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Bats join the ranks of oxpeckers and cleaner fish as partners in a pest-reducing mutualism

Meredith S. Palmer[1] | **Jim Krueger**[2] | **Forest Isbell**[1]

[1]Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota

[2]Cedar Creek Ecosystems Science Reserve, University of Minnesota, East Bethel, Minnesota

Correspondence
Meredith S. Palmer, Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN.
Email: palme516@umn.edu

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Abstract

While antagonistic species interactions such as predation or competition have a long history of study, positive inter-species interactions have received comparatively little attention. Mutualisms and commensalisms appear to be widespread in the animal kingdom, with examples of mammals, birds, fish, and reptiles from around the world engaging with other species in evidentially beneficial ways. Cleaning mutualism is a specific type positive inter-species interaction in which one species removes and feeds upon parasites infesting the other. Here, we document a new subset of positive inter-species "cleaning" interactions, in which one partner benefits from and reduces the abundance of pest species attracted by but not attached to their host. We observed in person and in camera trap footage numerous instances of insectivorous bats associating with white-tailed deer (*Odocoileus virginianus*) and feeding on the swarms of biting flies attracted to these large mammals. We call for the increased reporting of positive inter-species associations to better our understanding of the mechanisms leading to the formation of these interactions and the effects that these relationships may for the structuring of ecological communities.

KEYWORDS
cleaning mutualism, positive species interaction, species interactions

White-tailed deer (*Odocoileus virginianus*) are a natural host of a dozen or so species of deer and horse flies in the family *Tabanidae*. These hematophagous flies inflict painful, irritating bites that can cause extreme physical discomfort (Demain, 2003), create bleeding wounds and sores (Beier & McCullough, 1990; James & Harwood, 1969), and facilitate the spread of bacterial (Magnarelli, Anderson, & Barbour, 1986; Martinez, Salinas, Martinez, Cantu, & Miller, 1999; Petersen, Mead, & Schriefer, 2009) and viral (Grimstad, Williams, & Schmitt, 1987; Issel, 1973) diseases. There is little that deer can do to protect themselves from *Tabanidae* attacks, being unable to dislodge flies from the majority of their bodies. Often, the only options for relief are major alterations in overall patterns of diel activity or distribution, although these behavioral changes can in turn reduce access to forage or place animals at increased predation risk (Beier & McCullough, 1990; Nixon, Hansen, Brewer, & Chelsvig, 1991).

But while deer may suffer under these high loads of detrimental pests, the large volumes of flies they attract present a veritable buffet for sympatric insectivorous bat species such as little brown bats (*Myotis lucifugus*; Clare, Barber, Sweeney, Hebert, & Fenton, 2011), big brown bats (*Epitesicus fuscus*; Hamilton & Barclay, 1998), and Eastern red bats (*Lasiurus borealis*; Clare, Fraser, Braid, Fenton, & Hebert, 2009). During the summer (June–July) of 2014 at the Cedar Creek Ecosystem Science Reserve (CCESR; lat. 45°25′N, long. 93°10′W; 21 km^2), we repeatedly observed unique nocturnal interactions between deer and bats. CCESR is a long-term ecological research station positioned within a transitional vegetation zone which includes areas of prairies, evergreen forests, and leafy woodlands, and hosts moderate densities of white-tailed deer (8.5 deer/km^2; D'Angelo & Guidice, 2016). During the peak of the deer fly (*Chrysops callidus*) breeding season at CCESR, these insects are active at night as well as during day, swarming deer in the hundreds to thousands

FIGURE 1 Deer plagued with horseflies, image taken the previous year at the same location (July 16 2013 at 5:06 a.m.), demonstrating the degree to which deer suffer from nocturnal deer fly infestations at Cedar Creek Ecosystem Science Reserve

(Figure 1; Philip, 1931). Bats of an unidentified species were seen associating with deer, circling their heads and bodies and feeding on the attracted insects. On the first occasion, two bats were witnessed consuming flies concentrated around a doe and two fawns. On a separate evening, a single bat was seen feeding in association with a small buck.

Concurrent camera trap data suggest that this partnership is not an infrequent occurrence. An eight-week camera trap survey deployed during the same summer captured repeated incidences (N = 17 independent events) of same inter-species dynamic (Figure 2). We had deployed six remote camera traps (Cuddeback and Moultrie models, all programmed to capture a single image when triggered by motion) along game trails and areas of high mammal activity to document animal community composition. While bats are large enough to trigger the camera traps independently, ~94% of bats captured during the camera trap survey were photographed in association with deer. In these pictures, bats can clearly be seen foraging around deer on the clouds of flies attracted to these large herbivores. Multiple images were triggered for several of these occasions, suggesting that bats continue to associate with deer for sustained periods of time.

This association is a form of positive inter-species interaction, appearing to benefit at least one, perhaps even both participants, while harming neither. *Tabanidae* attraction to deer may decrease search time for foraging bats, saving bats valuable time, and energy by associating with fly hosts. As insectivorous bats can consume hundreds to thousands of insects per night, even a single associating bat could potentially cause a sizeable reduction in the pest load for an individual deer (Griffin, Webster, & Michael, 1960). The ecological relationship captured here is reminiscent of the symbioses observed between the tick-gleaning oxpeckers and ungulates in the African savannas (Tarakini et al., 2017) or cleaner fishes and their parasite-ridden “clients” in the tropical reefs (Grutter, 1999). Such “cleaning” mutualisms typically involve an association in which ectoparasites are provisioned and removed, resulting in net fitness benefits to both interacting participants (Cheney & Cote, 2005). These types of partnerships have been documented between a diversity of species in ecological communities across the world (Table 1). However, prior to the interaction described here, there were no recorded instances of associations in which one species is potentially decreasing the abundance of detached pests (vs. affixed parasites) attracted by the other.

Cleaning and other forms of mutualisms can be direct or indirect and range along a spectrum of more unbalanced, commensal-style relationships to completely obligate symbioses (Boucher, James, & Keeler, 1982). Here, we appear to be observing a direct but non-obligate interaction which may or may not be actively facilitated. From these initial observations, we cannot ascertain whether deer and bats are actively seeking each other out for this service nor assess whether either party gains demonstrable long-term fitness benefits from this association. For example, if the pest reduction benefits for individual deer are indeed negligible, we might classify this relationship as a commensalism (Boucher et al., 1982). Additional research at our site and others where deer and insectivorous bats are sympatric is necessary to establish whether this interaction is a common or especially beneficial occurrence.

Understanding how and why these types of relationships form is at the heart of inter-species-interaction research (Stachowicz,

FIGURE 2 Examples of nocturnal deer and bat associations, taken on June 11 2014 at 11:20 p.m. (left) and July 04 2014 at 3:52 a.m. (right). These are two of 17 independent occasions in which bats were captured by camera traps feeding on biting flies attracted to deer

TABLE 1 Examples of the diversity and geographic extent of cleaning mutualisms between a variety of classes of vertebrates and invertebrates

Interaction	Cleaner	Client	Geographic region	Reference
Mammal-Mammal	Northern raccoon (*Procyon lotor*)	Key deer (*Odocoileus virginianus clavium*)	North America	Cove, Maurer, and O'Connell (2017)
Mammal-Mammal	White-nosed coati (*Nasua narica*)	Barid's tapir (*Tapirus bairdii*)	Central America	McClearn (1992), Overall (1980)
Bird-Mammal	Black caracara (*Daptrius ater*)	Brazilian tapir (*Tapirus terrestris*)	South America	Peres (1996)
Bird-Mammal	African jacana (*Actophilornis africanus*)	Hippopotamus (*Hippopotamus amphibius*)	Africa	Ruggiero (1996)
Bird-Mammal	Wattled Jacana (*Jacana jacana*)	Capybara (*Hydrochoerus hydrochaeris*)	Central America	Marcus (1985)
Bird-Mammal	Caracara spp. (*Milvago chimachima, Caracara plancus*)	Capybara (*Hydrochoerus hydrochaeris*)	South America	Macdonald (1981), Tomazzoni, Pedó, and Hartz (2005)
Bird-Mammal	Cattle tyrant (*Machetornis rixosus*)	Capybara (*Hydrochoerus hydrochaeris*)	South America	Macdonald (1981)
Bird-Mammal	Rufous hornero (*Furnarius rufus*)	Capybara (*Hydrochoerus hydrochaeris*)	South America	Tomazzoni et al. (2005)
Bird-Mammal	Oxpecker spp. (*Buphagus africanus, B. erythrorhynchus*)	Ungulate spp. (*Aepyceros melampus, Ceratotherium simum, Connochaetes taurinus, Equus burchellii, Giraffa camelopardalis, Phacochoerus aethiopicus, Syncerus caffer, Tragelaphus oryx, T. angasii, T. strepsiceros*)	Africa	Atwell (1966), Hustler (1987), Hart, Hart, and Mooring (1990), Koenig (1997), Moreau (1933), Nunn, Ezenwa, Arnold, and Koenig (2011), Stutterheim and Panegis (1985), Tarakini et al. (2017)
Bird-Mammal	Pied fantail (*Rhipidura javanica*)	Bornean red muntjac (*Muntiacus muntjak*)	Asia	Silmi and Mislan (2013)
Bird-Mammal	Cattle egret (*Bubulcus ibis*)	White-tailed deer (*Odocoileus virginianus*)	North America	Halley and Lord (1978)
Bird-Mammal	Pale-winged Trumpeter (*Psophia leucoptera*)	Gray brocket deer (*Mazama gouazoubira*)	South America	Peres (1996)
Bird-Mammal	Black-billed Magpies (*Pica pica*)	Ungulate spp. (*Alces alces, Dama dama, Cervus canadensis, Odocoileus hemionus*)	Europe, North America	Genov, Gigantesco, and Massei (1998), Linsdale (1946), Samuel (1991)
Bird-Mammal	Scrub jays (*Aphelocoma coerulescens*)	Deer spp. (*Odocoileus hemionus columbianus, O. h. californicus*)	North America	Dixon (1944), Isenhart and DeSante (1985), Schulz and Budwiser (1970),
Bird-Mammal	Fan-tailed raven (*Corvus rhipidurus*)	Camel (*Camelus dromedarius*)	Africa	Lewis (1989)
Bird-Mammal	Pale-winged starlings (*Onychognathus nabouroup*)	Cape mountain zebra (*Equus zebra zebra*)	Africa	Penzhorn and Horak (1989)
Bird-Mammal	Yellow-bellied bulbul (*Chlorocichla flaviventris*)	Ungulate spp. (*Oreotragus oreotragus, Sylvicapra grimmia, Aepyceros melampus*)	Africa	Chalton (1976), Roberts (1993), Steyn (1975), Vernon (1972)
Bird-Reptile	Darwin's finch (*Geospiza fuliginosa*)	Galapagos tortoise (*Chelonoidis nigra*)	South America	MacFarland and Reeder (1974)
Bird-Reptile	Darwin's finch (*Geospiza fuliginosa*)	Marine iguana (*Amblyrhynchus cristatus*)	South America	Amadon (1967), Carpenter (1966)
Bird-Reptile	Common grackle (*Quiscalus quiscula*)	Map turtles (*Graptemys spp.*)	North America	Vogt (1979)
Bird-Reptile	Sandpiper (*Actitis hypoleucos*)	Nile crocodile (*Crocodilus niloticus*)	Africa	Cott (1961)

(Continues)

TABLE 1 (Continued)

Interaction	Cleaner	Client	Geographic region	Reference
Reptile-Reptile	Day gecko (*Phelsuma abbotti*)	Aldabra giant tortoise (*Aldabrachelys gigantea*)	Africa	Honegger (1966), Stoddart and Wright (1967)
Invertebrate-Reptile	Scarlet rock crab (*Grapsus grapsus*)	Marine iguana (*Amblyrhynchus cristatus*)	South America	Beebe (1924)
Invertebrate-Fish	Cleaning shrimp spp. (various)	Fish spp. (various)	Worldwide	Baensch and Debelius (1992), Chace (1958), Jonasson (1987), Limbaugh, Pederson, and Chace (1961), Randall (1958), Van Tassell, Brito, and Bortone (1994)
Fish-Fish	Freshwater fish spp. (various)	Fish spp. (various)	Worldwide	Abel (1971), Arndt (1973), Feder (1966), Powell (1984), Spall (1970), Sulak (1975)
Fish-Fish	Marine fish spp. (various)	Fish spp. (various)	Worldwide	Reviewed in: Bshary and Cote (2008, 1997), Cheney and Cote (2005), Van Tassell et al. (1994)

Note. Specific examples are given of mammal, bird, and reptile inter-species interactions; invertebrate-fish and fish-fish cleaning mutualisms are extensively reviewed elsewhere.

2001), and there is much work to be done examining the ecological and community contexts that promote the formation of such associations. Inter-species relationships play key roles in ecosystem structure and function (Goodale et al., 2017); however, positive interactions, including mutualisms and commensalisms, are traditionally under-reported (Stachowicz, 2001) and poorly studied (Goodale et al., 2017; Leung & Poulin, 2008). We suspect that bats and deer are not the only species to develop a pest-gleaning strategy and that many other occurrences within this new subset of cleaning mutualisms are yet to be discovered. Describing novel associations helps to elucidate the often surprising diversity of non-trophic interactions within ecological communities, the understanding of which is key for predicting community dynamics, particularly in the face of environmental manipulations (Estes et al., 2011; Goudard & Loreau, 2012). For example, apex predator loss or repatriation has been shown to have significant indirect effects via large herbivores on species as far removed in the interaction web as songbirds or pollinating insects (deCalesta, 1994; McShea & Rappole, 1997). Our work suggests that additional types of "outlying" species such as insectivorous bats might be affected by changing ecosystems in previously unanticipated ways. We hope that descriptions such as ours inspire others to add to the body of literature on positive inter-species associations, specifically investigation of mechanisms that promote these fundamental community connections and exploration of the community-level consequences of altering these associations under anthropogenic and other pressures.

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ORCID

Meredith S. Palmer https://orcid.org/0000-0002-1416-1732

REFERENCES

Abel, E. F. (1971). Zur Ethologie von Putzsymbiosen einheimischer Susswasserfische im naturlichen Biotop. *Oecologia*, *6*, 133–151.

Amadon, D. (1967). Galapagos finches grooming marine iguanas. *The Condor*, *69*, 3–11.

Arndt, R. G. (1973). Cleaning symbiosis in some Florida brackish water cyprinodonts. *Marine Aquarist*, *4*(3), 5–13.

Atwell, R. I. G. (1966). Oxpeckers, and their association with mammals in Zambia. *Puku*, *4*, 17–48.

Baensch, H. A., & Debelius, H. (1992). *Meerwasseratlas: Die gemeinsame Pflege von Wirbellosen Tieren und tropischen Meeresfischen im Aquarium*. Melle: Mergus, Verlag für Natur-und Heimtierkunde Baensch.

Beebe, C. W. (1924). *Galápagos: World's end*. New York, NY: G. P. Putnam's Sons.

Beier, P., & McCullough, D. R. (1990). Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs*, *109*, 3–51.

Boucher, D. H., James, S., & Keeler, K. H. (1982). The ecology of mutualisms. *Annual Review of Ecological Systems*, *13*, 315–347. https://doi.org/10.1146/annurev.es.13.110182.001531

Bshary, R., & Cote, I. M. (2008). New perspectives on marine cleaning mutualism In C. Magnhagen, V. A. Braithwaite, E. Forsgren, … B. G.Kapoor, (Eds), *Fish Behaviour* pp. 563–592. Enfield, NH: Science Publishers.

Carpenter, C. C. (1966). *The marine iguana of the Galapagos Islands, its behaviour and ecology*. Proceedings of the California Academy of Sciences, *34*, 329–376.

Chace, F. A. Jr. (1958). *A new shrimp of the genus Percilimenes from the West Indies*. Proceedings of the BiologicalSociety of Washington, *71*, 125–130.

Chalton, D. O. (1976). Another record of a Yellowbellied Bulbul perching on a mammal. *Ostrich*, *47*, 68.

Cheney, K. L., & Cote, I. M. (2005). Mutualism or parasitism? The variable outcome of cleaning symbioses. *Biology Letters*, *1*, 162–165. https://doi.org/10.1098/rsbl.2004.0288

Clare, E. L., Barber, B. R., Sweeney, B. W., Hebert, P. D. N., & Fenton, M. B. (2011). Eating local: Influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology*, *20*(8), 1772–1780. https://doi.org/10.1111/j.1365-294X.2011.05040.x

Clare, E. L., Fraser, E. E., Braid, H. E., Fenton, M. B., & Hebert, P. D. (2009). Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): Using a molecular approach to detect arthropod prey. *Molecular Ecology*, *18*(11), 2532–2542.

Cott, H. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Transactions of the Zoological Society London*, *29*(4), 211–356. https://doi.org/10.1111/j.1096-3642.1961.tb00220.x

Cove, M. V., Maurer, A. S., & O'Connell, A. F. (2017). Camera traps reveal an apparent mutualism between a common mesocarnivore and an endangered ungulate. *Mammalian Biology*, *87*, 143–145. https://doi.org/10.1016/j.mambio.2017.08.007

D'Angelo, G. J., & Guidice, J. H. (2016). *Monitoring population trends of white-tailed deer in Minnesota – 2016*. Minnesota Department of Natural Resources.

deCalesta, D. S. (1994). Effect of white-tailed deer on song-birds within managed forests in Pennsylvania. *Journal of Wildlife Management*, *58*, 711–718. https://doi.org/10.2307/3809685

Demain, J. G. (2003). Papular urticaria and things that bite in the night. *Current Allergy and Asthma Reports*, *3*(4), 291–303. https://doi.org/10.1007/s11882-003-0089-3

Dixon, J. S. (1944). California jay picks ticks from mule deer. *The Condor*, *46*, 204.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *33*, 301–306. https://doi.org/10.1126/science.1205106

Feder, H. M. (1966). Cleaning symbiosis in the marine environment. In S. M. Henry (Ed.), *Symbiosis* (Vol. *1*). New York, NY: Academic.

Genov, P. V., Gigantesco, P., & Massei, G. (1998). Interactions between Black-billed Magpie and fallow deer. *The Condor*, *100*, 177–179. https://doi.org/10.2307/1369914

Goodale, E., Beauchamp, G., & Ruxton, G. D. (2017). Mixed-species Groups of Animals: Behavior, Community Structure, and Conservation. New York, NY: Academic Press.

Goudard, A., & Loreau, M. (2012). Integrating trait-mediated effects and non-trophic interactions in the study of biodiversity and ecosystem functioning. In T. Ohgushi, O. J. Schmitz, & R. D. Holt (Eds.), *Trait-mediated indirect interactions: Ecological and evolutionary perspectives* (pp. 414–432). Cambridge, UK: Cambridge University Press.

Griffin, D. R., Webster, F. A., & Michael, C. R. (1960). The echolocation of flying insects by bats. *Animal Behaviour*, *8*(3–4), 141–154. https://doi.org/10.1016/0003-3472(60)90022-1

Grimstad, P. R., Williams, D. G., & Schmitt, S. M. (1987). Infection of white-tailed deer (*Odocoileus virginianus*) in Michigan with Jamestown Canyon virus (*California serogroup*) and the importance of maternal antibody in viral maintenance. *Journal of Wildlife Diseases*, *23*, 12–22. https://doi.org/10.7589/0090-3558-23.1.12

Grutter, A. S. (1999). Cleaner fish really do clean. *Nature*, *398*, 672–673. https://doi.org/10.1038/19443

Halley, M. R., & Lord, W. D. (1978). A cattle egret-deer mutualism. *The Wilson Bulletin*, *90*, 291.

Hamilton, I. M., & Barclay, R. M. (1998). Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta. *Journal of Mammalogy*, *79*(3), 764–771. https://doi.org/10.2307/1383087

Hart, B. L., Hart, L. A., & Mooring, M. S. (1990). Differential foraging of oxpeckers on impala in comparison with sympatric antelope species. *African Journal of Ecology*, *28*, 240–249. https://doi.org/10.1111/j.1365-2028.1990.tb01157.x

Honegger, R. E. (1966). Beobachtungen an der Herpetofauna der Seychellen. *Salamandra*, *1–2*, 20–36.

Hustler, K. (1987). Host preference of oxpeckers in the Hwange National Park, Zimbabwe. *African Journal of Ecology*, *25*(4), 241–245. https://doi.org/10.1111/j.1365-2028.1987.tb01115.x

Isenhart, F. R., & DeSante, D. F. (1985). Observations of scrub jays cleaning ectoparasites from black-tailed deer. *The Condor*, *87*(1), 145–147. https://doi.org/10.2307/1367147

Issel, C. J. (1973). Isolation of Jamestown Canyon virus (a California group arbovirus) from a white-tailed deer. *The American Journal of Tropical Medicine and Hygiene*, *22*(3), 414–417. https://doi.org/10.4269/ajtmh.1973.22.414

James, M. T., & Harwood, R. F. (1969). *Medical entomology*. New York: Macmillan.

Jonasson, M. (1987). Fish cleaning behaviour of shrimp. *Journal of Zoology*, *213*(1), 117–131. https://doi.org/10.1111/j.1469-7998.1987.tb03682.x

Koenig, W. D. (1997). Host preferences and behaviour of oxpeckers: Co-existence of similar species in a fragmented landscape. *Evolutionary Ecology*, *11*(1), 91–104. https://doi.org/10.1023/A:1018439614008

Leung, T. L. F., & Poulin, R. (2008). Parasitism, commensalism, and mutualism: Exploring the many shades of symbioses. *Vie Et Milieu*, *58*(2), 107–115.

Lewis, A. D. (1989). Notes on two ravens *Corvus* spp. in Kenya. *Scopus*, *13*, 129–131.

Limbaugh, C., Pederson, H., & Chace, F. A. Jr (1961). Shrimps that clean fish. *Bulletin of Marine Science*, *11*(1), 237–257.

Linsdale, J. M. (1946). American Magpie (*Pica pica*). Life histories of North American jays, crows, and titmice. *US National Museum Bulletin*, *191*, 133–154.

Macdonald, D. W. (1981). Feeding associations between capybaras *Hydrochoerus hydrochaeris* and some bird species. *Ibis*, *123*, 364–366. https://doi.org/10.1111/j.1474-919X.1981.tb04041.x

MacFarland, C., & Reeder, W. (1974). Cleaning symbiosis involving Galapagos tortoises and two species of Darwin's finches. *Zeitschrift Für Tierpsychologie*, *34*(5), 464–483.

Magnarelli, L. A., Anderson, J. F., & Barbour, A. G. (1986). The etiologic agent of Lyme disease in deer flies, horse flies, and mosquitoes. *The Journal of Infectious Diseases*, *154*(2), 355–358. https://doi.org/10.1093/infdis/154.2.355

Marcus, M. J. (1985). Feeding associations between capybaras and jacanas: A case of interspecific grooming and possibly mutualism. *Ibis*, *127*, 240–243. https://doi.org/10.1111/j.1474-919X.1985.tb05058.x

Martinez, A., Salinas, A., Martinez, F., Cantu, A., & Miller, D. K. (1999). Serosurvey for selected disease agents in white-tailed deer from Mexico. *Journal of Wildlife Diseases*, *35*(4), 799–803. https://doi.org/10.7589/0090-3558-35.4.799

McClearn, D. (1992). The rise and fall of a mutualism? Coatis, tapirs, and ticks on Barro Colorado Island, Panama. *Biotropica*, *24*(2), 220–222. https://doi.org/10.2307/2388678

McShea, W. J., & Rappole, J. H. (1997). Herbivores and the ecology of forest understory birds. In W. J. McShea, H. B. Underwood, … J. H. Rappole (Eds.), *The science of overabundance* (pp. 298–309). Washington, DC: Smithsonian Institution Press.

Moreau, R. E. (1933). The food of the Red-billed Oxpecker (*Buphagus erythrorhynchus*). *Bulletin of Entomological Research*, *24*(3), 325–335.

Nixon, C. M., Hansen, L. P., Brewer, P. A., & Chelsvig, J. E. (1991). Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs*, *118*, 3–77.

Nunn, C. L., Ezenwa, V. O., Arnold, C., & Koenig, W. D. (2011). Mutualism or parasitism? Using a phylogenetic approach to characterize the oxpecker-ungulate relationship. *Evolution*, *65*(5), 1297–1304. https://doi.org/10.1111/j.1558-5646.2010.01212.x

Overall, K. L. (1980). Coatis, tapirs, and ticks: A case of mammalian interspecific grooming. *Biotropica*, *12*(2), 158. https://doi.org/10.2307/2387731

Penzhorn, B. L., & Horak, I. G. (1989). Starlings, mountain zebras and ticks. *Koedoe*, *32*(1), 133–134. https://doi.org/10.4102/koedoe.v32i1.469
Peres, C. A. (1996). Ungulate ectoparasite removal by Black Caracaras and Pale-winged Trumpeters in Amazonian forests. *The Wilson Bulletin*, *108*(1), 170–175.
Petersen, J. M., Mead, P. S., & Schriefer, M. E. (2009). *Francisella tularensis*: An arthropod-borne pathogen. *Veterinary Research*, *40*, 07.
Philip, C. B. (1931). The Tabanidae (horseflies) of Minnesota with special reference to their biologies and taxonomy. Minnesota Agricultural Experiment Station Technical Bulletin 80:10.
Powell, J. A. (1984). Observations of cleaning behavior in the bluegill *Lepomis macrochirus*, a centrachild. *Copeia*, *1984*(4), 996–998.
Randall, J. E. (1958). A review of the labrid fish genus *Labroides*, with a description of two new species and notes on ecology. *Pacific Science*, *12*, 327–347.
Roberts, S. C. (1993). Yellowbellied bulbul gleaning on a klipspringer. *Ostrich*, *64*(3), 136–136.
Ruggiero, R. G. (1996). Interspecific feeding associations: Mutualism and semi-parasitism between Hippopotami *Hippopotamus amphibius* and African Jacanas *Actophilornis africanus*. *Ibis*, *138*, 346–348. https://doi.org/10.1111/j.1474-919X.1996.tb04352.x
Samuel, W. M. (1991). Grooming by moose (*Alces alces*) infested with the winter tick, *Dermacentor albipictus* (Acari): A mechanism for premature loss of winter hair. *Canadian Journal of Zoology*, *69*(5), 1255–1260.
Schulz, T. A., & Budwiser, P. D. (1970). Scrub Jay possibly feeding on ectoparasites of a black-tailed deer. *California Fish and Game*, *56*(1), 71.
Silmi, M., & Mislan, M. (2013). First evidence of mutualism between Pied Fantail (*Rhipidura javanica*) and Bornean Red Muntjac (*Muntiacus muntjak*). *Journal of Indonesian Natural History*, *1*(1), 42–44.
Spall, R. D. (1970). Possible cases of cleaning symbiosis among freshwater fish. *Transactions of the American Fisheries Society*, *99*(3), 599–600.
Stachowicz, J. J. (2001). Mutualism, facilitation, and the structure of ecological communities. *AIBS Bulletin*, *51*(3), 235–246.
Steyn, P. (1975). Yellowbreasted Bulbul feeding on an impala. *Lammergeyer*, *22*, 51.
Stoddart, D. R., & Wright, C. A. (1967). Ecology of Aldabra Atoll. *Nature*, *213*(5082), 1174. https://doi.org/10.1038/2131174a0
Stutterheim, I. M., & Panegis, K. (1985). Roosting behavior and host selection of oxpeckers (Aves: *Buphaginae*) in Moremi Wildlife Reserve Botswana and eastern Caprivi southwest Africa. *South African Journal of Zoology*, *20*(4), 237–240.
Sulak, K. J. (1975). Cleaning behaviour in the centrarchid fishes, *Lepomis macrochirus* and *Micropterus salmoides*. *Animal Behaviour*, *23*, 331–334. https://doi.org/10.1016/0003-3472(75)90080-9
Tarakini, T., Sithole, S., Utete, B., Muposhi, V. K., Madhlamoto, D., & Gandiwa, E. (2017). Host preferences, spatial distribution and interaction of oxpeckers with wild ungulates in and around southern Gonarezhou National Park, Zimbabwe. *Tropical Ecology*, *58*(4), 833–838.
Tomazzoni, A. C., Pedó, E., & Hartz, S. M. (2005). Feeding associations between capybaras *Hydrochoerus hydrochaeris* (Linnaeus) (Mammalia, *Hydrochaeridae*) and birds in the Lami Biological Reserve, Porto Alegre, Rio Grande do Sul, Brazil. *Revista Brasileira De Zoologia*, *22*(3), 712–716. https://doi.org/10.1590/S0101-81752005000300031
Van Tassell, J. L., Brito, A., & Bortone, S. A. (1994). Cleaning behavior among marine fishes and invertebrates in the Canary Islands. *Cybium*, *18*(2), 117–127.
Vernon, C. J. (1972). *Chlorocichla flaviventris* perching on *Sylvicapra grimmia*. *Ostrich*, *43*, 137.
Vogt, R. C. (1979). Cleaning/feeding symbiosis between grackles (*Quiscalus*: Icteridae) and Map Turtles (*Graptemys*: Emydidae). *The Auk*, *96*, 608–609.

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