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Cleaner birds: a worldwide overview

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RESUMO: Aves limpadoras: uma visão global. Diversas espécies de aves se alimentam de carrapatos e outros parasitos externos, insetos, tecido morto ou ferido, coágulos e sangue, secreções e sujeira orgânica presentes no corpo de outros vertebrados (hospedeiros ou clientes). Apresento uma visão geral das assim denominadas aves limpadoras, baseada em registros de literatura, observações de campo e arquivos fotográficos. Encontrei 101 espécies em 32 famílias agindo como limpadoras, ainda que diversas delas o façam muito ocasionalmente. As aves limpadoras abrangem desde a renomada búfaga-de-bico-vermelho (*Buphagus erythrorhynchus*) da África, até a pouco conhecida perdiz-de-crista (*Rollulus roulroul*) da Malásia. A maioria das espécies de aves limpadoras apresenta cores discretas, mas há as unicolores ou de plumagem contrastante e, ainda, algumas com colorido vivo. Os clientes são principalmente herbívoros de médio a grande porte como iguanas, tartarugas, capivaras, e ungulados silvestres e domésticos, mas também incluem carnívoros como pinípedes e aves marinhas. Algumas espécies de clientes adotam posturas características enquanto são limpas, ao passo que outras ficam indiferentes ou até perturbadas pela atividade de algumas espécies de aves limpadoras. Capivaras, tartarugas-gigantes e iguanas, estão entre os clientes que posam, ao passo que a maioria dos ungulados permanece indiferente. Características como dieta onívora e/ou comportamento oportunista, bem como o hábito de se associar de diversas outras maneiras a vertebrados maiores, estão relacionados ao comportamento de limpeza. A maioria das aves limpadoras habita áreas abertas, parecendo haver poucas que habitam áreas florestadas.

PALAVRAS-CHAVE: Simbiose de limpeza, remoção de ectoparasitos e tecidos, aves oportunistas, associação com mamíferos, aves, répteis e peixes.

ABSTRACT: Various bird species feed on a variety of insects, ticks and other external parasites, dead and wounded tissue, clots and blood, secretions and organic debris found on the body of other vertebrates (hosts or clients). Herein I present an overview of so called cleaner birds based on literature records, field observations, and photo surveys. I found that 101 bird species in 32 families practice cleaning even if some of them do so very occasionally. Cleaner birds range from the renowned Red-billed Oxpecker *Buphagus erythrorhynchus* from Africa to the little known Crested Partridge *Rollulus roulroul* from Malaysia. Clients are mostly medium-sized to large herbivores such as iguanas, tortoises, capybaras, and wild and domestic ungulates, but also include carnivores such as seals and seabirds. Some clients adopt particular, posing postures while being cleaned, whereas others are indifferent or even disturbed by the activity of some cleaner species. Capybaras, giant tortoises and iguanas are among the posing clients, whereas most ungulates remain oblivious to cleaners. Features such as omnivorous diet and/or opportunistic behaviour, and the habit of associating in other ways with larger vertebrates are related to cleaning behaviour. Most cleaner birds inhabit open areas, and forest-dwelling cleaners seemingly are few.

KEY-WORDS: Cleaning symbiosis, ectoparasite and tissue removal, opportunistic birds, association with mammals, birds, reptiles, and fish.

In cleaning symbiosis, cleaners remove external parasites and feed on wounded tissue and body secretions or fluids from so called clients or hosts, an association best documented among reef fishes (reviews in Losey 1987, Grutter 2005). There are several examples of cleaners among birds as well (e.g., Dean and MacDonald 1981, Ruggiero and Ewes 1988, Sazima 2007a), the most acknowledged association being that between oxpeckers (two species of *Buphagus*, Buphagidae) and ungulates in Africa (Craig 2009). There is a remarkable diversity among cleaner birds, including both non-passerine and passerine birds. In the Palearctic, Nearctic, Ethiopian, and Oriental regions several species of Corvidae,

Sturnidae, Turdidae, and even a species in the Anatidae and another in the Phasianidae are recorded as cleaners of ungulates (e.g., Dean and MacDonald 1981, Massei and Genov 1995, Fitzpatrick and Woolfenden 1996, Ruggiero and Eves 1998, Jaramillo and Burke 1999). In the Neotropical region, besides the relatively well studied cleaning interactions in the Galápagos Islands (e.g., MacFarland and Reeder 1974, Grant 1986, Cody 2005) and a few observations in Central and South America (e.g., Marcus 1985, Peres 1996, Sick 1997), this association type received attention only recently (e.g., Tomazoni *et al.* 2005, Sazima 2007a, Sazima and Sazima 2010a, b).

The purpose of this paper is to present an overview of cleaner birds worldwide. Thus, I herein: 1) provide a comprehensive picture of the species richness and variety of cleaner birds; 2) note the behavioural similarity among a few unrelated cleaner bird taxa; 3) point out the behavioural similarity among a few unrelated client taxa; 4) note that the great majority of cleaner birds associate with medium-sized to large herbivores; 5) offer a few new insights on this association type. I also point out the need for additional studies on cleaner birds and their clients, an association which remains poorly known for most of the involved species.

METHODS

For the purpose of this overview, I regard as a cleaner any bird that seeks food on the body of other animal, one extreme of which is picking external parasites and organic debris and the other is taking blood or tissue from wounds

(*e.g.*, Weeks 2000, Koenig 1997, Cody 2005, Sazima and Sazima 2010b). Catching insects attracted to clients are included in this broad view of cleaners, since the former may, like ticks, be a nuisance and transfer diseases to the clients. Data on cleaning associations between birds and other vertebrates were gathered mostly from literature, with a few data originating from image sites and/or banks and through brief interviews with professional biologists, amateur naturalists, and amateur and professional photographers or filmmakers who recorded cleaner birds in activity under natural conditions. Additionally, field data for several cleaner bird species and their clients in Brazil were recorded whenever spotted during field trips in the areas of Campinas ($-22^{\circ}54'S$, $47^{\circ}03'W$) and Ubatuba ($-22^{\circ}26'S$, $44^{\circ}04'W$) in São Paulo in the South-east, and in the Pantanal area near Poconé ($-16^{\circ}15'S$, $56^{\circ}37'W$), in Mato Grosso in the South-west. Cleaning associations were observed with naked eye, through 10×50 binoculars and a 70-300 telephoto zoom lens mounted on a SLR camera, from a distance of about 2-30 m. 'Ad libitum'

TABLE 1: Cleaner birds, approximate species richness, and their major client types (all records in nature). Plus sign (+) means that there is a great probability that additional species are involved in cleaning. Sources: *see* Appendix 1; families in alphabetical order.

Cleaners	Number of genera and species	Client types
Anatidae	One genus, 1 species	Buffalo, antelope
Ardeidae	Three genera, 3 species	Wild and domestic ungulates, capybara
Buphagidae	One genus, 2 species	Wild and domestic ungulates
Cathartidae	One genus, 1 species	Capybara, domestic dog
Chionidae	One genus, 2 species	Elephant and fur seals
Coraciidae	One genus, 1 species	Cattle
Corvidae	Eight genera, 23 + species	Wild and domestic ungulates
Cuculidae	One genus, 1 species	Capybara
Dicruridae	One genus, 3 + species	Wild and domestic ungulates, elephant
Emberizidae	One genus, 4 species	Land and marine iguanas, tortoise, seabirds
Falconidae	Four genera, 5 + species	Ungulates, capybara, elephant seal
Furnariidae	Two genera, 2 + species	Capybara, elephant seal
Glareolidae	One genus, 1 species	Antelope
Heliornithidae	One genus, 1 species	Buffalo, antelope
Icteridae	Three genera, 6 + species	Ungulates, capybara, freshwater turtles
Jacanidae	Two genera, 3 species	Hippopotamus, capybara, elephant
Laridae	One genus, 3 + species	Marine fish (ocean sunfish), right whale
Mimidae	One genus, 4 species	Land and marine iguanas, seabirds
Motacillidae	One genus, 1 species	Antelope
Numididae	One genus, 1 species	Warthog
Phasianidae	One genus, 1 species	Bearded pig
Podicipedidae	One genus, 1 species	Hippopotamus
Psophiidae	One genus, 1 species	Deer
Pycnonotidae	Two genera, 2 species	Antelopes
Rallidae	Two genera, 2 species	Warthog, hippopotamus, capybara
Rhipiduridae	One genus, 1 + species	Kangaroo, domestic ungulates
Scolopacidae	Two genera, 2 species	Hippopotamus, whale
Stercorariidae	One genus, 1 + species	Elephant seal
Sturnidae	Five genera, 15 + species	Wild and domestic ungulates
Sylviidae	One genus, 1 species	New Zealand sea lion and fur seal
Turdidae	Three genera, 5 + species	Antelopes, ibex
Tyrannidae	One genus, 1 species	Wild and domestic ungulates, capybara

and 'behaviour' sampling rules (Martin and Bateson 1986), both of which are adequate for opportunistic records and/or rare behaviours, were used throughout the observations. Photographs were used throughout the overview to describe and illustrate the behaviour of the birds and their clients. No attempt to quantify or compare the relative occurrence of cleaning behaviour among the bird species was made, due to the haphazard nature of the gathered data and the general lack of comparable data sets for cleaner bird species worldwide (e.g., MacFarland and Reeder 1974, Christian 1980, Marcus 1985, Tomazzoni *et al.* 2005, Sazima 2007a). Voucher copies of digital photographs, when copyright allowed, are on file at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

RESULTS

I found that 101 bird species in 32 families practice cleaning even if some of them do so very occasionally. Cleaner birds include both passerine and non-passerine species that range from the renowned Red-billed Oxpecker (*Buphagus erythrorhynchus*) from Africa to the little known Crested Partridge (*Rollulus roulroul*) from Malaysia, illustrating the remarkable variety among cleaner birds and their clients (Figures 1-38, Table 1). Bird groups that are most representative as cleaners include corvids (about 25 species) and sturnids (about 15 species). In the Neotropics, caracarine falcons and icterids (about 5 species each) are the most representative cleaners, and may be regarded as roughly equivalent to corvids and sturnids, respectively. Most bird groups have one to two recorded species acting as cleaners (Table 1). The majority of recorded cleaner bird species is found in Africa ($n = 37$), and South America including the Galápagos Islands ($n = 28$). Asia ($n = 17$) and North America ($n = 14$) have roughly similar numbers of recorded cleaners. Europe has nine cleaner bird species, and Australia including New Zealand has only three cleaners recorded to date (Appendix 1). The total by regions surpasses 101 due to the fact that some bird species occur in more than one region (e.g., the egret *Bubulcus ibis* and the myna *Acridotheres tristis*).

Most cleaners are monochromatic (white or black) or sport subdued colours, some of them have contrasting patterns, and very few are colourful. The egret *Bubulcus ibis*, the ani *Crotophaga ani*, the drongo *Dicrurus adsimilis*, and several corvids exemplify essentially monochromatic birds (Figures 7, 23 and 31); the oxpecker *Buphagus erythrorhynchus*, the cinclodes *Cinclodes antarcticus*, and the myna *Acridotheres fuscus* illustrate well drab or subdued colours (Figures 1, 6, 8 and 18); the magpie *Pica pica* and the gull *Larus dominicanus* exemplify contrasted patterns (Figures 4, 9), whereas the jacana *Actophilornis*

africanus, the scrub jay *Aphelocoma californica*, and the magpie *Urocissa erythrorhyncha* are among the most colourful cleaners (Figures 3, 10 and 20).

Clients are mostly medium-sized to large herbivores such as iguanas, tortoises, capybaras, and wild and domestic ungulates, but also include carnivores such as seabirds and seals (Table 1). Wild herbivorous mammals are mostly ungulates, but a giant rodent (the capybara) and kangaroos are included. Non-mammal clients are restricted to the Galápagos Islands or the open sea and include marine and land iguanas, giant tortoise, seabirds, and the ocean sunfish (Figures 11-14). Among wild ungulates of the Nearctic and Palearctic regions, deer are among favoured clients (Figures 15-20), whereas in the Neotropics deer are less important clients. On deer, the cleaner birds inspect mostly the back and head, although the rump and tail may be cleaned in resting clients (Figure 16). While perched on the head, the birds pick ticks and other food types from the ears, both externally and internally (Figures 17-18). The large, amphibious capybara (*Hydrochoerus hydrochaeris*) is the most favoured wild client of Neotropical cleaner birds, particularly in South America (Figures 21-26). While cleaning capybaras, some bird species perch on and inspect every body part exposed, including the throat (Figure 2), belly and inner thighs.

Among domestic ungulates, cattle seem most favoured by cleaner birds, albeit other livestock types are cleaned by these birds as well (Figures 27-32). Juvenile individuals also are inspected and cleaned by some cleaner birds (Figure 30). While on domestic ungulates, cleaner birds inspect mostly the back, albeit the head may be inspected as well. In some cases, the birds take ticks or horseflies from within the ears and even the nostrils (Figure 27). Domestic ungulates as clients of cleaner birds are increasingly replacing the wild ones as natural formations change to farmland.

Some clients adopt particular, inviting postures before or while being cleaned, whereas others are indifferent or even disturbed by the activity of cleaner birds. Capybaras, giant tortoises, and iguanas are among the inviting and/or posing clients (Figures 2, 12 and 13), whereas boobies try to dislodge the Sharp-billed Finch (*Geospiza difficilis*) while it drinks blood from wounds it makes on feathers' bases (Figure 11). However, when disturbed by wound pecking, even capybaras try to dislodge cleaner vultures, caracaras, and giant cowbirds by twitching the body, jerking the legs or moving the head towards the cleaner bird (Figure 21). Deer and other wild and domestic ungulates are generally indifferent to the activities of cleaners (Figures 15-20, and 27-32). The oceanic sunfish (*Mola mola*) may bask on the surface lying on its side, and adopts this pose for cleaners such as the Herring Gull (*Larus argentatus*) that approaches (Figure 14) to pick epibiotic and parasitic crustaceans.

Fledglings and even post-juvenile birds forage together with adult birds (presumably parents) on ticks and other food types on wild and domestic clients. For instance, an adult Red-billed Oxpecker (*Buphagus erythrorhynchus*) fed a fledgling with ticks it picked from a resting warthog (*Phacochoerus africanus*), the fledgling

vocalising and flapping its wings while near the adult (Figure 33; Peet van Schalkwyk *pers. comm.*). Another example is a post-juvenile Yellow-headed Caracara (*Milvago chimachima*) that picked ticks and pecked at the wounds to take blood from a capybara together with an adult for about three weeks in a row (IS *pers. obs.*).



FIGURES 1-6: Variety of cleaner birds and their wild mammal clients. (1) The most iconic cleaner bird, the Red-billed Oxpecker (*Buphagus erythrorhynchus*) of Sub-Saharan Africa: two individuals perching on the head of a giraffe (*Giraffa camelopardalis*), one of them scissoring with the bill through the short hair in search of ticks and/or flakes of dead skin. (2) A South American counterpart, the Yellow-headed Caracara (*Milvago chimachima*) picks a tick from the throat of a capybara (*Hydrochoerus hydrochaeris*) posing laid on its side. (3) A long-toed cleaner, the African Jacana (*Actophilornis africanus*) walks along the back of a hippopotamus (*Hippopotamus amphibius*) in search of flies and organic debris. (4) A marine cleaner, the Kelp Gull (*Larus dominicanus*) opens its wings to hold its balance on a swimming right whale (*Eubalaena australis*) while taking pieces of sloughed skin. (5) The largest of Australian fantails, the Willie Wagtail (*Rhipidura leucophrys*) perches on the occupied pouch of a female kangaroo (*Macropus cinereus*) to pick a prey, likely a tick, sheltered amidst the dense hair. (6) One of the southernmost Neotropical cleaners, the Black Cincloides (*Cinclodes antarcticus*) perches on the back of a moulting elephant seal male (*Mirounga leonina*), where it hunts flies and drink blood from wounds. Photographs by Gerda van Schalkwyk (1, 3), Ivan Sazima (2), Darío Podestá (4), João Paulo Krajewski (5) and Jan-Michael Breider (6).

Cleaner birds 'use' their clients in ways other than cleaning, displaying several behaviours that could be related to cleaning, albeit these are not cleaning activities. For instance, Cattle Egrets (*Bubulcus ibis*) closely follow the grazing activity of wild and domestic ungulates, which flush insect and other prey while doing so (Figure 34). Several birds use herbivorous vertebrates as hunting perches, from where they lunge after disturbed or otherwise active insect and other prey. In the Neotropics, a well known instance is the Cattle Tyrant (*Machetornis rixosa*), which perches on capybaras (Figure 35) and wild and domestic ungulates. At some localities in Brazil, this bird is called 'cavaleiro', which means horseman. The Southern Caracara (*Caracara plancus*) approaches cattle giving birth and feeds on the placenta, after which it may perch on the cattle and proceed foraging on ticks and wounds (Figure 36). Other foraging behaviours are not as clearly tied to cleaning, but may be related to it as well. One instance is feeding on dead mammals, a habit recorded mostly for crows, vultures, and caracaras (Figure 37), which may set a scenario for picking ticks and pecking at wounds on live clients (*see* Discussion). Another, particularly curious

behaviour is to pick hair from ungulates to line nests, a habit recorded for oxpeckers and crows (Figure 38).

DISCUSSION

Almost certainly I missed some, or even several, references on cleaner bird associations, but this will not influence much the main points I comment upon in this overview. Passeriformes (69 + species) dominate the cleaner guild worldwide. Corvidae and Sturnidae are by far the bird groups with the highest numbers of cleaner species recorded to date (corvids are 22.8% from the total). From the 123 species recognised within Corvidae (Anjos 2009), 23 are recorded as cleaners (18.7%), which is one of the highest ratios for any bird group other than the highly specialised oxpeckers (Buphagidae), of which the two recognised species are tickbirds (Craig 2009). The main reasons for the trend towards cleaning habits among corvids seem to be their broad diet and opportunistic foraging, besides their high cerebral capacity, proverbial learning ability, and complex social organisation of most



FIGURES 7-10: Colour patterns of cleaner birds. (7) The Cattle Egret (*Bubulcus ibis*) jumping to catch a horsefly on a cow (*Bos taurus*) exemplifies a monochromatic cleaner bird. (8) The Red-billed Oxpecker (*Buphagus erythrorhynchus*) searching within the ear of a common warthog piglet (*Phacochoerus africanus*) illustrates a cleaner with subdued colours. (9) The Common Magpie (*Pica pica*) on the rump of cattle is an iconic cleaner with contrasting pattern. (10) The Red-billed Magpie (*Urocissa erythrorhyncha*) perched on the head of a sambar deer (*Russa unicolor*) is one of the most colourful cleaner birds. Photographs by George Reszeter/Ardea (7), Peet van Schalkwyk (8), Henrique Oliveira Pires (9) and Somchai Kanchanasut (10).

species (e.g., Croze 1970, Anjos 2009). These attributes lead to their very variable foraging and ability to capitalise on almost any potential food opportunity (Anjos 2009). The second group with a high ratio of cleaner birds is Sturnidae, with 112 recognised species (Craig and Feare 2009) and 15 recorded cleaners (13.4%). Although sturnids are mostly omnivores and some species are highly opportunistic foragers (Craig and Feare 2009), they are not comparable to crows from this perspective. On the other hand, the falcons of the Caracarinae may be compared to crows in their broad diet and opportunistic foraging and, indeed, five (45.5%) out of the 11 recognised species within the five genera of caracarines (*sensu* Griffiths *et al.* 2004) are recorded as cleaners (Sazima 2007a, this paper). However, this ratio drops dramatically (8.2%) if the 61 species listed by White *et al.* (1994) within Falconidae are considered. Of the remaining bird groups, high ratios of cleaners are found, for instance, in the Jacanidae (37.5%), Psophiidae (33.3%), and Heliornithidae (33.3%), but these ratios are due to the overall low species richness of these taxa. Groups such as Icteridae, with 103 recognised species (Jaramillo and Burke 1999) have a

high ratio of cleaners (6.8%) as compared with most bird groups, even the very speciose Phasianidae and Anatidae among non-passerines and Tyrannidae and Sylviidae among passerines, each of which has one to two recorded cleaner species. The number of cleaner species within a given bird group does not reflect the group's species richness and, indeed, the highest ratios are found in a few small groups such as jacanas and trumpeters. Thus, the relative abundance of cleaners within a given bird group seem to reflect phylogenetic constraints (as some groups produce more cleaners than others), as well as ecological characteristics such as broad diets, variable foraging, and the ability to capitalise on almost any potential food source (*see* Dean and MacDonald 1981, Sazima 2007a for this latter view). From this double perspective, crows and caracarine falcons may again be regarded as roughly equivalent (Sazima 2007a, b).

Most cleaner birds dwell in open areas (e.g., Dean and MacDonald 1981, Swash and Still 2005, Sazima 2007a, Anjos 2009, Craig and Feare 2009), the forest-dwelling ones apparently being a handful of species (e.g., Frädriich 1972, Dean and MacDonald 1981, Ruggiero



FIGURES 11-14: Non-mammal clients of cleaner birds. (11) The Sharp-billed Ground Finch female (*Geospiza difficilis*), so called 'vampire finch', draws blood from the base of left wing feathers of a Nazca Booby (*Sula granti*). (12) The Small Ground Finch male (*Geospiza fuliginosa*) search diligently for ticks among the crest of a resting marine iguana (*Amblyrhynchus cristatus*). (13) The Small Ground Finch female search for ticks on the right forefoot of a head-high posing Giant Tortoise (*Chelonoidis nigra*). (14) The Herring Gull (*Larus argentatus*) approaches an ocean sunfish (*Mola mola*) posing laid on its side, to pick epibiotic and parasitic crustaceans. Photographs by Tui De Roy/Minden Pictures/Latinstock (11-13) and Paul Mingo (14).

and Eves 1988, Peres 1996, Maisels 2003, this paper for the Red-billed Blue Magpie). Cleaners are mostly drab or sport subdued colours, some of them have contrasting patterns, and very few are colourful. This feature is likely related both to phylogenetic and ecological constraints. For instance, forest-dwelling corvids tend to be colourful, whereas open areas species are mostly blackish

or greyish, sometimes mixed with white or blue, and the same may be said about sturnids (Anjos 2009, Craig and Feare 2009).

A glance at Appendix 1 reveals that the Ethiopian and Neotropical regions are the richest in cleaner bird species. I suspect that the relatively low numbers of cleaner species for the Indo-Malayan region may be



FIGURES 15-20: Deer as clients of cleaner birds. (15) A couple of Black-billed Magpies (*Pica hudsonia*) perch on the back of a grazing wapiti (*Cervus canadensis*) in search of ticks and flies. (16) A small group of Yellow-billed Magpies (*Pica nuttalli*) work on the back and rump of a resting California mule deer male (*Odocoileus hemionus*). (17) Three Jackdaws (*Corvus monedula*) search for ticks on a red deer male (*Cervus elaphus*), one of the birds holding its balance on the right ear of the resting client. (18) Perched on a chital (*Axis axis*) like a forehead ornament, a Common Myna (*Acridotheres tristis*) searches for ticks within the right ear of its undisturbed client. (19) Holding its balance among the antlers of a chital male, a Rufous Treepie (*Dendrocitta vagabunda*) searches for ticks and insect of its expectantly-looking client. (20) The showy Western Scrub Jay (*Aphelocoma californica*) searches for ticks and organic debris on the back of a resting mule deer. Photographs by Rian K. Long (15), Deborra Hanson (16), Graham (17), Paul Lathbury (18, 19) and Chris A. Cobb (20).

due to my missing some literature records and/or to lack of studies on the subject, as compared especially with the Ethiopian realm (*e.g.*, Dean and MacDonald 1981, Ruggiero and Ewes 1988, Anjos 2009, Craig and Feare 2009 and references therein). In the Neotropics, studies on cleaners concentrate in the Galápagos Islands (*e.g.*, MacFarland and Reeder 1974, Grant 1986, Cody 2005) and Brazil (Peres, 1996, Sick 1997, Tomazzoni *et al.*

2005, Sazima 2007a, Sazima and Sazima 2010a). A recent overview for the Neotropics reveals that 33 species in 16 families practice cleaning even if some of them do so very occasionally (Sazima and Sazima 2010b). Clearly, much more natural history-oriented studies on cleaning associations worldwide are needed to change this scenario, and I renew here once more the plea for more studies of organisms in nature (*see* Greene 2005



FIGURES 21-26: Capybaras as clients of cleaner birds. **(21)** A disturbed capybara (*Hydrochoerus hydrochaeris*) moves its head towards a Black Vulture (*Coragyps atratus*) that pulled ticks and pecked at sores. **(22)** The Wattled Jacana (*Jacana jacana*) perches on the back of a resting capybara female in search of insects and organic debris. **(23)** The Smooth-billed Ani (*Crotophaga ani*) searches intently for ticks on the back of a resting male. **(24)** The Shiny Cowbird (*Molothrus bonariensis*) searches for ticks and flies on the back of a resting female or young male. **(25)** Two Giant Cowbirds (*Molothrus oryzivorus*) feast on horseflies and other insects attracted to a resting female. **(26)** The Cattle Egret (*Bubulcus ibis*) remains unreported as cleaner of capybaras in the wild, but in an open air enclosure an individual approaches a resting female to catch a prey on her head. Photographs by Ivan Sazima (21, 23), M. Watson/Ardea (22), Luciano Candisani (24), Carlos Alberto Coutinho (25) and Alberto Alves (26).

for several reasons to do such type of research). It is clear that the help of amateur ornithologists and naturalists, as well as of professional wildlife photographers and/or filmmakers in bringing new data to the attention of professional biologists should be always sought and encouraged (see Sazima 2010b, Sazima and Sazima 2010a for this view).

Posing or facilitating behaviour while cleaned by birds is reported mostly for native clients, which may indicate co-evolved processes. For instance, iguanas and giant tortoises of the Galápagos Islands pose for cleaner finches and mockingbirds while being serviced (e.g., MacFarland and Reeder 1974, Cody 2005, this paper), tapirs and capybaras in Brazil pose for caracara falcons



FIGURES 27-32: Domestic mammals as clients of cleaner birds. (27) The Cattle Egret (*Bubulcus ibis*) stealthily approaches a resting cow (*Bos taurus*) to pick a horsefly from within the nostril. (28) A juvenile Yellow-headed Caracara (*Milvago chimachima*) walks on the back of a resting, undisturbed horse (*Equus caballus*) in search of ticks. (29) Perched on the back of a goat (*Capra hircus*), two Crested Mynas (*Acridotheres cristatellus*) diligently search for ticks along the hairy spine of their client. (30) A couple of Jungle Mynas (*Acridotheres fuscus*), representative of cleaner sturnids, search for ticks and flies on a resting, undisturbed calf. (31) Its feathers shining under the sun, a black drongo (*Dicrurus macrocercus*) perches on the rump of an ox, from whose body the bird would pick ticks and catch attracted flies. (32) A couple of Shiny Cowbirds (*Molothrus bonariensis*) pick ticks on the back of an ox. Photographs by Pedro Olivença (27), Wilfred Rogers (28), Neon Tomas B. Rosell II (29), Kristof Zyskowski and Yulia Bereshpolova (30), Rithwik Virunnukandi (31) and Romulo Campos (32).

(Peres 1996, Sazima 2007a), wild boars in Italy pose for magpies and crows (Massei and Genov 1995), and forest buffaloes in Congo pose for jacanas (Ruggiero and Eves 1998). However, when much disturbed by Black Vultures, Yellow-Headed Caracaras, or Giant Cowbirds pecking at wounds, capybaras try to dislodge the cleaner bird even if temporarily, with avoidance movements of

the body, legs, or head (Sazima 2007a, this paper). A few clients of the Red-billed Oxpecker are known not to tolerate well this cleaner bird and try to get rid of it or otherwise mitigate its presence (A. Turkalo *pers. comm.*). This avoidance-like behaviour is plausibly due to the sore-pecking and blood-feeding habits of oxpeckers (*e.g.*, Weeks 2000, Craig 2009). Likewise, hippos tolerate well



FIGURES 33-38: Bird behaviours related to cleaning associations. (33) Flapping its wings, a fledgling Red-billed Oxpecker (*Buphagus erythrorhynchus*) begs for food while a parent searches for ticks on a resting common warthog (*Phacochoerus africanus*). (34) Alert to insects flushed by a grazing ox (*Bos taurus*), the Cattle Egret (*Bubulcus ibis*) habitually associates with foraging ungulates. (35) Perched on the back of a grazing capybara (*Hydrochoerus hydrochaeris*), a Cattle Tyrant (*Machetornis rixosa*) waits for insects flushed by this giant amphibious rodent. (36) Attracted to birthing cows to feed on the afterbirth, a Southern Caracara (*Caracara plancus*) searches for food at the tail base of a cow. (37) Two Southern Caracaras and a Black Vulture (*Coragyps atratus*) dispute a South American coati (*Nasua nasua*) roadkill; several scavenging birds clean as well. (38) A small group of Jackdaws (*Corvus monedula*) pick hair from the mane of a horse (*Equus caballus*) to line their nests. Hair pulling and tick picking are similar from a behavioural perspective, although the former behaviour is not related to feeding. Photographs by Peet van Schalkwyk (33), Ivan Sazima (34), Luciano Candisani (35), Nelson de Luccia (36), Virginio Sanches (37) and Dawn Griesbach (38).

African Jacanas foraging on their backs but attempt to displace the birds when they peck at wounds (Ruggiero 1996). Curiously, the non-native banteng pose for crows in Australia, despite this client's obvious signs of discomfort and exertion due to the posing posture (Bradshaw and White 2006). Domestic ungulates in general are not known to pose and appear to be oblivious to the presence of cleaner birds or unable to drive them away, even when these latter peck at sores and take blood (Sick 1997, Weeks 1999, Sazima 2007a, Sazima and Sazima 2010b, this paper). Likewise, feral hogs showed no interactions with scrub jays that picked prey from their back (Baber and Morris 1980). For the Neotropics, Sazima and Sazima (2010a) note that deer and cattle do not pose, whereas capybara and tapir do, and relate these behavioural differences to the clients' morphological and behavioural features. However, in South-eastern USA cattle and feral hogs pose for the Common or American Crow *Corvus brachyrhynchos* (Kilham 1982). Thus, the issue of posing versus non-posing of wild, domestic, feral, and/or introduced ungulates merits a closer view and further studies of the possible causes for this apparently variable behaviour of clients towards cleaner birds. In some cases the cleaner species involved in the interaction and its cleaning behaviour are very likely among the underlying causes (IS *pers. obs.*).

The use of domestic animals by native bird cleaners likely began not much later after livestock were introduced in a given region and the trend was possibly driven by local extinction of wild ungulates (*e.g.*, Sick 1997, Ruggiero and Eves 1998). This view is highlighted by the example of the Caledonian Crow (*Corvus orru*) following the introduction of a non-native bovid ungulate, the banteng (*Bos banteng*) in Australia (Bradshaw and White 2006). Cleaning symbiosis between the crow and the bovid was first reported about 150 years after the introduction of this client type, the crow not being recorded as a cleaner of any native vertebrate (Bradshaw and White 2006). Another suggestive example is given by the Northern Jacana (*Jacana spinosa*) pulling off ticks from capybaras in central Panama (Marcus 1985). As capybaras were first reported in Central Panama in the late forties (Trapido 1947) and expanded their range from then (Glanz 1982), the association between jacanas and capybaras evolved within the very short span of about 30 years when reported by Marcus (1985). The cases of the banteng and the capybara illustrate well that behavioural adjustments between birds prone to clean and newly arrived hosts may evolve quickly.

One common way that birds learn food sources is fledglings following their parents and beg for food while the adults forage. This behaviour is well known and, for cleaner birds, is conveniently illustrated by a Red-billed Oxpecker fledgling near a warthog client from which a parent picks ticks (this paper). Even post-juvenile birds

may forage and pick ticks along with adults, as already noted for the Yellow-headed Caracara *Milvago chimachima* (Sazima 2007a). Additionally, the social habits of crows, starlings, some caracara species, and the Black Vulture possibly contributed to spread cleaning behaviour among these birds (*e.g.*, Dean and MacDonald 1981, Sazima 2007a, Anjos 2009, Craig and Feare 2009).

Some behaviours displayed by cleaner birds pose the intriguing question whether they may be related to the origin of cleaning. I adopt here the rationale that a more general and widespread habit may have set a favourable scenario for the origin of a more specialised one. Thus, following herbivorous land mammals and using them as flushers and/or hunting perches likely lead to foraging on blood-sucking and other types of flies attracted to the clients and eventually to pick blood-engorged ticks (*e.g.*, Dean and MacDonald 1981). Likewise, foraging on dead larger vertebrates may have lead to tick-picking as already suggested for crows, some starling species, and even the specialised oxpeckers (Dean and MacDonald 1981), besides the Black Vulture and the caracarine falcons (Sazima 2007a). The report of a vulture picking ticks and debris from a resting capybara and then joining another individual feeding on a capybara roadkill about 100 m away (Sazima and Sazima 2010b) seem to lend further support to these suggestions. The Southern Caracara and the Black Vulture feed on cattle afterbirth (Houston 1994, IS *pers. obs.*), this habit putting them in close proximity to the mammals. From feeding on afterbirth to pecking at sores or picking ticks from the resting cattle may be a simple behavioural adjustment for these highly opportunistic and quickly learning birds (*e.g.*, Sazima 2007a, b, c, 2010a). Taking blood from clients may be related to picking blood-engorged ticks, as already suggested for the oxpecker *Buphagus erythrorhynchus*, and the Galápagos mockingbirds of the genus *Nesomimus* (Curry and Anderson 1987, Craig 2009). Similarly, the caracaras pecking at sores and taking blood and tissue may be related to pick-ticking as well (Sazima 2007a), but the other way round is plausible too.

However, some cleaner birds display particular behaviours that are not related to foraging but may have lead to cleaning nevertheless. For instance, tick-picking by the Eurasian Jackdaw *Corvus monedula* may have originated from their pulling hair from wild and domestic ungulates for nest lining, or vice-versa as suggested by Anjos (2009). Cleaning associations involving birds and other vertebrates very likely had diverse starting points but resulted in similar relationships, sometimes with behavioural adjustments from both parties (*e.g.*, MacFarland and Reeder 1974, Dean and MacDonald 1981, Sazima 2007a, this paper).

As birds and fishes are the most important cleaners among vertebrates, I stress a fundamental difference between these two cleaner groups and their clients. Among

marine fishes in particular, cleaning interactions are mostly initiated by the clients, which adopt inviting and/or facilitating postures in front of the cleaner or its cleaning station (reviews in Losey 1987, Grutter 2005, Sazima *et al.* 2010). Among birds, however, cleaning association is always initiated by the cleaner (several references cited herein). This difference between cleaner fishes and birds and their clients may indicate a longer period of cleaning associations for the former group, which would allow for these behavioural adjustments. Additionally, being rid of ectoparasites is perhaps more important to fishes than to mammals and reptiles, the two major vertebrate groups cleaned by birds. The two above views are not mutually exclusive and, indeed, may be working together.

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APPENDIX 1

Cleaner bird species, general areas of cleaning records, and sources (all records in nature). Recent papers that summarise or cite others are favoured over earlier references (when there are two references, the data are different). Families, genera, and species in alphabetical order.

Cleaner species	General areas	Sources
Anatidae		
<i>Pteronetta hartlaubii</i>	Central Africa	Ruggiero and Eves 1998
Ardeidae		
<i>Ardea alba</i>	Central Africa	Ruggiero and Eves 1998
<i>Bubulcus ibis</i>	Circumtropical	Sazima and Sazima 2010a
<i>Egretta thula</i>	North to South America	Sazima and Sazima 2010b
Buphagidae		
<i>Buphagus africanus</i>	Africa	Craig 2009
<i>Buphagus erythrorhynchus</i>	East Africa	Craig 2009
Cathartidae		
<i>Coragyps atratus</i>	South America	Sazima 2007a, 2010a
Chionidae		
<i>Chionis albus</i>	South America, Antarctic	Burger 1996
<i>Chionis minor</i>	Antarctic	Burger 1996
Coraciidae		
<i>Coracias caudatus</i>	South Africa	Petney and Kok 1993
Corvidae		
<i>Aphelocoma caerulescens</i>	East North America	Fitzpatrick and Woolfenden 1996
<i>Aphelocoma californica</i>	West North America	Dixon 1944, Isenhardt and DeSante 1985
<i>Corvus albicollis</i>	South Africa	Anjos 2009
<i>Corvus albus</i>	Africa	Anjos 2009
<i>Corvus brachyrhynchos</i>	North America	Kilham 1982
<i>Corvus capensis</i>	Africa	Anjos 2009
<i>Corvus cornix</i>	South Europe	Massei and Genov 1995
<i>Corvus corru</i>	Australia	Bradshaw and White 2006
<i>Corvus edithae</i>	East Africa	Anjos 2009
<i>Corvus frugilegus</i>	Eurasia	Anjos 2009
<i>Corvus monedula</i>	Europe	Anjos 2009
<i>Corvus ossifragus</i>	North America	Bent 1946
<i>Corvus rhipidurus</i>	East Africa	Anjos 2009
<i>Corvus ruficollis</i>	North Africa	Anjos 2009
<i>Corvus splendens</i>	South Asia	Anjos 2009
<i>Dendrocitta vagabunda</i>	South Asia	Anjos 2009
<i>Perisoreus canadensis</i>	North America	Anjos 2009
<i>Pica hudsonia</i>	North America	Anjos 2009
<i>Pica nuttalli</i>	West North America	Lindsale and Tomich 1953
<i>Pica pica</i>	Eurasia, North America	Lindsale 1946, Massei and Genov 1995
<i>Ptilosomus afer</i>	North Africa	Anjos 2009
<i>Pyrhocorax pyrrhocorax</i>	Eurasia, Africa	Anjos 2009
<i>Urocissa erythrorhyncha</i>	South Asia	This paper (S. Kanchanasut in Flickr 2010)
Cuculidae		
<i>Crotophaga ani</i>	South America	Sazima 2008
Dicruridae		
<i>Dicrurus adsimilis</i>	Africa	Dean and MacDonald 1981
<i>Dicrurus leucophaeus</i>	South Asia	Rocamora and Yeatman-Berthelot 2009
<i>Dicrurus macrocercus</i>	South Asia	Rocamora and Yeatman-Berthelot 2009

Cleaner species	General areas	Sources
Emberizidae		
<i>Geospiza conirostris</i>	Galápagos Islands	Anderson <i>et al.</i> 2004
<i>Geospiza difficilis</i>	Galápagos Islands	Carpenter 1966, Swash and Still 2005
<i>Geospiza fortis</i>	Galápagos Islands	MacFarland and Reeder 1974
<i>Geospiza fuliginosa</i>	Galápagos Islands	Swash and Still 2005
Falconidae		
<i>Caracara plancus</i>	South America	Sazima 2007a
<i>Daptrius ater</i>	South America	Sazima and Sazima 2010a
<i>Milvago chimachima</i>	South America	Sazima 2007a
<i>Milvago chimango</i>	South America	Sazima 2007a
<i>Phalcoboenus australis</i>	South America	Sazima and Sazima 2010b
Furnariidae		
<i>Cinclodes antarcticus</i>	South America	Sazima and Sazima 2010b
<i>Furnarius rufus</i>	South America	Sazima 2007a
Glareolidae		
<i>Glareola pratincola</i>	East Africa	Dean and MacDonald 1981
Heliornithidae		
<i>Podica senegalensis</i>	Central Africa	Ruggiero and Eves 1998
Icteridae		
<i>Dives atrovioleaceus</i>	Central America	Jaramillo and Burke 1999
<i>Molothrus bonariensis</i>	South America	Sazima and Sazima 2010a
<i>Molothrus oryzivorus</i>	South America	Sazima 2007a
<i>Quiscalus mexicanus</i>	North and Central America	Johnson and Peer 2001
<i>Quiscalus niger</i>	Central America	Jaramillo and Burke 1999
<i>Quiscalus quiscula</i>	North America	Vogt 1979
Jacanidae		
<i>Actophilornis africana</i>	Central Africa	Ruggiero and Eves 1998
<i>Jacana jacana</i>	South America	Sazima and Sazima 2010a
<i>Jacana spinosa</i>	Central America	Marcus 1985
Laridae		
<i>Larus argentatus</i>	East Atlantic	King 1978, P. Mingo <i>pers. comm.</i>
<i>Larus dominicanus</i>	West Atlantic	Groch 2001, Sazima and Sazima 2010b
<i>Larus occidentalis</i>	East Pacific	Tibby 1936, Love 1996
Mimidae		
<i>Nesomimus macdonaldi</i>	Galápagos Islands	Cody 2005
<i>Nesomimus melanotis</i>	Galápagos Islands	Cody 2005
<i>Nesomimus parvulus</i>	Galápagos Islands	Cody 2005
<i>Nesomimus trifasciatus</i>	Galápagos Islands	Curry and Anderson 1987
Motacillidae		
<i>Motacilla capensis</i>	South Africa	Dean and MacDonald 1981
Numididae		
<i>Numida meleagris</i>	South Africa	Dean and MacDonald 1981
Phasianidae		
<i>Rollulus roulroul</i>	South Asia	Frädrich 1972
Podicipedidae		
<i>Tachybaptus ruficollis</i>	East Africa	Dean and MacDonald 1981
Psophiidae		
<i>Psophia leucoptera</i>	South America	Peres 1996
Pycnonotidae		
<i>Chlorocichla flaviventris</i>	South Africa	Dean and MacDonald 1981
<i>Nicator gularis</i>	East Africa	Roche and Kilpin 2003

Cleaner species	General areas	Sources
Rallidae		
<i>Amaurornis flavirostra</i>	South Africa	Dean and MacDonald 1981
<i>Gallinula galeata</i>	South America	Sazima and Sazima 2010b
Rhipiduridae		
<i>Rhipidura leucophrys</i>	Australia	Boles 2006, J. P. Krajewski <i>pers. comm.</i>
Scolopacidae		
<i>Phalaropus fulicarius</i>	Polar North America	Kumlien 1879
<i>Tringa hypoleucus</i>	South Africa	Dean and MacDonald 1981
Stercorariidae		
<i>Stercorarius antarcticus</i>	South America	Sazima and Sazima 2010b
Sturnidae		
<i>Acridotheres cristatellus</i>	South Asia	Craig and Feare 2009
<i>Acridotheres fuscus</i>	South Asia	Craig and Feare 2009
<i>Acridotheres ginginianus</i>	South Asia	Craig and Feare 2009
<i>Acridotheres grandis</i>	South Asia	Craig and Feare 2009
<i>Acridotheres javanicus</i>	South Asia	This paper (S. Sijanto in Flickr 2010)
<i>Acridotheres tristis</i>	South Asia, South Africa	Dean and MacDonald 1981
<i>Creatophora cinerea</i>	South Africa	Craig and Feare 2009
<i>Lamprotornis bicolor</i>	South Africa	Craig and Feare 2009
<i>Lamprotornis nitens</i>	South Africa	Craig and Feare 2009
<i>Onychognathus blythii</i>	East Africa	Craig and Feare 2009
<i>Onychognathus morio</i>	South Africa	Craig and Feare 2009
<i>Onychognathus nabouroup</i>	South Africa	Roberts 1995, Craig and Feare 2009
<i>Onychognathus tristramii</i>	West Asia	Yosef and Yosef 1991
<i>Sturnus unicolor</i>	West Europe	Craig and Feare 2009
<i>Sturnus vulgaris</i>	Europe	Craig and Feare 2009
Sylviidae		
<i>Megalurus punctatus</i>	New Zealand	Bairlein 2006
Turdidae		
<i>Alethe diademata</i>	Central Africa	Maisels 2003
<i>Alethe castanea</i>	Western Africa	Collar 2005
<i>Cossypha dichroa</i>	South Africa	Collar 2005
<i>Cossypha natalensis</i>	South Africa	Dean and MacDonald 1981
<i>Cercomela familiaris</i>	South Africa	Collar 2005
Tyrannidae		
<i>Machetornis rixosa</i>	South America	Sazima 2007a