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Bird-flower interactions in Brazil: a review

Luciana Baza Mendonça[1] e Luiz dos Anjos[2]
[1] *Universidade Estadual de Maringá, pós-graduação em Ecologia de Ambientes Aquáticos Continentais. E-mail: lu_baza@yahoo.com.br.*
[1] *Endereço para correspondência: Rua Serafim Nunes Diniz, 311, Centro, 86200-000 Ibiporã, PR, Brasil.*
[2] *Laboratório de Ornitologia e Bioacústica, Universidade Estadual de Londrina, depto de Biologia Animal e Vegetal, Caixa Postal 6001, 86051-970 Londrina, PR, Brasil. E-mail: llanjos@sercomtel.com.br*

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RESUMO. **Interações entre aves e flores no Brasil: uma revisão**. As interações aves-flores representam um campo bastante rico da Ecologia e, em muitos casos, podem ser vistas como relações mutualistas. Muitas plantas dependem das aves para a polinização e, do mesmo modo, muitas aves dependem do néctar como alimento. Considerando a importância do assunto, o presente trabalho oferece uma revisão das interações entre as aves e as flores no Brasil, com base na literatura publicada a partir de 1975. Diversos estudos abrangendo interações aves-plantas e assuntos relacionados foram conduzidos no país, especialmente em áreas de Floresta Atlântica do sudeste. Entretanto, para algumas regiões ou biomas brasileiros, os estudos são praticamente inexistentes. Os beija-flores, que se constituem no grupo dominante nas interações aves-plantas na região Neotropical, são as aves mais apontadas nos estudos. Contudo, alguns artigos mostram que uma ampla gama de aves, não necessariamente nectarívoras, também visitam as flores e podem, em alguns casos, desempenhar um papel importante na polinização.
PALAVRAS-CHAVE: interações aves-plantas, beija-flores, aves Passeriformes, polinização, Brasil.

ABSTRACT. Bird-flower interactions are a rich subject in Ecology and, in many cases, can be viewed as mutualistic relationships. Many plants rely on birds to pollination and, similarly, many birds depend on flower nectar for feeding. Taking into account the importance of the theme, the present work offers a review of the interactions between birds and flowers in Brazil, based on literature published since 1975. Many studies have been carried on bird-plant interactions and related subjects in Brazil, especially in the Atlantic Forest of southeastern Brazil. However, for some regions or biomes, studies are still virtually nonexistent. Hummingbirds, which represent the dominant group in bird-plant interactions in the Neotropics, are the birds most commonly cited. Nevertheless, some papers show that a wide range of perching birds, not necessarily adapted for nectar-feeding, also visit the flowers in search of nectar and, in some cases, can play an important role in pollination.
KEY WORDS: bird-plant interactions, hummingbirds, perching birds, pollination, Brazil.

Anthophiles or flower visitors are animals which feed on flowers (Kevan 1999) and may effect pollination or simply remove the floral resources sought by pollinators (Inouye 1980). When mutualistic, the relationship between plants and bird pollinators involves, basically, two processes: (1) the pollen transport between plants by foraging animals, promoting outcrossing, and (2) the production of resources which attracts pollinators to flowers (Brown and Kodrick-Brown 1979). The study of pollination is an extremely active field of Ecology and this is especially true with respect to bird pollination systems. The interest in foraging ecology, energetics, and social behavior of nectarivorous birds is leading to a broader appreciation of their role as pollinators (Stiles 1981).

Data on the interaction among organisms are important for understanding general functioning of communities and for fauna and flora management and conservation. Many birds depend on nectar as their major source of energy. In the same way, many plants rely on birds for pollination. Thus, the loss of such interactions may have important consequences for conservation. Snow and Snow (1986) have mentioned that the way in which the community of nectarivorous birds living in an area exploits the flowers is of both ornithological and botanical interest.

Nectarivorous birds are found in many parts of the world and five major groups, each one restricted to a geographical area, can be recognized. The Trochilidae (hummingbirds) occur in the Americas, the Meliphagidae (honeyeaters) occur in Australia, the Drepanididae (Hawaiian honeycreepers) are endemic to Hawaii, and the Promeropidae (sugarbirds) and Nectariniidae (sunbirds) are characteristically from Africa (Collins *et al*. 1990, Kearns and Inouye 1993). Furthermore a set of birds adapted in different degrees to nectarivory also visits the flowers and can act as pollen vectors (Faegri and Pijl 1979, Stiles 1981). In Brazil, we can recognize two major groups of birds that feed on floral nectar and differ both in morphology and feeding behavior: hummingbirds (Trochilidae) and perching birds, the latter represented mainly by Passeriformes.

Hummingbirds are the most specialized nectarivorous birds (Stiles 1981) and, in several communities, their coevolution (diffuse) with flowers is considered to have played an important role on community organization (Feinsinger 1983, Cotton 1998a). Compared with hummingbirds, Neotropical flower-visiting passerines exhibit a low to moderate degree of specialization for nectar feeding and some are often regarded as "parasites" on hummingbird-flower systems (Stiles 1981). Nevertheless, as Westerkamp (1990) have pointed out, perching birds may have a greater role on pollination than normally considered.

Taking into account the importance of the subject, this paper presents a review of information relevant to ecological interactions between birds and flowers in Brazil. The literature review was conduced in both national and international journals, related to Ornithology, Ecology, Zoology, and Botany, from 1975 to 2002. A search pattern based on the following keywords, presented in the title, abstract or author keywords, was used: hummingbird; bird; pollination; ornithophily; flower, floral, nectar and Brazil. Only studies developed in Brazil were included in the analysis. Unpublished works and academic thesis were not considered. Ornithological classification follows the Comitê Brasileiro de Registros Ornitológicos (2003).

GEOGRAPHIC DISTRIBUTION AND GENERAL SUBJECTS OF STUDIES

Bird pollination and related subjects have been studied a great deal in Brazil in the past 25 years (see also Willis 2002). Nevertheless, this knowledge is dispersed on the literature. A total of 72 publications that mention flower visiting or pollination by birds were found. Perhaps as a consequence of distribution of research groups in Brazil, the great proportion of the studies (ca. 76 %) was conducted in southeastern Brazil, especially in São Paulo State. The remaining studies were distributed among the northeastern, northern, and Central Brazil. The absence of publications on bird-plant interactions and related subjects for southern Brazil is remarkable (table 1).

Regarding biomes, up to 75% of the studies were carried out either in the Atlantic Forest or in the Cerrado (Brazilian Savanna). Other biomes studied were the Caatinga, the Amazon Forest, and the Pantanal. Some studies were developed in areas very altered by human activities, such as university's *campi*, roadsides, and cities, being treated here as separated cases, and denominated as urban sites (table 2).

The subjects and goals of the studies were varied. Only a few studies, restricted to southeastern Brazil, comprise communities of nectarivorous birds (hummingbirds) and their flowers. Most studies that report relationships between birds and flowering plants are concerned on floral biology, pollination, and/or reproduction of particular plant species or genus, in which birds are reported as pollinators or, at least, as anthophiles. Others, are focused on bird visitation to a given plant species or genus. In other cases, studies concerned on the feeding ecology and/or diet composition of birds only cite their consumption of nectar or flowers. Therefore, based on the goals of the studies, the particular set of flower traits related to specific groups of pollinators (pollination syndromes, see Faegri and Pijil 1979, Proctor *et al*. 1996), and the way which birds interact with flowers (Inouye 1980, 1983), studies were grouped and discussed in general topics, as follows:

COMMUNITY-LEVEL STUDIES: HUMMINGBIRDS AND THEIR FLOWERS

Only seven studies, restricted to southeastern Brazil and conducted mostly in the Atlantic Forest encompass communities of nectarivorous birds – hummingbirds – and their flowers (Snow and Teixeira 1982, Snow and Snow 1986, Sazima *et al*. 1996, Buzato *et al*. 2000, Vasconcelos and Lombardi 1999, 2000, 2001). Besides those, Varassin and Sazima (2000) observed hummingbird and butterfly visitation to bromeliads in the Espírito Santo. With regard to the flower assemblage used by a specific hummingbird species, the study of Sazima *et al*. (1995a) to *Ramphodon naevius* was the only one found.

As a general rule, the studies on hummingbirds and their flowers provide information about hummingbird and bird flower compositions, temporal and spatial distributions of flowers, floral features, and data on nectar volume and/or concentration. Some studies also encompass the nectar partitioning between the hummingbird species, their community roles, and their role as pollinators.

Table 1. Geographic distribution of studies conducted in Brazil that mention bird visits to flowers or concern subjects related to bird-flower interactions. Only published studies were considered (1975-2002).

Brazil's geographic regions	Number of studies[1]
Northern	5
Northeastern	8
Central Brazil	5
Southeastern	55*
Southern	0

1. Some studies were carried out in more than one state.
*Nectar samples by Perret at al. (2001) were performed either in southeastern Brazil or in glasshouses in Geneva, Switzerland.

Table 2. Number of published studies conducted in different Brazilian Biomes that mention bird visits to flowers or concern subjects related to bird-flower interactions. Only published studies were considered (1975-2002).

Biomes	Number of studies[1]
Atlantic Forest	37
Cerrado	19
Caatinga	4
Pantanal	2
Amazon Forest	5
Urban sites	8

1. Some studies comprise more than one state.

For instance, regarding the floristic composition of bird-pollinated flowers in Brazil, it was ascertained that hummingbirds feed on and pollinate a wide range of plant species. However, some families such as Gesneriaceae and especially Bromeliaceae are apparently more representative among the hummingbird-pollinated floras in the Atlantic Forest of southeastern Brazil, as well as in other Neotropical communities (Stiles 1978, Snow and Snow 1980).

Buzato *et al.* (2000), for example, gave an account that Bromeliaceae comprised about 36% of the 86 hummingbird-pollinated species at their study sites; according to the authors, this proportion associated with the nectar characteristics, qualify the bromeliads as the most important resources to hummingbirds in the Atlantic Forest of southeastern Brazil (see also Sazima *et al.* 1995a, 1999). Similarly, the study of Varassin and Sazima (2000) exemplify the importance of the Trochilidae as pollen vectors for bromeliads in the Atlantic Forest; hummingbirds accounted for 72-96% of the visits received by the bromeliad genera *Aechmea*, *Billbergia*, *Nidularium*, and *Vriesea*.

From the viewpoint of coevolution, it have been suggested the coevolution between the hermit *Phaethornis eurynome* and three particular plant species (*Heliconia vello-ziana*, *Sinningia polyantha*, and *Siphocampylus betulifolius*) in southeastern Brazil (Snow and Teixeira 1982). However, one of these species, *H. velloziana,* is also pollinated and dominated by another hermit, *Ramphodon naevius* (Sazima *et al.* 1996), and as pointed out by Sazima *et al.* (1996) there is still no convincing evidence of coevolution between a hummingbird and a particular plant species in southeastern Brazil. Actually, coevolutionary interactions of this nature are a rare event in nature and most hummingbirds and their food plants exemplify diffuse coevolution between two diverse groups of species (Feinsinger 1983).

Outside the Atlantic Forest range, the studies of Vasconcelos and Lombardi (1999, 2001) about hummingbirds and their flowers in the Campos Rupestres seem to be the only ones published to date. The importance of Asteraceae in the diet of *A. scutatus*, a hummingbird endemic to that vegetation type, is remarkable (Vasconcelos and Lombardi 2001).

Despite Amazon Forest being an area rich in both plants and birds, we found no publications regarding hummingbirds and hummingbird-pollinated flowers at the community-level for that biome in Brazil (but see Cotton 1998a, b, for studies in the Colombian Amazon). The same also seems true for the Caatinga. In effect, even in the Atlantic Forest and Cerrado, considered biodiversity hot spots – the former is actually considered one of the hottest hotspots of biodiversity and endemism of the planet (Myers *et al.* 2000) – only a few forest sites in southeastern Brazil have been studied. Therefore, certainly much more are to be examined about hummingbird-flower interactions in Brazil.

It would be very interesting to compare the composition and richness of ornithophilous flowers and diversity of hummingbirds in different communities occurring in different sites (see Buzato *et al.* 2000), Brazilian regions or Biomes. How species richness, floristic composition, diversity of floral traits of ornithophilous plants, as well as the composition and diversity of hummingbirds vary among different sites? Do hummingbird species richness and abundance correlate with flower availability? How hummingbird-plant interactions are affected by fragmentation or species loss? What is the role of other bird groups as anthophiles and pollinators on the level of community? How bird-flower networks function in urban sites? Perhaps, the evaluation of these questions might constitute good goals for future studies and contribute to outline patterns of bird-flower interactions in Brazil.

PARTICULAR INTERACTIONS: FLOWER VISITING AND POLLINATION BY BIRDS

Studies reporting interactions between birds and a particular plant species or genus were by far the most abundant (ca. 70%) and comprised mostly studies focused on pollination ecology and other aspects related to plant reproduction. Others studies focused chiefly on the feeding behavior of birds on plants (Piratelli 1997), patterns of bird visitation to flowers (Van Sluys and Stotz 1995, Van Sluys *et al.* 2001, Melo 2001) or territoriality at flowering plants (Raw 1996). At least 34 papers (out of 54 concerning particular interactions) reported birds as effective pollinators of one or more species, in some instances sharing this role with other animals.

Although studies comprising communities of nectarivorous birds and their flowers provide a broader view of bird-flower relationships than studies focused on the investigation of specific relationships between birds and flowers, the latter often provide detailed data of the flower traits (morphology and nectar rewards), floral biology, reproductive systems, and spectrum of visitors. Most also describe in detail the behavior and role of birds as pollinators. Therefore, these studies may lead to the discussion of the possible factors and mechanisms involved in such associations, as well as its consequences.

Considering that nectar is the floral reward most generally sought by birds (but see Sazima *et al.* 2001), variations on this reward are expected to affect many aspects of pollinator behavior (Torres and Galetto 1998). Studies that investigate the pattern of nectar production along the day or the flower lifespan were nearly absent in the beginning of 1990's but have increased substantially in recent years (Bittrich and Amaral 1996, Vicentini and Fisher 1999, Freitas and Sazima 2001, Melo 2001, Quirino and Machado 2001, Varassin *et al.* 2001). Some papers have suggested that the characteristics of nectar secretion pattern could influence bird visits to flowers or foraging behavior (Melo 2001, Quirino and Machado 2001, Freitas and Sazima 2001, Varassin *et al.* 2001). Nevertheless, until 2002, virtually no published study has investigated the existence of a significant correlation between bird visitation and nectar secretion rates – or patterns of nectar availability – and this hypothesis remains to be investigated.

With respect to bird morphology in relation to flower structure, bill lengths in relation to corolla lengths have been mentioned as an important factor in determining the ability of bird to access legitimately the nectar and, consequently, their aptitude as a pollen vector (Sazima and Machado 1983, Machado and Sazima 1995, Piratelli 1997). Actually, the anatomical and behavioral fit of the animal and the flower has been recognized as an important feature to determine if a given anthophile is a pollinator (Kevan 1999, Corbet 2000).

Perhaps, one of the best examples of the implications of morphological fit between flowers and pollinators in Brazil is given by the study of Sazima *et al*. (1994), concerning a species with features not uniquely related to bird-pollination. They observed that *Siphocampylus sulfureus* (Campanulaceae) presents intermediate floral features between hummingbird and bat syndromes of pollination and thus benefits from the activity of both groups as pollinators. The corolla morphology of this species allows both animals to contact the anthers and stigmas and pollinate the flowers. In contrast, another species observed by the authors, *S. umbelatus*, seems only bat-pollinated; the hummingbird *Leucochloris albicollis* also visited this species but usually did not contact the reproductive organs, therefore acting as a nectar thief. This study also exemplifies that classifying a given species into a pollination syndrome may be not so straightforward than previously though.

The concept of pollination syndromes recognizes functional groups of plants that share similar floral traits and spectrum of visitors, a possibly consequence of diffuse coevolution (Corbet 2000). The studies concerning pollination in Brazil usually take into account such concept, and often use the term ornithophily to refer to plants with features related to bird pollination (Sazima 1977, 1981, Barbosa 1999, Quirino and Machado 2001, Lopes *et al*. 2002). However, when species display features intermediate between two syndromes of pollination, with different groups of animals sharing the role of major pollinators, as exemplified by *S. sulfureus*, or present the "ability" to be pollinated by a diverse array of animals, classifying such species into one or other syndrome may be to some extent controversial (see also Machado and Sazima 1987, Buzato *et al.* 1994, Vieira and Carvalho-Okano 1996, Sigrist and Sazima 2002).

ANTHOPHILES BIRDS AND THEIR ROLE AS POLLINATORS

Studies on specific bird-plant relationships have revealed that there is a great diversity of anthophiles birds in Brazil (table 3) and that some ornithophilous plants appear to be adapted for perching birds. Hummingbirds represent both the ecologically and numerically dominant group in bird-plant interactions in the Neotropical region (Stiles 1981). But, despite the notability of hummingbird-plant interactions in Brazil and in the Neotropics as a whole, some researches have shown that a wide range of perching birds, some with no special adaptation for nectar-feeding, also visit the flowers and can, in some instances, exert an important role in pollination, as documented for *Norantea brasiliensis* (Sazima *et al*. 1993), *Mabea fistulifera* (Vieira and Carvalho-Okano 1996, Olmos and Boulhosa 2000), *Hortia brasiliana* (Barbosa 1999), *Moronobea coccinea* (Vicentini and Fisher 1999), some bromeliads with short corollas (Sazima and Sazima 1999), *Combretum fruticosum* (Quirino and Machado 2001), *Combretum lanceolatum* (Sazima *et al*. 2001), and *Erythrina dominguezii* (Ragusa-Netto 2002).

Perching birds are both taxonomically and ecologically diverse (see Willis 2002; table 3) and, except to those species highly nectarivorous as the Bananaquit, they may take advantage of a locally abundant resource – nectar – predictable both in time and space, as an alternative resource in periods of food scarcity (e.g. Barbosa 1999, Olmos and Boulhosa 2000, Ragusa-Netto 2002). The flowering of species such as *Norantea brasiliensis* (Sazima *et al*. 1993), *Hortia brasiliana* (Barbosa 1999), and *Combretum lanceolatum* (Sazima *et al.* 2001), for example, attracts a set of birds that find a rich and accessible source of energy and may, sometimes, represent better pollen vectors than hummingbirds.

Considering only those studies focused on particular interactions between plants and pollinators, birds were cited as pollinators (or potential pollinators) of at least 42 species. Although these plants are taxonomically diverse, many of them share floral traits such as bright colored flowers, diurnal anthesis, absence of odor, and copious and relatively dilute nectar, which are related to ornithophily (Faegri and Pijl 1979, Stiles 1981, Proctor *et al.* 1996).

Nevertheless, based on the literature, it is possible to observe that, corolla morphology of -flowers pollinated by perching birds is slightly different from that of hummingbird-flowers, since non-tubular corollas seem more frequent in the former (Sazima *et al*. 1993, Barbosa 1999, Sazima *et al.* 2001). Given that perching birds have bills that are often wider and shorter than those of hummingbirds, the existence of non-tubular flowers, as well as perches, allows them to reach the reward, that otherwise would be inaccessible – and also transport pollen among flowers.

In addition to corolla morphology, it is recognized that nectars of hummingbird-flowers and passerine-flowers differ in regard to sugar composition; in the former, sucrose is the prevailing sugar, whereas in the latter, there is a low proportion of sucrose and a high proportion of hexose (Baker and Baker 1983a, b, 1990, Baker *et al*. 1998). In Brazil, we found no studies explicitly dealing with such dichotomy, but reward composition of bird-pollinated flowers have been examined in some studies and, in general, support this perspective (Perret *et al*. 2001, Sazima *et al*. 2001).

If the differences on nectar sugar compositions – and floral architecture – really reflect adaptations to different kinds of Neotropical birds (hummingbirds and perching birds), these differences could be valuable in predicting or evaluating the pollinators of a given plant. Bittrich and Amaral (1996), for example, observed the hummingbird pollination of *Symphonia globulifera* in the Brazilian Amazon, but suspected that this was not a characteristic hummingbird-species. Two years latter, Gill *et al*. (1998) reported that the nectar of *S. globulifera* approaches those typical of passerine-pollinated species, with a high proportion of hexose.

Birds visit a wide range of plant species and may interact with them in different ways. Most relationships between birds and ornithophilous plants are mutually beneficial, given that foraging birds are provided with food and transport pollen among flowers, promoting pollination. In other cases, however, birds may obtain nectar without effecting pollination, even in bird-adapted flowers, due to morphological and behavioral constraints (Sazima *et al*. 1993, Machado and Sazima 1995, Vitali-Veiga and Machado 2000).

Moreover, studies have recorded birds, especially hummingbirds, probing flowers that display features related to pollination (and pollinated) by other animals, such as bees, butterflies and bats. In these cases, morphological and behavioral aspects of birds in relation to flowers may preclude pollination, and birds act most as nectar thieves, robbers or, sometimes, as additional pollinators (Sazima and Sazima 1978, Sazima *et al*. 1989, Bergallo 1990, Siqueira Filho 1998, Machado and Lopes 2000, Singer and Sazima 2001).

Hummingbirds appointed as nectar thieves or robbers are generally short-billed Trochilinae, but four studies have cited the hermit *Phaethornis ruber* as a nectar thief or robber (Machado *et al*. 1998, Machado and Lopes 2000, Singer and Sazima 2001, Lopes *et al*. 2002). Bergallo (1990), additionally, report *Phaethornis superciliosus* as an opportunist visitor to bat-pollinated flowers of *Bauhinia bongardii*, although it could eventually promote pollination.

In Brazil, bird utilization of non-ornithophilous species has been reported for several species (Sazima *et al*. 1982, 1989, Bergallo 1990, Oliveira and Gibbs 1994, Santos 1997, Machado *et al*. 1998, Gribel *et al*. 1999, Machado and Lopes 2000, Singer and Sazima 2001, Melo 2001). However, little is know about effects of nectar robbing on the reproduction of Brazilian plants. How does it affect pollinator visitation to flowers or pollinator movements among flowers? What are the effects on plant reproduction? To what extend hermit hummingbirds are involved in non-mutualistic relationships with flowers? These are questions which still need to be answered.

FEEDING ECOLOGY OF BIRDS: FLOWERS AND NECTARS AS FOOD SOURCES

We found some studies concerning feeding ecology and diet composition of birds. Although they are not focused on interactions between birds and flowers, they mention the use of floral resources (nectar or flower tissues). Such studies were included in this review because they lead to the appreciation of floral resources as a component of the diet for some species of non-nectarivorous birds and may help in the evaluation of the array of birds that make use of floral rewards as a food source. However, because they virtually never assess the mechanisms involved in such relationships, they will not be discussed in detail.

Birds reported as nectar or flowers consumers by these studies included the Black-legged Dacnis, *Dacnis nigripes* (Gonzaga 1983), the Red-rumped Cacique, *Cacicus haemorrous* and the Gold-winged Cacique, *C. cela* (Pizo 1996), the White-rumped Tanager, *Cypsnagra hirundinacea* (Ragusa-Netto 1997), the Cactus parakeet, *Aratinga cactorum* (Barros and Marcondes-Machado 2000), and the Saffron Toucanet *Baillonius bailloni* (Galleti *et al*. 2000).

For most of these birds, flowers and/or nectars represent a minor proportion of their diet and are consumed principally in periods of low availability of major food items; or non-nectarivorous birds may simply take advantage of a locally abundant resource predictable both in time and space, as an alternative energy source. However, *Mabea brasiliensis* (Euphorbiaceae), seems an important food source for *Dacnis nigripes* (Thraupinae) in Magé (RJ); the presence of the bird in that area during the winter was suggested to be influenced by the flowering of that species (Gonzaga 1983).

STUDIES ON RELATED SUBJECTS

Some publications explored other subjects related to plant-pollinator interactions, such as the nectar sugar composition of species belonging to different syndromes, including ornithophilous species (Perret *et al*. 2001) and the nutrient preferences of Brazilian hummingbirds (Bouchard *et al*. 2000). At the community-level, Silberbauer-Gottsberger and Gottsberger (1988) evaluated the pollination systems in Cerrado sites of southeastern and central Brazil. From the 279 species analyzed, only 5 were considered to be ornithophilous and in only one, the hummingbirds acted as exclusive pollen vectors. Pizo (1994), on the other hand, investigated the use of bromeliads by birds in the Fazenda Intervales (SP); the author observed that bromeliads represent important resources for birds living in that area, not only with respect to nectar, but also to other food sources (fruits and animals), water and nesting sites or nest-building material.

CONCLUSIONS AND PERSPECTIVES

The study of bird-flower interaction represents a rich field in Ecology, regarding both ecological and evolutionary aspects. Many of these interactions present a mutualistic character, and understanding such relationships is nowadays imperative to ecosystem management and conservation. An array of birds, with emphasis to hummingbirds, relies – in different degrees – on flower nectar for feeding and, similarly, many angiosperms rely on birds for pollination. Thus, the maintenance of interactions between pollinating animals and flowering plants should be taken into account in the proposal of conservation and management strategies.

Many studies have been carried on bird-plant interactions and related subjects in Brazil, but certainly much more still remain to be studied. For example, little information exists on the consequences of habitat fragmentation and species loss on pollinator-plant networks. Also, in some Brazilian states or biomes, only a few studies on bird-pollination of particular plant species have been carried out, being notable the absence of studies on the level of communities. It is particularly remarkable the absence of publications for southern Brazil regarding bird-flower interactions at any level.

Studies concerning relationships between birds and flowers on the community level offer a broad view of such interactions, creating a good opportunity for outlining patterns of bird-flower interactions, as well as to define the major factors involved. On the other hand, studies dealing with particular bird-plant interactions, by concentrating the efforts on only a few plant species, make it possible detailed investigation of the mechanisms governing such interactions as well as its consequences for birds and plants. Therefore, these two scales of investigation appear to be complementary to a better understanding on the ecology and evolution of bird-plant interactions and the maintenance of plant-pollinator systems within communities.

Hummingbirds certainly are the major bird group of pollinators in Brazil, as well as in other Neotropical sites. However, given that some plant species appear to be more suited for pollination by perching birds, an increasing focus to them could lead to a broader appreciation of their role as flower visitors and pollinators. Because few Brazilian studies have investigated the proportion of sugars in nectars of ornithophilous flowers, it would be also of interest for future studies to examine possible variations in nectar sugar composition as well as in other characteristics of flowers pollinated by hummingbirds and perching birds in Brazil.

Table 3. Bird visited or pollinated species in Brazil. Compiled from papers published since 1975. Studies concerning hummingbird communities and their flowers are not included here.

Family/species	Avian visitors	State/Font
ACANTHACEAE		
Ruellia asperula (O)	*Eupetomena macroura*, *Amazilia lactea*, *Amazilia versicolor*, *Chrysolampis mosquitus*, *Hylocharis sapphirina* (Trochilidae)	PE, Machado and Sazima (1995)
R. brevifolia (O-P)	*Colibri sp.*, *A. lactea*, *A. versicolor*, *E. macroura*, *Phaethornis pretrei*, *Thalurania glaucopis* (Trochilidae)	SP, Sigrist and Sazima (2002)
AMARYLLIDACEAE		
Hippeastrum atibaya (O)	*Phaethornis pretrei*, *Leucochloris albicollis*, *Thalurania glaucopis*, *Chlorostilbon aureoventris* (Trochilidae)	SP, Piratelli (1997)
H. psittacinum (O-P?)	*P. pretrei*, *T. glaucopis*	SP, Piratelli (1997)
ASTERACEAE		
Mutisia coccinia (O)	*A. lactea*, *Anthracothorax nigricollis*, *Colibri serrirostris*, *P. pretrei* (Trochilidae)	SP, Sazima and Machado (1983)
BIGNONIACEAE		
Lundia cordata (O)	*Phaethornis ruber*, *P. pretrei*, E. *macroura*, *Amazilia fimbriata* (Trochilidae)	PE, Lopes *et al.* (2002)
Pyrostegia venusta (O)	*E. macroura*, *A. lactea*, *P. pretrei* (Trochilidae)	SP, Gobatto-Rodrigues and Stort (1992)
BOMBACACEAE		
Ceiba petandra (Q)	Unidentified Trochilidae	AM, Gribel *et al.* (1999)
Pseudobombax sp. (Q)	Cacicus haemorrhous *(Emberezidae: Icterinae)*	SP, Pizo (1996)
Spirotheca passifloroides (O)	Cacicus haemorrhous	SP, Pizo (1996)
BROMELIACEAE		
Acanthostachys strobilaceae (O)	*C. aureoventris*, *A. lactea*, *P. pretrei* (Trochilidae); *Coereba flaveola* (Emberezidae: Coerebinae)	SP, Sazima and Sazima (1999)
Aechmea bomeliifolia (O)	*C. aureoventris* (Trochilidae); *Coereba flaveola* (Coerebinae)	SP, Sazima and Sazima (1999)
A. distichanta (O)	*A. fimbriata* (Trochilidae); *C. flaveola* (Coerebinae)	SP, Sazima and Sazima (1999)
Encholirium glaziovii (Q)	*E. macroura* (Trochilidae)	MG, Sazima *et al*. (1989)
Hohenbergia ridleyi (M)	*A. fimbriata, Amazilia leucogaster, C. aureoventris, E. macroura, Phaethornis ruber* (Trochilidae)	PE, Siqueira Filho (1998)
Pitcairnia flammea (O?)	*Phaethornis pretrei*, *Thalurania glaucopis*, unindentified hummingbird (Trochilidae)	RJ, Wendt *et al*. (2002)
Vriesea carinata (O)	*Ramphodon naevius* (Trochilidae)	SP, Araujo *et al*. (1994)

Table 3. Cont'd

Family/species	Avian visitors	State/Font
V. ensiformis (O)	*Ramphodon naevius*	SP, Araujo *et al*. (1994)
V. incurvata (O)	*Ramphodon naevius*	SP, Araujo *et al*. (1994)
V. neoglutinosa (O)	*A. fimbriata, C. aureoventris, Phaethornis idaliae, Polytmus guainumbi* (Trochilidae)	ES, Van Sluys and Stotz (1995)
V. procera (O)	*A. fimbriata, C. serrirostris, T. glaucopis, E. macroura, Melanotrochilus fuscus* (Trochilidae)	RJ, Van Sluys *et al.* (2001)
V. sazimae (Q)	*Stephanoxis lalandi* (Trochilidae)	SP, Sazima *et al*. (1995)
Bromeliads (species not mentioned)	*Phaethornis eurynome, Phaethornis squalidus, Thalurania glaucopis* (Trochilidae); *Euphonia pectoralis* (Emberezidae: Thraupinae)	SP, Pizo (1994)
CACTACEAE		
Melocactus salvadorensis (O)	*Chrysolampis mosquitus* (Trochilidae)	BA, Raw (1996)
CAMPANULACEAE		
Siphocampylus sulfureus (Q-O)	*Clytolema rubricauda, Leucochloris albicollis, Stephanoxis lalandi* (Trochilidae)	SP, Sazima *et al.* (1994)
S. umbellatus (Q)	*L. albicollis*	SP, Sazima *et al.* (1994)
CARYOCARACEAE		
Caryocar brasiliense (Q)	*Amazilia fimbriata, Eupetomena macroura, Thalurania furcata* (Trochilidae); *Cyanocorax cristatellus* (Corvidae); *Dacnis cayana, Hemithraupis guira, Tangara cayana, Thraupis sayaca, Thraupis palmarum, Tachyphonus rufus, Piranga flava* (Thraupinae)	DF, Melo (2001)
CLUSIACEAE		
Symphonia globulifera (O)	*Chlorestes notatus, T. furcata* (Trochilidae); *Cacicus cela* (Icterinae); other unidentified birds	AM, Bittrich and Amaral (1996)
Moronobea coccinea (O) (1998)	*Phaethornis superciliosus, Florisuga mellivora, T. furcata, Campylopterus largipennis, Heliothrix aurita* (Trochilidae); *Brotogeris chrysopterus* (Psittacidae).	AM, Vicentini and Fischer
COMBRETACEAE		
Combretum lanceolatum (O)	*Amazilia versicolor* (Trochilidae); *Columba cayannensis, Columba picazuro* (Columbidae); *Diopsittaca nobilis, Aratinga aurea, Aratinga leucophtalmus, Brotogeris chiriri* (Psittacidae); *Melanerpes candidus* (Picidae); *Pseudoseidura cristata* (Furnariidae); *Elaenia flavogaster, Maxetornis rixosa, Pitangus sulphuratus* (Tyrannidae); *Turdus leucomelas, Turdus rufiventris* (Muscicapidae:Turdinae); *Coereba flaveola* (Coerebinae); *Ramphocelus carbo, Tachyphonus rufus, Thraupis palmarium, T. sayaca, Euphonia chlorotica* (Thraupinae); *Coryphospingus cucullatus, Paroaria capitata* (Emberezidae: Emberezinae); *Cacicus cela, Gnorimospsar chopi, Icerus cayanensis, Icerus jamacaii, Psarocolius decumanus* (Icterinae); *Saltator coerulescens* (Emberezidae: Cardinalinae).	MT, Sazima *et al.* (2001)
C. fruticosum (O)	*Chlorostilbon aureoventris* (Trochilidae); *C. flaveola* (Coerebinae); *Cyanerpes cyaneus* (Thraupinae)	PE, Quirino and Machado (2001)
CONVOLUACEAE		
Ipomoea hederifolia (O)	*Amazilia lactea, A. versicolor, Calliphox amethystina, Chlorostilbon aureoventris, Eupetomena macroura, Phaethornis pretrei* (Trochilidae)	SP, Machado and Sazima (1987)
I. Quamoclit (P)	*Amazila versicolor, Chlorostilbon aureoventris* (Trochilidae)	SP, Machado and Sazima (1987)
EUPHORBIACEAE		
Jatropha mollissima	*Aratinga cactorum* (Psittacidae)	BA, Barros and Marcondes-Machado (2000)

Table 3. Cont'd

Family/species	Avian visitors	State/Font
Mabea brasiliensis	*Dacnis nigripes* (Thraupinae)	RJ, Gonzaga (1983)
M. fistulifera (Q-O)	*Anthracothorax nigricollis*[C], *C. amethystina*[C], *Eupetomena macroura*[A,B,C], *Hylocharis chrysura*[C], *Leucochloris albicollis*[C], *Melanotrochilus fuscus*[C], *Phaethornis pretrei*[C] (Trochilidae); *Coereba flaveola*[A,B] (Coerebinae); *Elaenia flavogaster*[C], *Elaenia chiriquensis*[C] (Tyrannidae); *T. leucomelas*[C] (Turdinae); *Dacnis cayana*[C], *C. cyaneus*[C], *Conirostrum bicolor*[C], *Tangara cayana*[C], *T. sayaca*[A,B,C], *T. palmarum*[C], *Tachyphonus coronatus*[A], *Trichothraupis melanops*[A], *Nemosia pileata*[C], *Pipraeida melanota*[A] (Thraupinae), *Mimus saturninus*[A] (Mimidae); *Pitangus sulphuratus*[A] (Tyrannidae)	A. MG, Vieira *et al.* (1992) B. MG, Vieira and Carvalho-Okano (1996); C. SP, Olmos and Boulhosa (2000)
FABACEAE		
Bauhinia bongardii (Q)	*Amazilia versicolor*, *Phaethornis superciliosus* (Trochilidae)	PA, Bergallo (1990)
Bowdichia virgilioides	*Amazilia lactea*, *Amazilia sp.*, *Colibri serrirostris*, *C. aureoventris*, *C. amethystina*, *E. macroura* (Trochilidae); *C. flaveola* (Coerebinae); *D. cayana* , *T. cayana*, *T. sayaca* (Thraupinae); *Aratinga aurea* (Psittacidae)	MG, Rojas and Ribon (1997)
Erythrina speciosa (O)	*Amazilia sp.*, *Chlorostilbon aureoventris*, *Eupetomena macroura* (Trochilidae); *Passer domesticus* (Passeridae); *Coereba flaveola* (Coerebinae)	SP, Vitali-Veiga and Machado (2000)
Erythrina dominguezii (O)	*Brotogeris chiriri*, *Nandayus nanday*, *Aratinga acuticaudata* (Psittacidae); *Psarocolius decumanus*, *Icterus cayanensis*, *Icterus icterus* (Icterinae)	MS, Ragusa-Netto (2002)
GENTIANACEAE		
Irlbachia alata (Q)	*Phaethornis ruber* (Trochilidae)	PE, Machado and Sazima (1998)
GESNERIACEAE		
Nematanthus fritschii (O)	*Ramphodon naevius* (Trochilidae)	SP, Franco and Buzato (1992)
MALVACEAE		
Abutilon rufinerve (Q-O)	*Phethornis eurynome*, *C. rubricauda*, *S. lalandi*, *Thalurania furcata* (Trochilidae)	SP, Buzato *et al*. (1994)
A. regnellii (Q-O)	*C. rubricauda*, *L. albicollis*, *T. furcata*	MG, Buzato *et al*. (1994)
Abutilon aff. regnellii (Q-O)	*P. eurynome*, *C. rubricauda*, *L. albicollis*, *S. lalandi* (Trochilidae)	SP, Buzato *et al*. (1994)
Pavonia montana (O)	*Phaethornis pretrei* (Trochilidae)	MG, Sazima (1981)
P. malvaviscoides (O)	*P. pretrei*, *Thalurania glaucopis* (Trochilidae)	MG, Sazima (1981)
MARCGRAVIACEAE		
Norantea brasiliensis (O)	*Amazilia fimbriata*[A], *Anthracothorax nigricollis*[A], *Aphantochroa cirrichloris*[A], *Chlorestes sp*[B]., *Eupetomena macroura*[A,B], *Hylocharis cyanus*[A], *Lophornis chalybea*[A], *Melanotrochilus fuscus*[A], *T. glaucopis*[A] (Trochilidae); *Coereba flaveola*[A] (Coerebinae), *Chlorophanes spiza*[A], *Dacnis cayana*[A], *Euphonia violaceae*[A], *Hemithraupis ruficapilla*[A], *Ramphocelus bresilius*[A], *Tachyphonus cristatus*[A], *Tangara cyanocephala*[A], *Tangara desmaresti*[A], *Tangara seledon*[A] (Thraupinae)	A. SP, Sazima *et al.* (1993); B. RJ, Pinheiro *et al.* (1995)
Souroubea guianensis (P?)	*Phaethornis ruber* (Trochilidae)	PE, Machado and Lopes (2000)
MIMOSACEAE		
Inga sp. (Q)	Cacicus haemorrhous *(Icterinae)*	SP, Pizo (1996)
ONAGRANACEAE		
Fuchsia sp. (O)	*Cacicus chrysopterus* (Icterinae)	SP, Pizo (1996)

Table 3. Cont'd

Family/species	Avian visitors	State/Font
ORCHIDACEAE		
Stenorrhynchos lanceolatus (O)	*Phaethornis eurynome, Leucochloris albicollis, T. glaucopis* (Trochilidae)	RJ, Singer and Sazima (2000)
Aspidogyne longicornu (M)	*P. ruber* (Trochilidae)	SP, Singer and Sazima (2001)
PASSIFLORACEAE		
Passiflora mucronata (Q)	Unidentified Trochilidae	ES/SP, Sazima and Sazima (1978)
P. speciosa (O)	*Phaethornis idaliae* (Trochilidae)	ES, Varassin *et al*. (2001)
RUBIACEAE		
Ferdinandusa speciosa (O)	*P. pretrei, C. aureoventris* (Trochilidae)	MG, Castro and Oliveira (2001)
Kerianthera preclara (O)	*Eupetomena macroura* (Trochilidae)	AM, Marques-Souza *et al*. (1993)
Manettia luteo-rubra (O)	*Phaethornis squalidus, P. eurynome, T. glaucopis* (Trochilidae)	SP, Passos and Sazima (1995)
RUTACEAE		
Hortia brasiliana (O)	*Saltator atricollis* (Cardinalinae), *Coryphospingus cucculatus, Volatinia jacarina, Zonotrichia capensis* (Emberezidae: Emberezinae); *Mimus saturninus* (Mimidae); *Schistochlamys ruficapilus* (Thraupinae)	MG, Barbosa (1999)
SAPOTACEAE		
Pouteria torta	*Cypsnagra hirundinacea* (Thraupinae)	SP, Ragusa-Netto (1997)
SCROPHULARIACEAE		
Esterhazya macrodonta (O)	*Leucochloris albicollis* (Trochilidae)	SP, Freitas and Sazima (2001)
STERCULIACEAE		
Helicteres brevispira (O)	*Amazilia lactea, Chlorostilbon aureoventris* (Trochilidae)	SP, Franceschinelli and Kesseli; Franceschinelli and Bawa (2000)
TILIACEAE		
Luehea speciosa (Q)	*Eupetomena macroura* (Trochilidae)	SP, Sazima *et al.* (1982)
VELLOZIACEAE		
Barbacenia flava (O)	*Colibri serrirostris, Augastes scutatus* (Trochilidae)	MG, Sazima (1977)
Vellozia leptopetala (O)	*C. serrirostris, A. scutatus*	MG, Sazima and Sazima (1990)
V. declinans (M-O)	*C. serrirostris, A. scutatus*	MG, Sazima and Sazima (1990)
VOCHYSIACEAE		
Vochysia elliptica (M)	*Amazilia fimbriata* (Trochilidae)	DF, Oliveira and Gibbs (1994)
V. rufa (M)	*A. fimbriata*	DF, Oliveira and Gibbs (1994)
V. thyrsoidea (M)	*A. fimbriata, C. serrirostris* (Trochilidae)	DF, Oliveira and Gibbs (1994)
V. tucanorum (M)	*A. fimbriata, C. serrirostris*	DF, Oliveira and Gibbs (1994)
V. pyramidalis (M)	*A. fimbriata, C. serrirostris*	DF, Oliveira and Gibbs (1994)
V. cinnamomea (M)	*Amazilia sp.*; other unidentified Trochilidae	MG, Santos *et al*. (1997)

Pollination Syndromes: (O) Ornithophily; (Q) Quiropterophily; (P) Psichophily; (M) Melithophily

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