Cleaning Associations between Birds and Herbivorous Mammals in Brazil: Structure and Complexity

CLEANING ASSOCIATIONS BETWEEN BIRDS AND HERBIVOROUS MAMMALS IN BRAZIL: STRUCTURE AND COMPLEXITY

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Abstract.—Birds that remove ectoparasites and other food material from their hosts are iconic illustrations of mutualistic–commensalistic cleaning associations. To assess the complex pattern of food resource use embedded in cleaning interactions of an assemblage of birds and their herbivorous mammal hosts in open habitats in Brazil, we used a network approach that characterized their patterns of association. Cleaning interactions showed a distinctly nested pattern, related to the number of interactions of cleaners and hosts and to the range of food types that each host species provided. Hosts that provided a wide range of food types (flies, ticks, tissue and blood, and organic debris) were attended by more species of cleaners and formed the core of the web. On the other hand, core cleaner species did not exploit the full range of available food resources, but used a variety of host species to exploit these resources instead. The structure that we found indicates that cleaners rely on cleaning interactions to obtain food types that would not be available otherwise (e.g., blood-engorged ticks or horseflies, wounded tissue). Additionally, a nested organization for the cleaner bird–mammalian herbivore association means that both generalist and selective species take part in the interactions and that partners of selective species form an ordered subset of the partners of generalist species. The availability of predictable protein-rich food sources for birds provided by cleaning interactions may lead to an evolutionary pathway favoring their increased use by birds that forage opportunistically. *Received 30 June 2011, accepted 10 November 2011.*

Key words: cleaner birds, herbivorous mammal hosts, interspecific interactions, nestedness, network organization.

Asociaciones de Limpieza entre Aves y Mamíferos Herbívoros en Brasil: Estructura y Complejidad

Resumen.—Las aves que remueven ectoparásitos y otros alimentos de sus hospederos son ejemplos icónicos de asociaciones mutualistas-comensalistas de limpieza. Para establecer el complejo patrón de uso de recursos alimenticios embebido en las interacciones de limpieza de un ensamblaje de aves y sus mamíferos herbívoros hospederos en hábitats abiertos en Brasil, usamos una aproximación basada en redes para caracterizar sus patrones de asociación. Las interacciones de limpieza mostraron un patrón claramente anidado, relacionado con el número de interacciones de los limpiadores y de los hospederos, y con el rango de tipos de alimento diferentes que provee cada especie hospedera. Los hospederos que proveen un espectro amplio de tipos de alimento (moscas, garrapatas, tejido y sangre, restos orgánicos) fueron atendidos por más especies de limpiadores y formaron el centro de la red. Por otro lado, las especies limpiadoras centrales no explotaron el espectro completo de recursos disponibles, pero sí usaron una variedad de especies hospederas para explotar tales recursos. La estructura que encontramos indica que los limpiadores dependen de las interacciones de limpieza para obtener tipos de alimento que no hubiesen estado disponibles de otra manera (e.g., tábanos o garrapatas llenas de sangre, o tejidos heridos). Además, una organización anidada para la asociación entre aves limpiadoras y mamíferos herbívoros significa que tanto especies generalistas como especialistas toman parte en las interacciones y que los compañeros de las especies selectivas forman un subconjunto ordenado de los compañeros de las especies generalistas. La disponibilidad de fuentes predecibles de alimento rico en proteínas para las aves que provienen de interacciones de limpieza puede conducir a caminos evolutivos que favorecerían el incremento en su uso por aves oportunistas.

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CLEANING ASSOCIATIONS ARE a widespread form of interspecific interactions that occur both on land and in water, typically with two types of participants: the cleaner and the host or client (MacFarland and Reeder 1974, Losey et al. 1999, Grutter 2005, Sazima 2011). During cleaning interactions, cleaner species forage on ectoparasites that they remove from the hosts, but they can also capitalize on other food types found on hosts (Dean and MacDonald 1981, Losey et al. 1999, Sazima and Sazima 2010). These additional food types vary according to the interacting species and the type of environment where the association takes place, and they include a variety of materials, such as dead or live tissue, blood, secretions, scales, and organic debris (Burger 1996, Losey et al. 1999, Sazima 2007c, Craig 2009, Sazima and Sazima 2010).

Many positive heterospecific relationships (Stachowicz 2001), such as plant pollination or cleaning in reef fishes, generally comprise several species in a dense web of interactions (i.e., connections) rather than isolated interactions between pairs of species (Bascompte et al. 2003, Bascompte and Jordano 2007, Guimarães et al. 2007). General properties, such as specific organizing patterns rather than random interactions among species, were found to be pervasive in several of the positive associations described so far (e.g., Lewinsohn et al. 2006, Bascompte and Jordano 2007). A specific type of arrangement of interactions called "nestedness" was originally described in the field of island ecology for patterns of species presences across islands (Atmar and Patterson 1993) and is particularly common in mutualistic assemblages of species (Bascompte et al. 2003, Guimarães et al. 2007, Verdú and Valiente-Banuet 2008). The nestedness concept, as applied to webs of interacting species, describes assemblages in which species with few interactions (i.e., selective species) display a tendency to interact with species that have many interactions (generalists). Thus, if we rank species in a nested system from the most to the least selective, we will observe that the interactions recorded for one species form a subset of the interactions recorded for the next more connected species, as in "Russian dolls" with smaller ones contained in larger ones (Bascompte et al. 2003, Lewinsohn et al. 2006). An important property that arises in nested systems is that generalist species interact among themselves to form a highly cohesive (i.e., with redundancy) core of interacting species (Bascompte et al. 2003, Bascompte and Jordano 2007).

A search for patterns of interactions among species may provide information about the causes and consequences of these interactions and provide insight for understanding the ecology and evolution of multispecies assemblages (Bascompte et al. 2006, Lewinsohn et al. 2006, Bascompte and Jordano 2007). Here, we use a network approach to examine the complexity of terrestrial cleaning interactions, frequently considered only in terms of their curiosity or anecdotal components. Associations between cleaner birds and vertebrate herbivores have sometimes been interpreted as casual (e.g., Kilham 1982, Fennessy 2003) and were never considered from the perspective of an interaction web whose specific dependencies among partners may depart from a random collection of serendipitous interactions. Here, we search for organizing patterns and mechanisms that contribute to network structure through analysis of associations between Brazilian cleaner birds and their herbivorous mammalian hosts living in open habitats. Our main working hypothesis was that the web organization of interactions between hosts and their cleaners in terrestrial associations resembles that which is described for cleaning associations in marine habitats (Guimarães et al. 2007). Accordingly, three questions guided our study: (1) Are interactions between cleaner birds and their herbivorous mammalian hosts arranged in a nested pattern? (2) What are the implications of this type of web arrangement for the species involved? (3) What mechanisms could contribute to build nestedness? If the association between cleaner birds and their mammalian hosts is arranged in a nested pattern, we expected that selective cleaner species would visit only a subset of the host species visited by the generalist cleaner species. Additionally, since nested assemblages are considered cohesive because of the generalist–generalist interactions (Jordano et al. 2006), a nested pattern would suggest that selective cleaner species have access to food sources provided by hosts, because this relationship is maintained mostly by the interactions among generalist species.

METHODS

Our data set for the web of cleaning interactions between birds and herbivorous mammals was built upon records during field activities in open habitats of southeastern (Campinas area in São Paulo) and southwestern Brazil (Poconé area in Mato Grosso). Observations lasted 1–6 h per day for 1–4 days on 17 field trips, which yielded 108 direct observations of cleaner birds feeding on hosts. This type of procedure follows methods usually adopted in studies of mutualistic networks, including nestedness analysis (e.g., Guimarães et al. 2007, Ollerton et al. 2007). The "behavior sampling" rule (Martin and Bateson 1986) or "all occurrences sampling" (Lehner 1998), which provides an adequate record of the occurrence of particular behavior types, was used throughout our observations, which we occasionally documented with photographs. When recording interactions in the field, we opted for naturalistic observations (i.e., we studied the behavior of the animals as it occurred naturally and minimized intrusion; see Lehner 1998). Thus, we sought sites that could harbor potential hosts for the cleaner birds, and our working protocol included the identification of the cleaners and the hosts, records of the food type consumed by the cleaners and their behavior while cleaning, and records of the postures and avoidance movements (if any) adopted by the hosts while interacting. We observed the interaction until the cleaner or the host retreated. We made our observations with the naked eye, through 10 × 50 binoculars, or through a 70–300 mm telephoto zoom lens mounted on an SLR camera, from a distance of about 2–30 m. It was possible to distinguish the type of food taken from a host by a bird, because the behaviors of the birds differ when they catch a fly, pull a tick, glean organic debris, drink blood, or rip off a piece of tissue (e.g., Sazima 2007c, Sazima and Sazima 2010). Time spent observing native fauna and livestock was roughly similar because we attempted to minimize bias toward one or another host type. Native hosts were observed in protected areas where they are habituated to people, thus avoiding or minimizing the potential effect of the observer. All species considered here are widespread in eastern South America (Table 1), resident in the areas where our observations were made (Sick 1997, Parera 2002), and found in the same habitats.

Heterospecific interactions can be described as webs in which species may be depicted as nodes and interactions between pairs of species as links (e.g., Sazima et al. 2010). To evaluate whether the web composed by cleaner birds and their hosts is arranged in a nested pattern, we organized a qualitative matrix using data of the record of interactions among different species on the basis of information that we collected in the field. Thus, our network of cleaning can be defined by an adjacency matrix R

Table 1. Cleaner birds and their herbivorous mammal hosts studied in open habitats in southeast and southwest Brazil. Families are in systematic order, species in alphabetical order.

Families	Scientific names and authorities	General distribution
Cleaners		
Ardeidae	*Bubulcus ibis* (Linnaeus)	Cosmopolitan
Cathartidae	*Coragyps atratus* (Bechstein)	North to South America
Falconidae	*Caracara plancus* (Miller)	South America
	Milvago chimachima (Vieillot)	Central to South America
	M. chimango (Vieillot)	South America
Jacanidae	*Jacana jacana* (Linnaeus)	Central to South America
Cuculidae	*Crotophaga ani* (Linnaeus)	North to South America
Furnariidae	*Furnarius rufus* (Gmelin)	South America
Tyrannidae	*Machetornis rixosa* (Vieillot)	Central to South America
Icteridae	*Molothrus bonariensis* (Gmelin)	North to South America
	M. oryzivorus (Gmelin)	Central to South America
Hosts		
Tapiridae	*Tapirus terrestris* (Linnaeus)	South America
Equidae	*Equus asinus* (Linnaeus)	Cosmopolitan
	E. caballus (Linnaeus)	Cosmopolitan
Cervidae	*Blastocerus dichotomus* (Illiger)	South America
Bovidae	*Bos taurus* (Linnaeus)	Cosmopolitan
Caviidae	*Hydrochoerus hydrochaeris* (Linnaeus)	Central to South America

with host species assigned to columns and cleaner species to rows; an element of the matrix representing an interaction received the value of 1, but zero otherwise. Throughout the text, we refer to a given species' number of interactions, which we consider as equal to the number of links per species (i.e., the number of species that a given species interacts with, which in our case is the number of cleaner species attending each host species or the number of host species visited by each cleaner species).

We estimated an index of nestedness in our adjacency matrix of cleaning interactions using a recently proposed metric (NODF: Nestedness metric based on Overlap and Decreasing Fill), which accounts for the two structural properties that a nested matrix should have: "decreasing fill" and "paired overlap" (Almeida-Neto et al. 2008). Decreasing fill is the gradual diminution of the number of interactions from the most generalist to the most selective species in the matrix; paired overlap determines whether the number of interactions of a selective species overlaps those in the subset of interactions from the next most generalist species (Almeida-Neto et al. 2008). Traditional metrics of matrix temperature (a measure of how a matrix departs from a perfect nested structure) and discrepancy often overestimate the degree of nestedness observed in real networks because they do not consider decreasing fill and paired overlap. The NODF metric, on the other hand, is directly based on both properties and seems to be less prone to Type I statistical error, consistently rejecting nestedness for random networks (Almeida-Neto et al. 2008). The NODF's values range from zero in a non-nested matrix to 100 in a perfectly nested one (for further details, see Almeida-Neto et al. 2008). We used ANINHADO software (Guimarães and Guimarães 2006) to perform analyses of nestedness.

After we estimated the index of nestedness in the cleaning matrix, it was necessary to assess the significance of the index by comparing the observed value with a benchmark provided by a null model (Bascompte et al. 2003). Models that fix column or row totals from the original incidence matrix and that randomize interactions may greatly increase the occurrence of Type II error (Ulrich and Gotelli 2007, Ulrich et al. 2009, Joppa et al. 2010). Additionally, because the observed number of interactions for each species is intrinsically probabilistic while representing estimates of the actual number of interactions, we opted for a model that accounted for the number of interactions recorded for each species in a probabilistic way, thus controlling for differences between species. The null model we used in our analyses considered that the probability that a host i will interact with a cleaner j depends on the observed number of interactions of both species, and thereby tests whether the observed value of nestedness is higher than expected for random webs that are similar to ours in terms of the heterogeneity of species' interactions. This null model accounts for random and stochastic processes (e.g., sampling biases) that might generate structure by maintaining differences in the number of interactions between species in the observed network. Thus, it seems correct to consider that the nested structure that we describe for the analyzed network is related to interaction patterns between the involved species rather than to other processes such as differences in species' local abundance (i.e., a passive sampling effect based only on the probability of interspecific encounters). Our results were compared with 1,000 replicates generated by the null model that we selected.

Each species in the assemblage of cleaners and hosts contributes to overall nestedness. Using our adjacency matrix, we ran ANINHADO to calculate the contribution of each row (cleaner species) and column (host species) to the value of the observed nestedness. The contribution of each cleaner species (or host) to overall nestedness quantifies how much its pattern of interaction fits in the expected pattern when a perfectly nested web is assumed. Nestedness contribution values range from zero (no contribution to the nested pattern) to 100 (maximum contribution to the nested pattern). Under a perfectly nested pattern, each species has a nestedness contribution value of 100. In our set of cleaners, those species with many interactions would have high contributions to nestedness if they interact with core hosts and these latter also interact with cleaners with few interactions. Accordingly, cleaners with few interactions would have high contributions if they visit a subset of partners also visited by cleaners with many interactions. The same reasoning is valid to understand how host species contribute to nestedness. To gain insight into the mechanisms that may contribute to nestedness, we performed Spearman rank correlations using the value of each species' contribution to nestedness (Almeida-Neto et al. 2008) and four traits from this system. The four traits included (1) number of food types provided by each host species, (2) number of food types exploited by each cleaner species, (3) number of interactions of each cleaner species, and (4) number of interactions of each host species.

Results

The web of interactions between Brazilian cleaner birds and their herbivorous mammalian hosts in open habitats is composed of 11 species of birds and 6 species of mammals (Figs. 1 and 2; Table 1). The cleaners range from the starling-sized Shiny Cowbird (*Molothrus bonariensis*) to the crow-sized Yellow-headed Caracara (*Milvago chimachima*) and the raven-sized Black Vulture (*Coragyps*

atratus). The hosts range from the pig-sized rodent Capybara (*Hydrochoerus hydrochaeris*) to larger ones such as the Marsh Deer (*Blastocerus dichotomus*), the Brazilian Tapir (*Tapirus terrestris*), and livestock. Five distinct food types were available on the host's assemblage, ranging from ticks and flies to tissue and organic debris, although food types available to cleaners varied among host species (Fig. 2). Cleaner birds exploited one to three food types available on hosts (Fig. 2). Flies and ticks were the food types present in all host species (Fig. 2). On the other hand, wounded or dead tissue and blood from wounds were present in four host species (Fig. 2)—the ones that are bitten during chasing and fighting, such as the highly social Capybara (see Schaller and Crawshaw 1981), and those that injure themselves on wire fences or have sores caused by botfly larvae, such as livestock. Additionally, organic debris was a food item present in the Capybara only, because of its amphibious habits and mud-wallowing behavior (Schaller and Crawshaw 1981, C. Sazima et al. pers. obs.). Except for the Cattle Egret (*Bubulcus ibis*) and the Cattle Tyrant (*Machetornis rixosa*), which feed on insects and small vertebrates, most of the cleaner birds that we studied are, more or less, omnivores. For instance, the Southern Caracara (*Caracara plancus*), the Yellow-headed Caracara, the Chimango Caracara (*Milvago chimango*), and the Black Vulture feed on carrion, small vertebrates, fruits, and other plant material. The Wattled Jacana (*Jacana jacana*), the Smooth-billed Ani (*Crotophaga ani*), the Giant Cowbird (*Molothrus oryzivorus*), the Shiny Cowbird, and the Rufous Hornero (*Furnarius rufus*) feed on insects and other invertebrates but also take seeds and fruits (Sick 1997, C. Sazima et al. pers. obs.).

We found that the network of interactions between cleaner birds and their hosts was highly nested (NODF = 82.39). This level of nestedness is significantly higher than expected by the null model (mean ± SE = 54.87 ± 0.293, $P < 0.001$). The number of interactions of hosts was negatively related to their nestedness contribution ($r_s = -0.88$, $P = 0.02$, $n = 6$). On the other hand, number of interactions of cleaners was positively correlated with their nestedness contribution ($r_s = 0.755$, $P = 0.007$, $n = 11$). The range of food types provided by each host species was negatively related to their nestedness contribution ($r_s = -0.819$, $P = 0.045$, $n = 6$). Interestingly, there was no correlation between the range of food types exploited by cleaner species and their nestedness contribution ($r_s = 0.304$, $P = 0.362$, $n = 11$). We also performed correlations between the number of interactions of species and the range of food types provided and used, as follows: the number of interactions of host species was not related to the range of food types they provided ($r_s = 0.617$, $P = 0.191$, $n = 6$), but these variables became significantly related when the Donkey (*Equus asinus*) was grouped with the Horse (*E. caballus*) ($r_s = 0.948$, $P = 0.013$, $n = 5$); these two species provided the same food types, so we summed the number of interactions for each of them and used this total under the genus *Equus* to conduct this analysis. On the other hand, the number of interactions of cleaner species was not correlated with the range of food types they exploited ($r_s = 0.198$, $P = 0.558$, $n = 11$).

DISCUSSION

All of the host species that we included have mobile parasites (ticks and horseflies), but hosts that provide additional food types have the highest number of interactions, and these comprise the

web's core. Thus, the variety of food types on hosts could be one of the underlying causes that build up the web structure. On the other hand, cleaner birds that visit many host species (i.e., core cleaners) do not necessarily exploit a wider range of food types when compared with cleaners that visit only one or a few hosts. Therefore, core cleaners are not those that exploit a greater variety of food resources, but those that exploit resources on a wider variety of host species. The nested structure (i.e., the existence of a core of cleaners and hosts, and a peripheral subset of species that interacts with it) that we describe for terrestrial cleaning interactions, as opposed to a random assignment of cleaners to hosts, indicates that cleaners rely on such types of interaction to obtain a variety of food types that otherwise would not be available (blood-engorged ticks and horseflies, wounded tissue). The availability of these predictable and protein-rich food sources for cleaner birds, provided via such interactions, may lead to an evolutionary pathway that favors the increased use of these interactions, especially in the case of the generalist species (i.e., those with many interactions). Accordingly, in marine cleaner–client networks, core cleaners such as cleaner gobies (*Elacatinus* spp.) are supergeneralists (*sensu* Thompson 2005) that rely on a diversity of partners to survive (Guimarães et al. 2007, Sazima et al. 2010).

The Capybara is the host visited by the greatest number of cleaner species and, thus, seems to be favored by a varied assemblage of cleaner birds. We suggest that this pattern is related to this mammal's natural history: (1) it is appealing to a wide diversity of cleaner birds because it provides the greatest variety of food types; and (2) it often adopts inviting poses, which allow the birds to work on body areas that would not be accessible otherwise, such as belly and inner thighs (Sazima 2007c, Sazima and Sazima 2010). Livestock, on the other hand, is mostly indifferent to the activity of cleaner birds (Sazima 2011). Therefore, in addition to the number of food types provided, behavior before or during cleaning likely influences the number of interactions for the hosts, because web structure may be influenced by a combination of several determinants (Vázquez et al. 2009), which includes ecological and behavioral characteristics of interacting species (Stang et al. 2007). Factors that influence the number of interactions for the cleaners, on the other hand, seem to be more difficult to define. Most of the cleaners that we recorded are omnivores, but even if omnivory likely renders the birds inclined to engage in cleaning activities, it seems that the cleaners' diet has little influence on the number of partner species they visit. This suggestion is supported by our observations that cleaners, independently of their number of partners, exploit only one to three food types available in the hosts' assemblage. On the other hand, cleaners vary in their opportunism level (Sazima 2007b, c) and bill morphology (Sick 1997; Telfair 2006; Sazima 2007c, 2011), and these traits may influence the number of host species they interact with. Body size is also likely to influence a cleaner's role, given that hosts generally did not seem comfortable in the presence of the two largest cleaners we recorded, the Southern Caracara and the Black Vulture, and attempted to discourage or avoid their cleaning (Sazima 2011). The hosts' wariness presumably explains the few interactions that we recorded between these two bird species and hosts because their behavioral plasticity and ability to capitalize on almost any feeding opportunity would suggest more numerous interactions (Sazima 2007a, b, c). Thus, it is possible to infer that a combination of opportunistic foraging and behavioral versatility, limited or mediated by

FIG. 1. Selected Brazilian cleaner birds and their hosts. (A) Its head covered with mud, organic debris, and flies, a Capybara is attended by the Giant Cowbird that deftly hunts flies attracted to this host. (B) Gashes on a Capybara's back and rump (due to aggression by dominant individuals) are sought by the Yellow-headed Caracara, which may capitalize on blood and wounded or dead tissue while picking ticks. (C) Posing or facilitation behavior is usual for Capybaras during tick-picking sessions by a cleaner, here the Yellow-headed Caracara. (D) Holding its grasp on a ruminating bovine (*Bos taurus*), a female Shiny Cowbird removes a tick from the host. (E) Close to a resting and ruminating bovine, the Cattle Egret deftly removes a tick from within the ear of this host. (F) Holding its balance on the tail of a grazing Horse, an immature Yellow-headed Caracara removes a tick from its client's rump. Photographs by Carlos A. Coutinho (A), Ivan Sazima (B, C), Romulo Campos (D), Margot K. Castro (E), and Wilfred Rogers (F).

bill morphology (and possibly body size as well), could have played a role in the number of partner species each cleaner visited. However, no bird cleaner in South America or other parts of the world (Sazima and Sazima 2010, Sazima 2011) is as dependent on herbivorous ungulates as the specialized African tick-picking and blood-drinking oxpeckers (*Buphagus* spp.), the epitomes of tickbirds (Weeks 1999, 2000; Craig 2009). Their South American rough equivalent would be the Yellow-headed Caracara (Sazima 2011), the cleaner bird for which we recorded the highest number of host species.

Studies of cleaning interactions and relationships between cleaner organisms and their hosts are far more advanced in marine than in terrestrial habitats. For instance, it is well known that cleaner fishes do not feed only on ectoparasites picked from their clients, because they also forage on noninfected parts of the client's body and ingest mucus, skin, and scales (Cheney and Côté 2005, Grutter 2005). In the terrestrial cleaning interactions recorded in Brazil, a similar situation may occur while cleaners feed on blood and tissue from their hosts. However, this situation is mostly
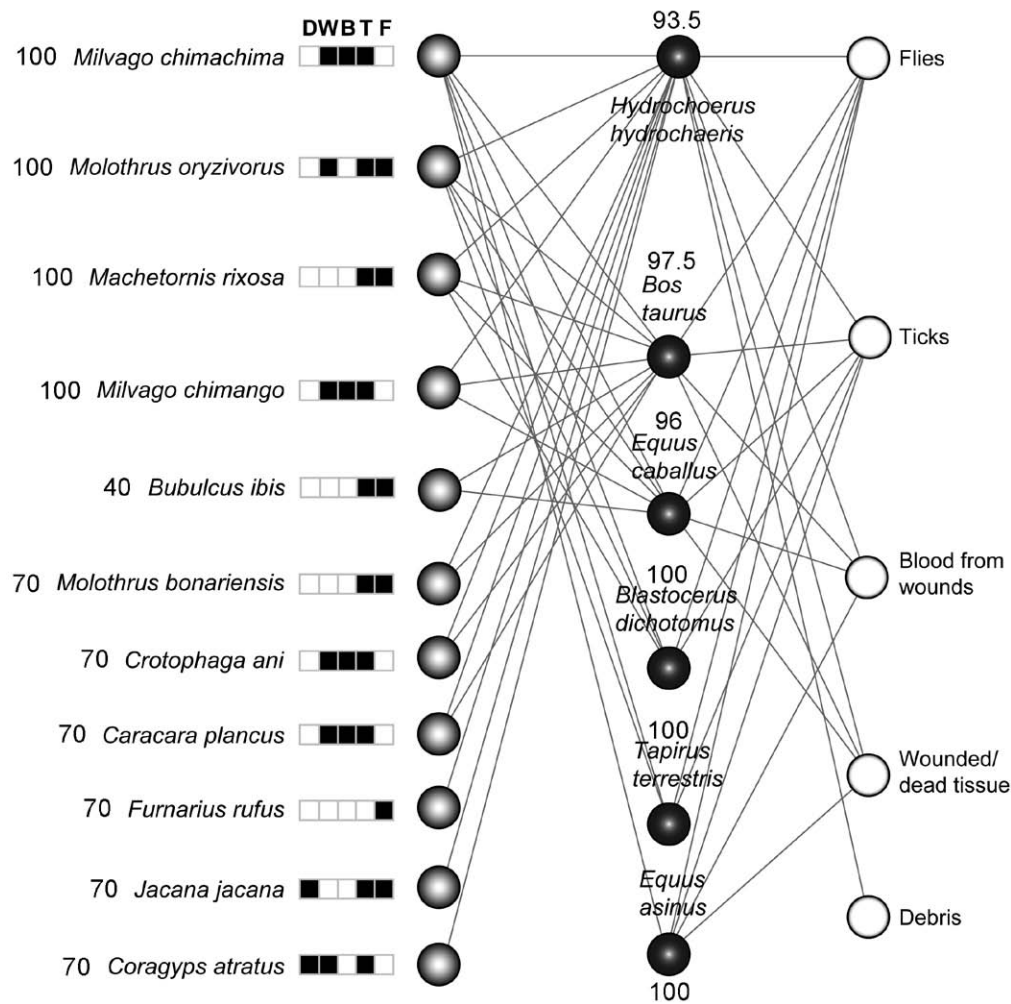
Fig. 2. Web of interactions between Brazilian cleaner birds (gray circles, left), herbivorous mammal hosts (black circles, middle), and food types available on each mammal species (white circles, right). The row of squares next to the birds is the range of food types exploited (black squares) or not (white squares) by each cleaner species. D = debris, W = wounded/dead tissue, B = blood, T = ticks, and F = flies. Numbers next to specific name of cleaners and hosts refer to values of nestedness contribution for each species.

restricted to interactions between carnivorous or necrophagous birds and wounded hosts, in which the cleaner may ingest blood or tissue while primarily picking parasites (Sazima 2011). Client fishes disturbed by the cleaner's feeding react with jolts (a sudden jerky motion of the body), whereas herbivore hosts try to dislodge the bird with avoidance movements of the body, legs, or head, and sometimes retreating (Grutter 2005, Sazima 2011, C. Sazima et al. pers. obs.). Cleaner fishes that feed on material other than ectoparasites from their hosts would suggest a nonmutualistic interaction, but the consensus is that the overall outcome of the association indeed benefits the hosts, mainly by reducing parasite loads (Grutter 2005). Although little evidence on reduction of parasite densities on hosts is presently available for terrestrial cleaning interactions (but see Weeks 2000), it is very likely that the outcome of such interactions is also mutualistic, because blood or tissue consumption is restricted to specific situations and only occasionally do the hosts try to dislodge the cleaner or end the interaction. Another resemblance between marine and terrestrial cleaning interactions is that in both

habitat types, hosts pose to cleaners and facilitate the association (Grutter 2005, Sazima and Sazima 2010, Sazima 2011). Posing in reef fishes is interpreted as a signal of the client's intention to be cleaned, behavior that also guides the cleaner to infected areas and provides it with better access to the parasites (Grutter 2005). Inviting postures are recorded for cleaning interactions between cleaner birds and their herbivore hosts as well (Sazima 2011) and likely serve the same purposes as in marine cleaning associations.

Among the cleaner species that we studied, species with many interactions contributed heavily to building the nested pattern because their host partners included a range of species that had both many and few interactions. Thus, this type of cleaner visited host species as expected given the level of nestedness of the entire web. By contrast, some cleaner species with fewer interactions did not interact according to the nestedness of the real web (i.e., with a well-defined subset of the generalist hosts) as would be expected (Bascompte et al. 2003), thereby decreasing their contributions. Among hosts, those with few interactions contributed

the most to the nested pattern. The latter trend is related to two aspects: (1) selective hosts were visited mainly by generalist cleaners, as expected for a nested assemblage; and (2) some generalist hosts were not visited by some of the selective cleaners. For instance, the nestedness contribution found for the Capybara was limited by the absence of a link between this mammal and the cleaner Cattle Egret, which is believed to have evolved next to larger herbivores such as African Buffalo (*Syncerus caffer*; Telfair 2006). Thus, this cleaner likely prefers cattle to Capybara, as the former is an approximate ecological equivalent of Buffalo.

We also found that domestic ungulates predominated over the native fauna as hosts (the Capybara is an exception). This result is likely related to the fact that domestic species have for the most part replaced large native herbivores (Marsh Deer and Brazilian Tapir) that have either gone extinct or experienced greatly diminished population sizes since the beginning of European colonization (Sick 1997). A similar finding has been recorded in several parts of Africa for the highly specialized tickbirds *Buphagus* spp. (Weeks 1999). It should be noted that hosts for cleaner birds worldwide are mostly herbivorous ungulates, exceptions being reptiles and seals on oceanic islands, and seals on the southern tip of South America (Sazima and Sazima 2010, Sazima 2011). Thus, substitution of native ungulates by livestock as hosts of cleaner birds is to be expected worldwide.

We have made the first attempt to characterize the web structure of cleaner–host interactions among birds and herbivorous mammals, which is an important step for understanding the organizing patterns of such iconic associations. The high level of nestedness that we found indicates that this cleaner–host system is not randomly organized but has a distinctly nested structure. Two important properties emerge from this type of organization: (1) both generalist and selective species participate in the association, and (2) partners of selective species form an ordered subset of the partners of generalist species. Thus, we could predict the composition of species in the subset of partners for new additions to our web. Overall, the nested organization indicates that generalist species of cleaners and hosts are the ones that potentially drive the ecology and the evolution of the entire web of interactions. An example of such influence is that the generalist species are the ones more likely to attract new species to the web (e.g., an additional host species would be cleaned by the Yellow-headed Caracara and an additional cleaner species would clean the Capybara). Future research on associations between cleaner birds and herbivorous mammals may look, for instance, at the topology of interactions in African assemblages that include the food-specialized oxpeckers (Craig 2009) and the diverse extant megafauna. Our view is that African webs are richer in the food types exploited and species involved (e.g., Dean and MacDonald 1981, Ruggiero and Eves 1998) and that the associations are more intimate in a few cases than those that we presented here for South American species.

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