juncos (*Junco hyemalis*), Song Sparrow (*Melospiza melodia*) and Eastern Towhees (*Pipilo erythrophthalmus*) rarely fed as close to cover as possible. Caldwell (1986) found that various heron species (Ardeidae) avoided areas of high vegetation that might conceal attacking hawks (*Buteo* spp). These birds perceived cover as a source of attacks.

In studies of giving-up densities where birds were allowed to trade food and safety in depletable food patches, Kohlmann and Risenhoover (1996) found that Northern Bobwhites (*Colinus virginianus*) had lower giving-up densities in patches under a canopy of cover than those devoid of an umbrella of vegetation. Conversely, in the Negev desert, Crested Larks (*Galerida cristata*; Brown et al. 1997) had higher giving-up densities under shrub cover than in the open microhabitat. Differences among bird species in escape tactics, vigilance behavior, and sources of threat probably determine the risk ranking of microhabitat relative to cover (Lima 1998). Such effects probably contribute greatly to different bird species' use of space.

Our results indicate that birds were more active in shrubs and tree canopies in the morning, but moved to more open areas in the afternoon (Fig. 2A). This suggests that birds depleted food patches closer to cover in the morning before they began to use the distant and more dangerous ones in the afternoon. When the trays close to cover reached a low density, at which the food was buried in the substrate and difficult to obtain, the birds then switched to the next higher density food patch. At this time, the birds faced a dilemma in that higher energy intake rates could be achieved only when feeding farther from cover. Schneider (1984) reported that White-throated Sparrows fed as close to cover as possible, unless food was greatly depleted close to cover. Evidently, birds were maximizing energy intake by moving increasingly far from cover. However, this increased the predation risk, and

with greater predation risk may come an increase in energetic demands (e.g., increased vigilance).

Measures of feeding activities among the microhabitats showed that there were more European Starlings than American Robins in the study area. Despite their abundance, starlings were more likely to reject the opportunity to forage in a tray than were the robins. Thus the giving-up densities more likely indicate the foraging efficiencies of robins than of starlings. Furthermore, starlings were common only in the mornings, and rare in the afternoon. Robins were widespread throughout the day giving them more opportunities to visit the food patches.

In summary, giving-up densities revealed spatial and temporal habitat preferences of robins and starlings. Both species had lower giving-up densities near cover than away, and near shrub cover than tree canopy cover without understory shrubs, and presumably perceived the habitat as safer. The concepts and methods involved in this experiment are relatively accessible, inexpensive and straightforward. This method holds promise for the understanding of habitat preferences, habitat quality, and foraging decisions of easily observed animals such as diurnally foraging birds.

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THE RELATIVE IMPORTANCE OF ARTHROPODS AND FRUITS IN FORAGING BEHAVIOR OF OMNIVOROUS TANAGERS (THRAUPIDAE): THE COMPARISON OF THREE METHODS

KAZUYA NAOKI¹

*Department of Biological Sciences and Museum of Natural Science, 119 Foster Hall,
Louisiana State University, Baton Rouge, LA 70803*

Abstract. I quantified the foraging ecology of omnivorous *Tangara* tanagers with three methods commonly used in the study of foraging behavior. The relative importance of two food types, arthropods and fruits, varied largely depending on which method was used for data analyses. Arthropod foraging was more important than fruit foraging when calculated using the duration of foraging. In contrast, fruit foraging was more important when characterized by the food taken at initial observation and the total number of food items taken. This bias was probably caused by the difference in distribution and abundance of these two food types. Although numerous studies have used the frequency of initial observations to quantify bird for-

aging behavior, this method tends to underestimate the importance of highly rewarding but scarce food types in time budgets and tends to overestimate the same food type in the number of food items in birds' diets.

Key words: *duration, Ecuador, foraging behavior, frequency, omnivorous birds, Tangara.*

Importancia Relativa de Artrópodos y Frutos en el Comportamiento de Forrajeo de las Tangaras Omnívoras (Thraupidae): Comparación de Tres Métodos

Resumen. Cuantifiqué la ecología de forrajeo de las tangaras omnívoras del género *Tangara* con tres métodos comúnmente utilizados en el estudio del comportamiento de forrajeo. La importancia relativa de dos tipos de alimento, artrópodos y frutos, varió significativamente dependiendo de qué método se utilizó para analizar los datos. El forrajeo de artrópodos fue

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¹ E-mail: knaoki@lsu.edu

más importante que el forrajeo de frutos cuando calculado utilizando duración del forrajeo. En contraste, el forrajeo de frutos fue más importante cuando caracterizado por el tipo de alimento consumido en observación inicial y el número total de alimentos consumidos. Este sesgo fue causado probablemente por la diferencia en distribución y abundancia de estos dos tipos de alimento. Muchos estudios han utilizado la frecuencia de observaciones iniciales para cuantificar el comportamiento de forrajeo de las aves. Sin embargo, este método tiende a subestimar la importancia de aquellos alimentos, de alta recompensa pero escasos, en términos del tiempo invertido en su búsqueda. Al mismo tiempo, este método tiende a sobrestimar estos mismos tipos de alimento cuando se considera el número de artículos alimenticios en la dieta de las aves.

Studies of foraging behavior and food resources constitute part of an overall effort to comprehend diverse aspects of avian biology such as population dynamics, community structure, ecomorphology, physiology, and predator-prey relationships (Morrison, Ralph, and Verner 1990). Behavioral observation generally yields four main types of measures (Martin and Bateson 1993) of which frequency and duration are most commonly used to study foraging behavior of birds (Morrison, Ralph, et al. 1990). These two measures, however, represent different aspects of foraging behavior, and the observers' preference for one measure over the other may hide or even distort a true biological pattern. In addition, various sampling methods can be used to quantify both frequency and duration, and different methods can affect the estimates of mean and standard errors of foraging parameters (Morrison 1984, Hejl et al. 1990). Evidently, no study has compared the data sets taken using different measures to understand the potential bias associated with each measure.

Here I present quantitative analyses of two measures of foraging behavior using three different sampling methods. These three sampling methods were "food type taken at initial observation" and "total number of food items taken" for quantifying foraging frequency, and "duration" for foraging duration. All the data were taken from the same set of foraging observations gathered from four *Tangara* species in Ecuador during 1999. The genus *Tangara* includes 50 species of small canopy-dwelling tanagers endemic to the Neotropics. Their diverse diet consists of fruits, arthropods, nectar, flower buds, and Müllerian bodies (Isler and Isler 1999, Naoki and Toapanta 2001) although fruits and arthropods account for over 95% of their diet (Snow and Snow 1971, Rodrigues 1995, Isler and Isler 1999). I here compare these three methods and discuss how they can lead to different conclusions concerning the relative importance of fruits and arthropods in the biology of these omnivorous tanagers.

METHODS

From October to December 1999, I quantified foraging behavior of *Tangara* tanagers in the vicinity of Mindo, Pichincha province, Ecuador (0°02'S, 78°46'W, 1300–1600 m). The area corresponds to the transitional zone from foothill forest to subtropical montane forest (Ridgely and Greenfield 2001); average annual rainfall

in the area is ca. 2700 mm, and annual mean temperature is 20.3°C ($n = 13$ years, Instituto Nacional de Meteorología e Hidrología, unpubl. data). The observations were conducted along a 10-km trail southeast of the village of Mindo and a 4-km trail in a private farm, 1 km west of Mindo. The vegetation along the trail was a mosaic of young and old secondary forest with some large trees over 25 m high.

Birds were opportunistically encountered as I slowly walked along the trail. At every encounter, I followed one individual for as long as possible and recorded the following data to microcassettes: time spent foraging for arthropods, time spent foraging for fruit, the number of arthropods attacked, the number of fruits attacked, and food type taken at initial observation. Hereafter, each encounter is referred to as a foraging bout. I used two stopwatches to quantify the time spent foraging for arthropods and for fruits. Foraging behavior was defined as any behavior used for obtaining food, including searching, attacking, and handling maneuvers (Remsen and Robinson 1990). Fruit searching was usually short in duration because *Tangara* tanagers flew directly to fruits and rapidly moved from one fruit to another. When the birds hopped and stared at substrates with no fruits, such as moss, branch undersides, or leaf surfaces, the searching activity was considered toward arthropods. Each *Tangara* species searched a distinct substrate for arthropods by using a unique searching maneuver (KN, unpubl. data). I carefully excluded the time spent flying between trees and moving between branches without typical searching maneuvers to avoid inflating arthropod foraging time. Attacks, usually brief, consisted of a quick capture attempt for arthropods or fruits. Handling included mashing of fruit or large arthropods. Small fruits, such as genera *Miconia* and *Trema*, and most arthropods were swallowed without a long handling time. The number of arthropods or fruits attacked represented the total number of individual arthropods or fruits to which capture attempts were made. *Tangara* species often bit or poked one food item more than once to finish ingesting a whole or part of a large fruit or arthropod. These multiple bites toward one food item were considered as one attack. Food type taken at initial observation was the initial capture attempt made in each foraging bout and was noted as arthropod or fruit. The initial observation is the most commonly used method to study foraging behavior of birds (e.g., Morrison, Ralph, et al. 1990, Sillett 1994, Rodrigues 1995). I calculated foraging efficiency by dividing the number of arthropods or fruits attacked by the time spent arthropod and fruit foraging respectively (the number of arthropods or fruits eaten per minute). Müllerian bodies and flower buds were included in the fruit category because they resembled fruits more than arthropods in being conspicuous and stationary.

STATISTICAL ANALYSES

Because most observations were short and showed large variation in duration (60.2 ± 61.2 sec; range 1–450, $n = 267$), I pooled all foraging bouts and presented the results as the proportion of arthropod foraging to total foraging activity (Table 1). As a result, the data presented here were cumulative and did not

TABLE 1. Relative importance of arthropods and fruits in foraging behavior of four *Tangara* species in Mindo, Ecuador. Bias-corrected mean and 95% confidence limits (in parentheses) were calculated using 1000 bootstrap replicates.

Species	Percentage of arthropod foraging per total foraging activity			
	Duration	Frequency		No. of foraging bouts
		Initial observation	No. of food items	
<i>Tangara arthus</i>	57% (48–67)	31% (21–40)	20% (12–27)	138
<i>T. parzudakii</i>	58% (41–74)	45% (30–61)	23% (9–38)	51
<i>T. labradorides</i>	70% (56–84)	50% (32–68)	35% (17–52)	41
<i>T. rufigula</i>	64% (49–78)	58% (39–77)	46% (21–70)	37
Total	59% (53–66)	41% (34–48)	25% (17–33)	267

allow calculation of confidence limits by themselves. To overcome this problem, I bootstrapped the original sample data 1000 times to calculate confidence limits and to correct the bias of the estimators (Manly 1997). To compare two percentages or two foraging efficiencies, I applied the modified version of bootstrap tests of significance described in Manly (1997, chapter 3.10). This test consists of (1) generation of the pseudodistributions by bootstrapping the original sample data, (2) formation of a third distribution by comparing the two pseudodistributions, and (3) test of null hypotheses and calculation of P -values using the third distribution. For example, to test the difference between two percentages $\alpha\%$ and $\beta\%$ ($\alpha > \beta$), I bootstrapped the original sample data, A and B, 1000 times to obtain 1000 A_i and B_i , each of which supposedly represents a pseudodistribution of α and β . Then I calculated the difference between A and B for each bootstrap result: $D_i = A_i - B_i$. P -value was calculated as the proportion of negative D_i to total D_i . I conducted all the statistical analyses including the bootstrap procedure using SYSTAT 8.03 (SPSS 1998). All results are reported as mean \pm SD unless otherwise indicated.

RESULTS

During the study, *Tangara* tanagers were observed in mixed-species flocks in 68% of the total encounters ($n = 244$). The relative importance of arthropod foraging varied largely depending on which of the three measures was used to analyze the data (Table 1). When foraging duration was used, arthropod foraging was more important than fruit foraging: four *Tangara* species spent over half of their foraging time foraging for arthropods (59%; Table 1). When food type at initial observation or the total number of food items taken was used, fruits were more important than arthropods: fewer than half of the initial observations and of the total number of food items were arthropods (41% and 25% respectively; Table 1). Although the four *Tangara* species differed in the percentage of arthropod foraging under each measure, all four showed the same trend: the percentage of arthropod foraging was the

largest using the duration of foraging, followed by the food type at initial observation, and then the total number of food items. These differences were significant in 13 out of 15 pairwise comparisons ($P < 0.05$): the differences between foraging duration and food type at initial observation were significant in *T. arthus* ($P < 0.001$), *T. parzudakii* ($P < 0.05$), *T. labradorides* ($P < 0.01$), and for all four species combined ($P < 0.001$), but not in *T. rufigula* ($P = 0.3$). The differences between the foraging duration and total number of food items methods were significant in *T. arthus*, *T. parzudakii*, *T. labradorides*, and all four species combined ($P < 0.001$), and *T. rufigula* ($P < 0.05$). The differences between food type at initial observation and total number of food items were significant in *T. arthus* and *T. parzudakii* ($P < 0.001$), *T. labradorides* ($P < 0.01$), and all four species combined ($P < 0.01$), but not in *T. rufigula* ($P = 0.08$).

Fruit foraging was 3.7–4.9 times more efficient than arthropod foraging, except for *T. rufigula*, which showed higher arthropod foraging efficiency than the other *Tangara* species (Table 2). However, the data for *T. rufigula* were heavily influenced by a single foraging bout in which a large number of arthropods were gleaned from a spider web (19 attacks during 65 sec). When this unusual foraging bout was eliminated from the analysis, arthropod foraging efficiency of *T. rufigula* became 1.7 attacks per min, and fruit foraging became 2.5 times more efficient than arthropod foraging. *Tangara* tanagers did not attack arthropods in 48 percent of foraging bouts that included arthropod searching (Table 2). In contrast, *Tangara* tanagers failed to pick a fruit in only 13% of foraging bouts considered as fruit searching.

DISCUSSION

The study showed that the relative importance of two food types, arthropods and fruits, varied largely depending on which measure and method was used to quantify foraging behavior of omnivorous *Tangara* tanagers. The percentage of foraging time spent for arthropod foraging was significantly higher than per-

TABLE 2. Foraging efficiency and percentage of foraging bouts without an attack in four *Tangara* tanagers of Ecuador. Bias-corrected mean and 95% confidence limits (in parentheses) were calculated using 1000 bootstrap replicates.

Species	Foraging efficiency				Foraging bouts without an attack			
	Arthropods		Fruits		Arthropods		Fruits	
	No. of attacks per min	<i>n</i>	No. of attacks per min	<i>n</i>	Percentage	<i>n</i>	Percentage	<i>n</i>
<i>Tangara arthus</i>	1.0 (0.8–1.2)	75	4.9 ^a (4.1–5.7)	62	62% (51–72)	89	10% ^b (3–17)	74
<i>T. parzudakii</i>	1.5 (0.8–2.1)	23	7.1 ^a (3.9–10.3)	13	34% (19–51)	32	4% ^b (–3–10)	28
<i>T. labradorides</i>	1.4 (0.8–2.1)	20	5.3 ^a (2.4–8.2)	23	37% (19–55)	27	25% (6–44)	20
<i>T. rufigula</i>	3.4 (0.5–7.3)	13	4.3 (3.4–5.3)	15	27% (10–44)	26	29% (9–48)	21
Total	1.4 (1.0–1.8)	131	5.4 ^a (4.5–6.2)	113	48% (40–55)	174	13% ^b (8–19)	143

^a Differences of foraging efficiency between arthropods and fruits highly significant ($P < 0.001$ in 1000 bootstrap replicates, one-tailed test).

^b Differences of percentage of foraging bouts without attack between arthropods and fruits highly significant ($P < 0.001$ in 1000 bootstrap replicates, one-tailed test).

centage of arthropods in the number of food items (all five pairwise comparisons). This pattern was especially pronounced in *T. arthus*, which spent 57% of its foraging time searching for arthropods, but arthropods accounted for only 20% of food items. This difference was due to the difference in foraging efficiency: arthropod foraging was 3.9 times less efficient than fruit foraging. As a consequence of this low efficiency, arthropods formed a small percentage of the diet of *Tangara* (25%) despite their spending almost 60% of their foraging time searching for arthropods.

The percentage of arthropods in initial observations was significantly lower than the percentage of foraging time spent for arthropod foraging (four out of five pairwise comparisons). This seems puzzling because the two measures should be approximately the same if at least one arthropod attack was observed in all foraging bouts that contained arthropod searching. However, *Tangara* species failed to attack in 3.7 times more arthropod-foraging bouts than when foraging for fruits. Thus, the higher percentage of failure in finding arthropods than fruits appears to have caused the discrepancy between initial observations and foraging duration.

The fruits eaten by these tanagers are produced for facilitating the dispersal of seeds by birds and other animal dispersers; thus, most fruiting trees in the study area bore conspicuous fruits easily found by visual cues, and the ripeness of an individual fruit was easily predicted by both birds and humans due to its color, allowing the birds to assess abundance and distribution of fruits in the area. For example, *Acnistus arborescens* (Solanaceae) bore conspicuous orange fruits that attracted many bird species, including *Tangara* species. These same birds, however, did not stop at the trees when only unripe, green fruits were present.

In contrast to fruits, most arthropods are cryptic as one of their antipredatory traits, which presumably lower the foraging efficiency for the birds and increase the percentage of unsuccessful foraging bouts in arthropod foraging. Despite these drawbacks, *Tangara* tanagers spent considerably more time, and therefore more energy, searching for arthropods than for fruits. This suggests that arthropods are important in tanagers' diets for supplying nutritional resources that fruits do not provide.

Although numerous studies have used the frequency of initial observations to quantify bird foraging behavior (see Morrison, Ralph, et al. 1990), my study showed that this may be misleading when the study involves very different food types, such as highly rewarding but scarce arthropods and less rewarding but abundant fruits. The frequency of initial observations tends to underestimate the importance of such valuable food types in time budgets and tends to overestimate the same food type in the number of food items in birds' diet. Thus, it is probably advisable to employ multiple methods and analyses when studying species with diverse or poorly known behavioral repertoires.

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COMPARATIVE ANALYSIS OF THE RATTLE CALLS IN *CORVUS* AND *NUCIFRAGA*: THE EFFECT OF BODY SIZE, BILL SIZE, AND PHYLOGENY

PAOLA LAIOLO¹ AND ANTONIO ROLANDO

Dipartimento di Biologia Animale e dell'Uomo, Via Accademia Albertina 17, 10123 Turin, Italy

Abstract. We assessed the effect of body size and bill length on the acoustic properties of the rattle calls of 15 corvid species. First, we correlated body traits and the acoustic properties of rattles, regardless of the evolutionary history of the study species. Then we repeated the analysis, taking into account phylogeny and thus excluding its effect on morphological and acoustic characters. When the potential effects of phylogeny were ruled out, the second frequency peak was negatively correlated to body size. The carrying frequency also decreased with decreasing body size, but the relationship was weaker than that resulting from a phylogeny-free analysis. This pattern is consistent with the demonstrated body-size–frequency allometry in the vocalizations of many birds. Bill length also influenced

rattle spectral properties. We emphasize that patterns and processes elucidated with comparative studies can be biased if species relatedness is not considered.

Key words: *bill size, body size, corvids, phylogeny, short-range communication, vocalizations.*

Análisis Comparativo de las Llamadas de Matraqueo entre *Corvus* y *Nucifraga*: Efecto del Tamaño Corporal, Tamaño del Pico y Filogenia

Resumen. Evaluamos el efecto del tamaño corporal y la longitud del pico sobre las propiedades acústicas de los llamados de matraqueo de 15 especies de córvidos. Primero, correlacionamos los caracteres corporales con las propiedades acústicas del matraqueo independientemente de la historia evolutiva de las especies estudiadas. Luego, repetimos el análisis tomando en cuenta la filogenia, excluyendo su efecto sobre

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¹ E-mail: paola.laiolo@unito.it

los caracteres morfológicos y acústicos. Cuando los potenciales efectos filogenéticos fueron removidos, el segundo pico en la frecuencia se correlacionó negativamente con el tamaño corporal. La frecuencia principal también decreció con la disminución del tamaño corporal, pero esta relación fue más débil que la resultante de un análisis sin considerar la filogenia. Este patrón es consistente con la alometría entre el tamaño corporal y la frecuencia de las vocalizaciones de muchas aves. La longitud del pico también influyó sobre las propiedades espectrales del matraqueo. Enfatizamos que los patrones y procesos elucidados a través de estudios comparativos pueden encontrarse sesgados si no se consideran las relaciones entre las especies.

Acoustic communication systems have received much attention from evolutionary biologists (Hopp et al. 1998). Several studies have shown that bird vocalizations are influenced by morphology. In particular, a negative relationship between body mass and frequencies of signals has been demonstrated below and above the species level (Ryan and Brenowitz 1985), although studies that failed to find this relationship are not rare (Bowman 1979, Shy 1983). The body-size–frequency relationship has been associated with morphological features: larger birds emit calls with a lower fundamental frequency because of their larger syrinxes. Thus, selection for larger body size will cause an allometric increase of the syringeal membranes, and will indirectly change the signal spectral properties (Wallschläger 1980, Ryan 1988). The impact of the length of the suprasyringeal vocal tract is less clear. In some species, the length of the tract from trachea through buccal cavity to beak constrains the lower frequencies that can be produced at high intensity (the carrying frequencies), and determines the harmonic content of sounds (Ryan and Brenowitz 1985, Hoese et al. 2000). In these species, individuals with longer oropharyngeal tubes (and, in general, longer beaks) can produce lower carrying frequencies. In the Collared Dove (*Streptopelia decaocto*), however, vocal-tract resonances do not play an active role in the modification of vocalizations, although they might enhance the fundamental frequency passively (Ballintijn and ten Cate 1998). All things considered, it seems likely that different sound-producing structures may underlie different types of vocalizations, and constrain sound output in a variety of ways.

In this paper, we assess the effect of body size and bill length on the acoustic properties of rattle calls in 15 corvid species (genera *Nucifraga* and *Corvus*). Rattles are guttural, mechanical-sounding calls. The typical call used by *Corvus* and *Nucifraga* for long-range communication is the *caw*, a loud and harsh self-assertive signal that may also serve as territorial advertisement (Goodwin 1986). Conversely, rattles may play a role in short-range communication, since they are not markedly loud and are produced only when the recipient is very close. Although they differ among species and genera, as do the postures in which they are given, it is highly probable that rattles are homologous within the Corvidae (Goodwin 1986).

We first correlated body traits with the acoustic properties of rattles. Then we repeated the analysis,

taking into account phylogeny and thus excluding its effect on morphological and acoustic characters. The latter perspective should produce a more robust figure of morphologic-acoustic trait covariation because it is framed in a phylogenetic context. Too often, studies of body-trait–frequency allometry have not accounted for the lack of independence among species generated by their phylogeny (Tubaro and Mahler 1998). Because species are descended in a hierarchical fashion from common ancestors, they cannot be considered as independent data points in statistical analysis (Harvey and Purvis 1991). In the case of our study species, Cibois and Pasquet's (1999) molecular analysis emphasized a strict relationship between the genera *Corvus* and *Nucifraga*, which are considered by Goodwin (1986) to be the youngest offshoot within the corvine group. To avoid any bias due to nonindependence of the dataset, we incorporated phylogenetic information by using Felsenstein's (1985) independent contrasts procedure, and tested for correlated evolution of call acoustic properties and morphometric traits after removing the effect of phylogeny. The phylogenetically independent contrasts procedure produces weighted differences (contrasts) of the character values between pairs of sister species, which can be considered as independent and therefore used for statistical analyses (Garland et al. 1992). This method is appropriate for analyses on any continuous trait that is inherited from ancestors, regardless of the mechanism of inheritance (cultural or genetic; Garland et al. 1992).

METHODS

Rattles used in this study were recorded either in the field with a Sony DC D7 tape recorder and a Sony ECM672 microphone (*Corvus frugilegus*, *C. corone*, *C. corax*, *Nucifraga caryocatactes*) or obtained from the sound archive of the British Library, London (*Corvus albicollis*, *C. crassirostris*, *C. rhipidurus*, *C. ruficollis*, *C. capensis*, *C. validus*, *C. mellori*, *C. coronoides*, *C. caurinus*, *C. brachyrhynchos*, *C. imparatus*; Table 1). Goodwin (1986) suggested that only females give rattles, and only in sexual or self-assertive situations. The rattles used in this study were produced by females in the case of the Rook (*C. frugilegus*) and the Black Crow (*C. capensis*), but in the other species, the sex of the calling bird was unknown. Rattles recorded in the field were given by birds in pairs, in flocks, or by solitary birds mobbing birds of prey. Consequently, the strict association advocated by Goodwin (1986) between rattles and females does not seem to be confirmed.

Rattles are atonal, pulsed calls (Fig. 1). We generated spectrograms using Avisoft SASLab Pro Software (Specht 2001) performing a fast Fourier transform (sampling frequency 22 050 Hz, FFT length 512, time resolution 8.9 msec, frequency resolution 43 Hz, window function: Bartlett). We measured the following variables: rattle duration (D), pulse duration (DP; mean value of three measurements: at the beginning, at the middle, and at the end of the rattle), carrying frequency (F1; first frequency peak measured on the mean spectrum of the entire spectrogram), second carrying frequency (F2; second frequency peak measured on the mean spectrum of the entire spectrogram), pulse rate

TABLE 1. Mean values \pm SD of the acoustic features of rattles, wing and bill lengths (after Madge and Burn 1994), and phylogenetic position^a of 15 species of corvids.

Species	No. calls sampled	Rattle duration (sec)	Carrying frequency (kHz)	Second carrying frequency (kHz)	Pulse duration (sec)	Pulse rate (pulses sec ⁻¹)	Wing length (cm)	Bill length (cm)	Phylogenetic position
Northwestern Crow	5	0.48 \pm 0.14	1.64 \pm 0.09	1.50 \pm 0.45	0.016 \pm 0.003	52.3 \pm 16.3	292	49	CBBABB
<i>Corvus caurinus</i>									
American Crow	9	0.31 \pm 0.02	1.05 \pm 0.03	0.56 \pm 0.03	0.016 \pm 0.002	48.1 \pm 3.6	325	50	CBBABA
<i>Corvus brachyrhynchos</i>									
Tamaulipas Crow	39	0.30 \pm 0.06	1.24 \pm 0.13	1.57 \pm 0.25	0.017 \pm 0.001	78.7 \pm 5.6	253	42	CBBAAA
<i>Corvus imparatus</i>									
Australian Raven	4	0.37 \pm 0.07	1.68 \pm 0.09	1.05 \pm 0.05	0.013 \pm 0.002	39.1 \pm 11.8	397	66	CBBCBBBBBB
<i>Corvus coronoides</i>									
Little Raven	4	0.94 \pm 0.42	1.51 \pm 0.13	2.76 \pm 0.41	0.012 \pm 0.001	37.6 \pm 16.2	370	56	CBBCBBBBBC
<i>Corvus mellori</i>									
Long-billed Crow	4	0.24 \pm 0.16	0.67 \pm 0.13	0.51 \pm 0.27	0.022 \pm 0.002	33.6 \pm 19.1	365	85	CBBCBBBBBF
<i>Corvus validus</i>									
Hooded Crow	14	0.26 \pm 0.07	1.68 \pm 0.22	1.50 \pm 0.49	0.022 \pm 0.003	27.4 \pm 4.6	330	61	CBBBAA
<i>Corvus corone</i>									
Common Raven	4	0.17 \pm 0.01	1.03 \pm 0.06	1.00 \pm 0.41	0.020 \pm 0.003	34.2 \pm 4.8	473	80	CBBBBCAA
<i>Corvus corax</i>									
Black Crow	19	0.65 \pm 0.23	0.86 \pm 0.18	1.48 \pm 0.37	0.019 \pm 0.004	25.3 \pm 11.4	350	63	CBBBBB
<i>Corvus capensis</i>									
White-necked Raven	12	0.31 \pm 0.04	1.45 \pm 0.25	0.92 \pm 0.42	0.016 \pm 0.002	47.8 \pm 3.6	430	66	CBBBBCBA
<i>Corvus albicollis</i>									
Brown-necked Raven	22	0.64 \pm 0.17	1.03 \pm 0.05	1.42 \pm 0.09	0.017 \pm 0.004	53.3 \pm 19.2	432	73	CBBBBCAC
<i>Corvus ruficollis</i>									
Thick-billed Raven	24	0.35 \pm 0.09	0.89 \pm 0.19	1.77 \pm 0.42	0.020 \pm 0.004	40.3 \pm 11.5	472	85	CBBBBCBB
<i>Corvus crassirostris</i>									
Fan-tailed Raven	13	0.34 \pm 0.11	1.28 \pm 0.09	1.06 \pm 0.57	0.024 \pm 0.005	30.6 \pm 11.7	424	62	CBBBBCBC
<i>Corvus rhipidurus</i>									
Rook	15	1.50 \pm 0.49	1.32 \pm 0.04	1.85 \pm 0.06	0.013 \pm 0.001	76.4 \pm 4.3	330	57	CA
<i>Corvus frugilegus</i>									
Spotted Nutcracker	4	1.35 \pm 0.82	2.17 \pm 0.19	2.76 \pm 0.10	0.010 \pm 0.001	27.2 \pm 4.3	195	52	AA
<i>Nucifraga caryocatactes</i>									

^a Phylogeny after Goodwin (1986). Starting from the root, at each node of the phylogeny a letter is assigned to each daughter branch, creating a unique code for each species (Purvis and Rambaut 1995).

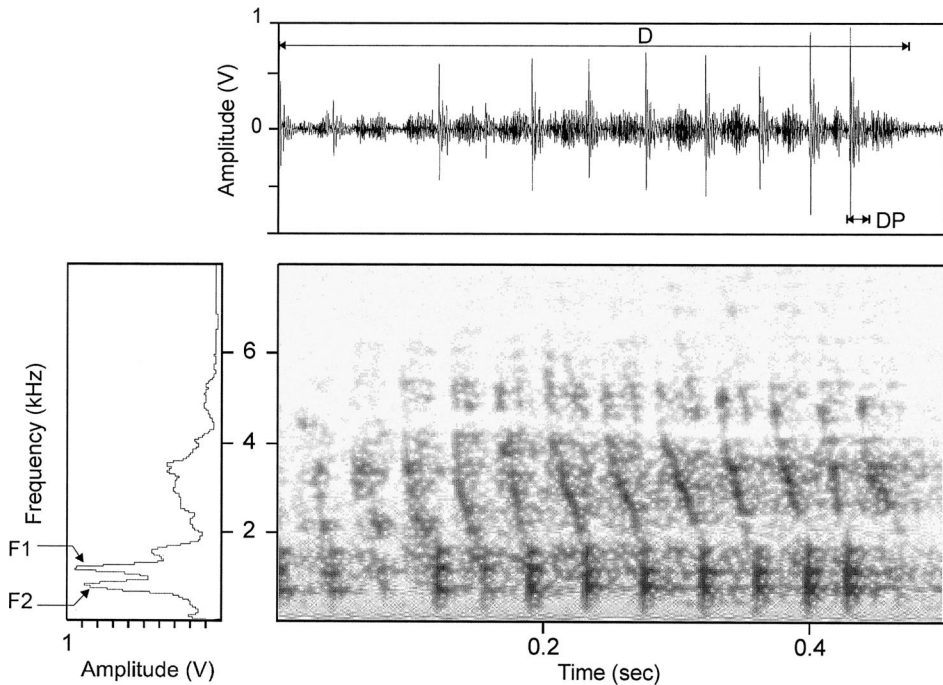


FIGURE 1. Waveform (top), sonogram (center) and mean power spectrum (left) of a typical corvid rattle. The call of the Thick-billed Raven (*Corvus crassirostris*) from Ethiopia is shown. Rattle calls of *Nucifraga* and other *Corvus* species have the same general structure. Labels indicate variables defined in Methods: D = call duration, DP = pulse duration, F1 = carrying frequency, F2 = second carrying frequency.

(V; number of pulses divided by the duration of the call [D]). Acoustic characteristics of calls were measured in the time domain on envelopes and in frequency domain on fast Fourier transform mean spectra.

Overall, we analyzed 192 rattles from 15 species (4 to 39 calls per taxon). Since all recordings were obtained from unmarked birds, analyses were carried out using species mean values, thus avoiding problems of pseudoreplication. To justify the use of mean values, we assessed the magnitude of spectrotemporal variation within and among species by means of the coefficient of variation. Interspecific variability ranged from 24% (interspecific CV of pulse duration) to 75% (interspecific CV of call duration), whereas intraspecific variability was lower for each call variable, ranging from 10% (mean within-species CV of the carrying frequency) to 30% (mean within-species CV of call duration).

We used published data on wing length and bill size (using the maximum values from the ranges quoted in Madge and Burn 1994). In keeping with Gosler et al. (1998), wing length was used as an indicator of body size; our choice was corroborated by the fact that the heavier species here considered also have longer wings ($r = 0.9$). We first regressed the spectrotemporal variables on body size and bill length, using log-transformed data. To incorporate phylogenetic information into statistical analyses of correlated evolution of continuous traits, we performed the comparative method of independent contrasts (Felsenstein 1985) using

CAIC software, version 2.0 (Purvis and Rambaut 1995). This method allowed us to analyze relationships among acoustic properties of rattles and bird morphology, after controlling for phylogeny. We based our analysis on Goodwin's (1986) phylogeny of *Corvus* and *Nucifraga*. Since this phylogenetic hypothesis was not built with a cladistic methodology, it could cause comparative problems (Tubaro and Mahler 1998). As Garland et al. (1992) pointed out, if the taxonomy is not cladistic, the independent-contrasts method could be misleading, but it does allow some kind of analysis in the absence of actual phylogenetic information. Furthermore, all the species here considered are closely related (Goodwin 1986, Cibois and Pasquet 1999), thus reducing the potential source of error induced by a phylogenetic topology that is not cladistic (Felsenstein 1988). Hence, based on the phylogeny proposed by Goodwin (1986) and in keeping with Palacios and Tubaro (2000), we estimated the ancestral states of the characters using the punctuated model (Harvey and Purvis 1991), which assumes that change occurs only at speciation events. As this model is likely to perform better if the phylogeny contains all the species in the group, not just those in the dataset (Purvis and Rambaut 1995), we constructed a topology using the uppermost branches of the corvid phylogeny proposed by Goodwin (1986). Details of the general procedure for estimating the ancestral character values are summarized in Felsenstein (1985). The independent-contrasts method produces comparisons between pairs of

sister species (nodes) as indicated in the phylogenetic topology, and each pairwise comparison produces a new parameter (a "contrast"), resulting from the difference between the values of the variable for the species pair. Contrasts should be independent of one another because they result from the evolutionary divergence after the origin of the pair. In keeping with Palacios and Tubaro (2000), we detected associations between standardized contrasts of spectrotemporal variables versus body size and bill length by means of standard linear regression models adjusted to pass through zero. Regressions were carried out with Microsoft Excel 2000.

Although we performed multiple comparisons with the same null hypothesis, we chose not to adjust our probability levels using a Bonferroni correction. We believe that with our small sample of 10 contrasts, such a correction would risk accepting a false null hypothesis (type II error). It is worth noting that our small sample is not a result of low sampling effort, but rather reflects the rarity of rattle calls in the repertoires of the species here considered (present in only 15 of 38 species).

RESULTS

Without controlling for phylogeny, carrying frequency decreased and pulse duration increased with body size ($F1 = 1.31 - 0.37(\text{BODY SIZE})$, $r^2 = 0.28$, $F_{1,14} = 4.9$, $P = 0.04$; $DP = -0.01 + 0.008(\text{BODY SIZE})$, $r^2 = 0.26$, $F_{1,14} = 4.5$, $P = 0.05$), whereas rattle duration, second carrying frequency, and pulse rate were not significantly affected by body size. Since bill length was positively correlated to body size ($\text{BILL LENGTH} = 0.16 + 0.64(\text{BODY SIZE})$, $r^2 = 0.57$, $F_{1,14} = 17.1$, $P = 0.001$), we regressed the acoustic variables on the residuals of bill length, thus excluding the effect of body size. The only relationship between any acoustic variable and bill length was a weak association with pulse rate ($V = 1.62 - 0.07(\text{residual of BILL LENGTH})$, $r^2 = 0.24$, $F_{1,14} = 4.0$, $P = 0.07$).

When we controlled for phylogeny, we found a negative correlation between the second carrying frequency and body size ($F2 = -0.81(\text{BODY SIZE})$, $r^2 = 0.38$, $F_{1,10} = 6.1$, $P = 0.03$; Fig. 2); the carrying frequency was weakly related to body size, but not significantly ($F1 = -0.45(\text{BODY SIZE})$, $r^2 = 0.23$, $F_{1,10} = 3.0$, $P = 0.1$). Pulse duration was not affected by body size.

Independent-contrasts analysis also revealed that bill length and body mass were positively correlated ($\text{BILL LENGTH} = 0.39(\text{BODY SIZE})$, $r^2 = 0.44$, $F_{1,10} = 7.8$, $P = 0.02$). In the regressions of independent contrasts of acoustic variables and bill length, we used residuals of those variables that were significantly affected by body size (F2 and bill length). In this way, we removed the confounding effect of the covariation between body size, bill length, and F2. There was no relationship between bill length and pulse rate, pulse duration, rattle duration, or carrying frequency, whereas the second carrying frequency was positively correlated to bill length (independent contrasts in residuals, $F2 = 0.62(\text{BILL LENGTH})$, $r^2 = 0.37$, $F_{1,10} = 5.3$, $P = 0.05$). Since the significance of the relationship between contrasts of F2 and contrasts of body mass

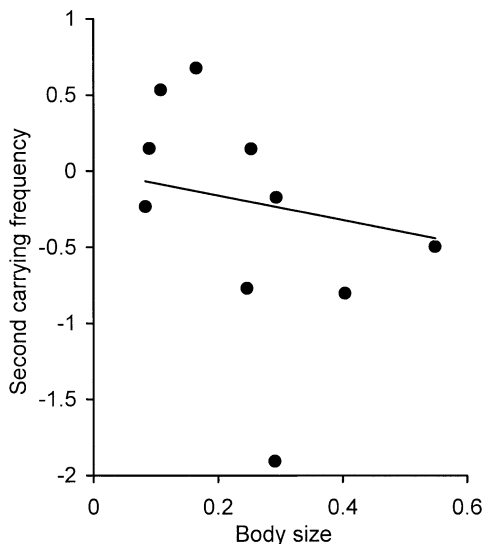


FIGURE 2. Second carrying frequency (F2) plotted against body size for 10 standardized independent contrasts of 15 species of *Nucifraga* and *Corvus*. Regression line is adjusted to pass through zero.

largely depended on one contrast (corresponding to the node *Corvus brachyrhynchos-C. caurinus*; Fig. 2), we repeated the former analysis using raw values of F2 instead of residuals, but the same positive correlation resulted ($F2 = 0.61(\text{BILL LENGTH})$, $r^2 = 0.37$, $F_{1,10} = 5.4$, $P < 0.05$).

DISCUSSION

Most research on bird vocalizations involves songs, the advertising vocalizations uttered by males (and females in some species) during the breeding season. Corvids, though songbirds, mostly produce calls, or simple signals that are not structured in multi-unit phrases. Unlike songs, calls are given throughout the year (Kroodsma and Miller 1996). To date, calls often have been neglected by studies on the acoustic communication systems of birds, and few of these studies have accounted for phylogeny when investigating the morphological constraints acting on the acoustic features of calls.

Our study showed that the results of comparative analyses can change when considered in a phylogenetic context. In corvid rattles, pulse duration appeared to be significantly affected by body size, but the relationship was not significant when taking into account the evolutionary history of the species. Moreover, when the effects of phylogeny were ruled out, the second carrying frequency was negatively correlated with body size; the carrying frequency also tended to decrease with decreasing body size, but the relationship was weaker than that resulting from a phylogeny-free analysis. Phylogeny apart, however, the pattern we found is consistent with the demonstrated body-size-frequency allometry in the vocalizations of many bird species: smaller birds can produce higher-pitched vocalizations because of their smaller syrinxes or shorter

trachea (Wallschläger 1980, Ryan and Brenowitz 1985).

Phylogeny also confounded relationships between bill size and acoustic features: when considering phylogeny, only the second carrying frequency was significantly affected by bill length, whereas pulse rate increased in longer-billed species in phylogeny-free analyses. The existence of a relationship between residuals of beak size and second carrying frequency is in line with the idea that the bill has resonating properties that affect the frequency spectrum of the vocalizations (Nowicki 1987), but the positive relationship we found contrasts with other empirical studies that show a negative correlation (Palacios and Tubaro 2000). However, a negative correlation is actually expected when beak maximum aperture is constant among species. If birds were constrained in their beak gapes, longer-billed species would produce lower-pitched vocalizations because of their elongated vocal tracts (Palacios and Tubaro 2000). Conversely, if the angle between the upper and lower mandible could change during sound emission, birds with longer beaks could produce maximum frequencies as high as (or even higher than) shorter-beaked species, because of the change in length of the orotracheal tube. Unfortunately, almost nothing is known about the mechanisms of sound production in corvids, and we cannot dismiss any of these hypotheses.

In conclusion, despite being based on a small sample of independent contrasts, this study supports the negative relationship between body size and call frequencies found in other bird species, and also suggests that bill length might have an influence on call spectral properties. Moreover, we emphasize that results of comparative studies can change when analyses are framed in a phylogenetic context, and that ignoring this context can bias our observations of patterns and processes.

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