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Authors: Nyffeler, Martin, Maxwell, Michael R., and Remsen, J. V.

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BIRD PREDATION BY PRAYING MANTISES: A GLOBAL PERSPECTIVE

MARTIN NYFFELER,¹ MICHAEL R. MAXWELL,² AND J. V. REMSEN, JR.³

ABSTRACT.—We review 147 incidents of the capture of small birds by mantids (order Mantodea, family Mantidae). This has been documented in 13 different countries, on all continents except Antarctica. We found records of predation on birds by 12 mantid species (in the genera *Coptopteryx*, *Hierodula*, *Mantis*, *Miomantis*, *Polyspilota*, *Sphodromantis*, *Stagmatoptera*, *Stagmomantis*, and *Tenodera*). Small birds in the orders Apodiformes and Passeriformes, representing 24 identified species from 14 families (Acanthizidae, Acrocephalidae, Certhiidae, Estrildidae, Maluridae, Meliphagidae, Muscicapidae, Nectariniidae, Parulidae, Phylloscopidae, Scotocercidae, Trochilidae, Tyrannidae, and Vireonidae), were found as prey. Most reports (>70% of observed incidents) are from the USA, where mantids have often been seen capturing hummingbirds attracted to food sources in gardens, i.e., hummingbird feeders or hummingbird-pollinated plants. The Ruby-throated Hummingbird (*Archilochus colubris*) was the species most frequently reported to be captured by mantids. Captures were reported also from Canada, Central America, and South America. In Africa, Asia, Australia, and Europe, we found 29 records of small passerine birds captured by mantids. Of the birds captured, 78% were killed and eaten by the mantids, 2% succeeded in escaping on their own, and 18% were freed by humans. In North America, native and non-native mantids were engaged in bird predation. Our compilation suggests that praying mantises frequently prey on hummingbirds in gardens in North America; therefore, we suggest caution in use of large-sized mantids, particularly non-native mantids, in gardens for insect pest control. Received 22 June 2016. Accepted 11 August 2016.

Key words: gardens, hummingbird feeders, Mantidae, natural enemy, Passeriformes, Trochilidae.

Praying mantises (order Mantodea, family Mantidae) are globally distributed predators that are mainly insectivorous; however, they can also subdue and consume vertebrates, as reported anecdotally from nature and from captivity, including small frogs, lizards, salamanders, newts, shrews, mice, snakes, tiny soft-shelled turtles, and even once a small bat (Teale 1953, Nash 1962, Johnson 1976, Ridpath 1977, Nickle and Harper 1981, Kevan 1985, Ehrmann 1992, Ehrmann and Schmidt 1992, Jehle et al. 1996, Tomasinelli 2000, Dale 2005, Costa-Pereira et al. 2010, Mebs et al. 2016). Although predation on birds by arthropods including mantises is well documented (e.g., McCormick and Polis 1982, Miller and Gass 1985, Brooks 2012), a synthesis focusing on mantises has not been published. Here, we compile and review records of predation on birds by mantises.

Several species of large mantids (*Mantis religiosa*, *Tenodera angustipennis*, *Tenodera si-*

nensis) were released across North America as biological control agents in the 1900s (Davis 1918, Bromley 1932, Gurney 1950, Vickery and Kevan 1983). These species have become established in the eastern USA, and they show mixed effects on arthropod community structure (Fagan et al. 2002). The introduced large mantids now constitute novel potential predators for hummingbirds and other small birds.

METHODS

An extensive bibliographic search was conducted to locate all available published reports on bird predation and predation attempts by mantids using the Thomson-Reuters database, Scopus databases, SORA (Searchable Ornithological Research Archive), Google Scholar, Google Books, and ProQuest Dissertations and Theses. Social media were also searched. The following books not included in the large data-bases were hand-searched: Bedichek (1961), Russell (1961), Bridges and Guppy (1980), Toops (1992), True (1993), Ehrmann (2002), and Shackelford et al. (2009).

We found 147 reports of predation (or predation attempts) on birds by mantids, of which fewer than one third had previously been published (Tables 1–2). The remaining reports were found on social media sites (e.g., Hummingbird Society, Bird Watcher's Digest, National Geographic, Audubon Society, Discovery Channel, YouTube, etc.).

¹ Section of Conservation Biology, Department of Environmental Sciences, University of Basel, CH-4056 Basel, Switzerland.

² Department of Mathematics and Natural Sciences, National University, La Jolla, California 92037, USA.

³ Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803, USA.

⁴ Corresponding author; e-mail: martin.nyffeler@unibas.ch

TABLE 1. Mantid species engaged in the capture of birds. Sources for adult female body length—de Saussure (1871): *C. argentina*. Ehrmann (1992): *H. patellifera*, *H. weneri*, *P. aeruginosa*. Arnett (2000): *T. sinensis*. Battiston et al. (2010): *M. religiosa*, *S. viridis viridis*. Rodrigues (2013): *S. septentrionalis*. Maxwell (2014): *S. carolina*, *S. limbata*.

Species#	Mantid species	Number of incidents	Location	Adult female body length (cm)	Source
1	<i>Coptopteryx argentina</i>	1	Argentina	7	Burmeister 1864
2	<i>Hierodula patellifera</i>	1	India	6–7	Browne 1899
3	<i>Hierodula weneri</i>	2	Australia	7.5–8.5	Ridpath 1977
4	<i>Mantis religiosa</i>	16, 3	Spain; USA	4–9	This paper (Figs. 1C, 3A), Bigas et al. 2006
5	<i>Miomantis</i> sp.	1	South Africa	N/A	Restall 2010
6	<i>Polyspilota aeruginosa</i>	1	Angola	8	Beier 1969
7	<i>Sphodromantis viridis viridis</i>	1	Tunisia	6–7.5	Trouessart 1912
8	<i>Sphodromantis</i> sp. ^a	1	Democratic Republic of the Congo	large	Vrydagh 1946
9	<i>Stagmatoptera septentrionalis</i>	1	Panama	6–9	Smithsonian Tropical Research Institute 2012
10	<i>Stagmomantis carolina</i>	3	USA	4–6.5	Lorenz 2007
11	<i>Stagmomantis limbata</i>	10	USA	4.5–6	This paper (Figs. 1B, 3B), Richman 2013
12	<i>Tenodera sinensis</i>	25	USA	7.5–10.5	This paper (Figs. 1A, 2A–D), Laurent 1933, Prescott 1968
N/A	<i>Stagmomantis</i> spp.	5	USA	4–6.5	www.hummingbirdssociety.org; and others
N/A	Unidentified	67	USA	4–10.5	Butler 1949, Hildebrand 1949, Williams 1974, Carignan 1988, Fisher 1994, Kesterson and Kesterson 1999, and others
N/A	Unidentified	6	Australia	10	Morse 1922, Dale 2005
N/A	Unidentified	1	Belize	N/A	Toops 1992
N/A	Unidentified	1	Trinidad	large	Bridges and Guppy 1980
N/A	Unidentified	1	Canada	N/A	Russell 1961

^a *Sphodromantis* sp. from D.R. Congo is a different species than *Sphodromantis viridis viridis* since the latter species does not exist in the D.R. Congo (Roy 2010).

Our search produced 45 published accounts, 37 accounts from bloggers, three newspaper accounts, five published photos, 48 photos or videos uploaded to internet sources, and nine unpublished accounts (D. Bigas, pers. comm.). Of these predation events, 4% had been reported prior to the year 1920, 29% from 1920 to 1999, and 67% between 2000–2015. The rapid increase in the number of incidents reported since 2000 is most certainly because of the uploading of photos and media to the internet as well as the growing popularity of artificial feeding stations for hummingbirds. For 43 photos, North American hummingbirds and mantids were identified to the lowest taxon possible. Hummingbirds were identified by Remsen. Mantids were identified by Reinhard Ehrmann (Staatliches Museum für Naturkunde Karlsruhe, Germany), William F. Fagan (University of Maryland, College Park, USA), and

Michael R. Maxwell (National University, La Jolla, CA, USA), using Helfer’s (1987) key. Reinhard Ehrmann verified identifications of *Mantis religiosa*. One mantid in a photo from Panama (Figs. 2E–F) was identified by Reinhard Ehrmann, Julio Rivera (University of Toronto, Canada), and Henrique Miranda Rodrigues (Case Western Reserve University, Cleveland, OH, USA). Kai Schütte (University of Hamburg, Germany) identified a mantid to genus based on the shape of the pronotum in a photo in Vrydagh (1946). Bird taxonomy follows Dickinson and Remsen (2013) and Dickinson and Christidis (2014).

RESULTS

The 147 predation events involved 12 mantid species as predators, representing nine genera

(Table 1). Birds captured were all in the orders Apodiformes and Passeriformes, and represented 24 identified species from 14 families (Table 2). The reported incidents originate from 13 different countries and from all continents except Antarctica (Table 1). The vast majority of cases originate from regions of warmer climate ($<41^{\circ}$ latitude). In the following, we summarize the documented incidents grouped by geographic region.

Reports from North and South America ($n = 118$).—Most reports (113 of 147) are from the USA (Tables 1–2), where 110 of 113 incidents were in gardens and yards, nature centers, bird sanctuaries, and state parks, where hummingbirds were attracted to feeders or flowers (Figs. 1, 2A–D). Hummingbirds captured included immatures and adults of both sexes. Incidents of hummingbird predation by mantids were reported for 26 states, with most incidents from New York, North Carolina, Texas, Arizona, and California.

In the eastern USA, the mantids engaged in bird predation preyed almost exclusively on the only breeding hummingbird species of that region, the Ruby-throated Hummingbird *Archilochus colubris* (e.g., Edwards 1934, Butler 1949, Hildebrand 1949, Murray 1958, Weingartner 1976, Conway 1992, Kesterson and Kesterson 1999). In the western USA, mantids captured a broader diversity of hummingbird species (Table 2).

Five cases of predation are reported outside of the USA (Tables 1–2): one in Canada, two in Central America, one in Trinidad, and one in Argentina. Four of these cases were mantids eating hummingbirds, and the remaining case was the mantid *Coptopteryx argentina* eating a White-crested Tyrannulet (*Serpophaga suberistata*) in Argentina (Burmeister 1864).

Reports from Australia and Asia ($n = 9$).—One predation event was reported for Asia (India), and 8 were reported for Australia (Tables 1–2). Morse (1922) encountered an unidentified mantid eating a “tiny naked” Yellow-rumped Thornbill (*Acanthiza chrysorrhoa*) near a bird nest in New South Wales. After finishing its meal, the mantid dropped the dead bird. Three other tiny unidentified birds were lying on the ground, each with a hole in its head through which its brains had been extracted, presumably by the same mantid. In the Northern Territory, Ridpath (1977) witnessed two incidents of a Brown Honeyeater (*Lichmera indistincta*) being captured by *Hierodula wernerii*. In one

instance, the captured bird was able to escape through its own efforts; in the second, the bird, held firmly by the mantid, was unable to escape until the human observer intervened (Ridpath 1977).

Reports from Europe and Africa ($n = 20$).—Four incidents were recorded for Africa, all involving the predation of small passerine birds by large mantids (*Polyspilota aeruginosa*, *Miomantis* sp., and *Sphodromantis* spp.; Tables 1–2). For Europe, all reports are from mantid attacks on living birds captured in mist-nets in Spain. Bigas et al. (2006) reported seven predation events, and nine additional events were relayed by D. Bigas (pers. comm.) during a multi-year banding project. Mantids (*Mantis religiosa*) entered the mist-nets to attack and eat entangled birds (Fig. 3A). Bigas et al. (2006) stated that the mantids were always large and heavy—most likely gravid females. Five species of birds were attacked (Tables 1–2). Bigas et al. (2006:237) described the feeding behavior of the mantids in the mist-nets:

“The *modus operandi* of the mantis seems to be to approach the bird, which is always hanging downwards, and then enter the cranial cavity via one of the eyes, feeding on the brain tissues. Although we have not seen the direct attack on the birds, we think that the mantis is most probably attacking the birds when they are still alive, rather than feeding on recently dead birds. We found several instances of the mantis feeding on the head of the bird, and on at least two occasions the mantis cut the head when it finished. ... On the days when the attacks were noted, there were not any other losses in the ringing session caused by weather effects or by stress. In some cases the bird still had fresh blood on the head, which indicated a very recent attack and death. ...”

DISCUSSION

Mantid and Bird Species Involved.—We found 147 cases of mantids preying upon small birds, involving nine genera in the Mantidae and 24 identified small bird species in the Apodiformes and Passeriformes. Not surprisingly, the mantid species tended to be relatively large, typically at least 6 cm in body length. Well-fed adult females of some of the larger genera in this study, such as

TABLE 2. Bird species reported to be captured by praying mantises in different parts of the world. Standard bird mass data taken from the *Handbook of the Birds of the World Alive* (del Hoyo et al. 2016).

Common name	Latin name	Number of records	Bird mass (g)	Geographic area	Observed mantis / bird-interaction	Source
GERYGONES AND THORNBILLS	ACANTHICIDAE					
Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>	4	Tiny naked bird (nestling) N/A	Australia	Predation	Morse 1922
REED WARBLERS	ACROCEPHALIDAE					
Common Reed Warbler	<i>Acrocephalus scirpaceus</i>	1	8.0–19.7	Spain	Predation in mist-net	Bigas et al. 2006
TREECREEPERS	CERTHIIDAE					
Eurasian Treecreeper	<i>Certhia familiaris</i>	1	7.8–10.0	USA	Feeding on a live bird trapped in mist-net without killing it	Prescott 1968
WAXBILLS	ESTRILIDAE					
Common Waxbill	<i>Estrilda astrild occidentalis</i>	1	6.0–11.0	D.R. Congo	Predation	Vrydagh 1946
Black-and-white Mammikin	<i>Spermestes bicolor</i>	1	8.0–11.0	South Africa	Predation	Restall 2010
FAIRYWRENS	MALURIDAE					
Red-backed Fairywren	<i>Malurus melanocephalus</i>	1	6.0–8.0	Australia	Rescued	Dale 2005
HONEYEATERS	MELIPHAGIDAE					
Brown Honeyeater	<i>Lichmera indistincta</i>	3	7.0–14.0	Australia	Predation (1 case), Escape (1 case), Rescued (1 case)	Ridpath 1977
CHATS AND FLYCATCHERS	MUSCICAPIDAE					
European Robin	<i>Erithacus rubecula</i>	4, 1	14.0–25.0	Spain	Predation in mist-net (4 cases), Feeding on a live bird trapped in mist-net without killing it (1 case)	Bigas et al. 2006
European Pied Flycatcher	<i>Ficedula hypoleuca</i>	4, 1	9.7–22.2	Spain	Predation in mist-net (4 cases), Feeding on a live bird trapped in mist-net without killing it (1 case)	Bigas et al. 2006

TABLE 2. Continued.

Common name	Latin name	Number of records	Bird mass (g)	Geographic area	Observed mantis / bird-interaction	Source
SUNBIRDS	NECTARINIIDAE					
Crimson-backed Sunbird	<i>Lepidocoma minima</i>	1	4.0–6.0	India	Predation	Browne 1899
WOOD WARBLERS	PARULIDAE					
Northern Parula	<i>Setophaga americana</i>	1	7.1–10.2	USA	Rescued	Mahler 1977
OLD WORLD LEAF WARBLERS	PHYLLOSCOPIDAE					
Willow Warbler	<i>Phylloscopus trochilus</i>	1, 2	6.3–14.6	Tunisia, Spain	Predation: Tunisia / Predation in mist-net: Spain	Trouessart 1912, Bigas et al. 2006
BUSH WARBLERS	SCOTOCERCIDAE					
Cetti's Warbler	<i>Cettia cetti</i>	3	8.0–18.5	Spain	Predation in mist-net	Bigas et al. 2006
HUMMINGBIRDS	TROCHILIDAE					
White-bellied Emerald	<i>Amazilia candida</i>	1	3.4–3.8	Belize	Predation	Toops 1992
Black-chinned Hummingbird	<i>Archilochus alexandri</i>	5	2.7–4.7	USA	Predation (4 cases), Rescued (1 case)	This paper (Fig. 1C), Shackelford et al. 2009, Richman 2013
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	37, 1	3.0–3.3	USA, Canada	Predation (32 cases), Escape (1 case), Rescued (5 cases)	This paper (Figs. 1A, 2A–D), Edwards 1934, Butler 1949, Hildebrand 1949, Murray 1958, Russell 1961, Weingartner 1976, Conway 1992, Kesterson and Kesterson 1999, and others
Anna's Hummingbird	<i>Calypte anna</i>	4	3.3–5.8	USA	Predation (3 cases), Escape (1 case)	This paper (Fig. 3B), and others
Garden Emerald	<i>Chlorostilbon assimilis</i>	1	3.0–3.2	Panama	Predation	Smithsonian Tropical Research Institute 2012
Broad-billed Hummingbird	<i>Cynanthus latirostris</i>	1	3.2–4.4	USA	Predation	Allen 1961
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	2	2.6–4.1	USA	Predation	Lorenz 2007, and another source
Rufous Hummingbird	<i>Selasphorus rufus</i>	6	2.9–3.9	USA	Predation (5 cases), Rescued (1 case)	Carignan 1988, Fisher 1994, and others
Allen's Hummingbird	<i>Selasphorus sasin</i>	4	2.5–3.8	USA	Predation (2 cases), Rescued (2 cases)	This paper (Fig. 1B), and others
Unknown	Unknown	51	N/A	USA	Predation (38 cases), Rescued (13 cases)	Alexander 1888, Laurent 1933, Ross 1984, Smith 1992, Schwetman 1995, and others

TABLE 2. Continued.

Common name	Latin name	Number of records	Bird mass (g)	Geographic area	Observed mantis / bird-interaction	Source
Unknown TYRANT-FLYCATCHERS	Unknown TYRANNIDAE	1	N/A	Trinidad	Predation	Bridges and Guppy 1980
White-crested Tyrannulet	<i>Serpophaga subcristata</i>	1	6.0–7.0	Argentina	Predation	Burneister 1864
VIREOS	VIREONIDAE					
Blue-headed Vireo	<i>Vireo solitarius</i>	1	14.1–19.0	USA	Rescued	Lauro 1976
UNKNOWN FAMILY	UNKNOWN FAMILY					
Unknown	Unknown (Suborder Passeri)	1	N/A	Angola	Predation	Beier 1969

Hierodula and *Tenodera*, can weigh up to 7 g (Ridpath 1977, Eisenberg et al. 1981). We note that 11 of the 24 reported bird species have masses <7 g; thus, mantids may frequently outweigh small birds and other vertebrates. Indeed, four mantid genera in the present study (*Hierodula*, *Mantis*, *Stagmomantis*, *Tenodera*) have been observed eating other small vertebrates, such as frogs, lizards, and mice (Rau and Rau 1913, Ridpath 1977, Vickery and Kevan 1983, Kevan 1985, Ramsay 1990, Ehrmann 1992, Ehrmann and Schmidt 1992, Jehle et al. 1996, Tomasinelli 2000, Mebs et al. 2016). As far as can be determined, all mantids engaged in bird predation were females. In two cases, mantid females were feeding on a bird while mating with a male mantid (e.g., Fig. 2C).

Most cases of bird capture were of hummingbirds (family Trochilidae) in North America and South America (114 of 147 total events). The weights of these hummingbird species ranged from 3–6 g, and so it is likely that almost all hummingbird species are vulnerable to predation by large mantises where they co-occur. Since mantids prey on small, vulnerable birds, one may wonder if they sometimes take nestlings. The only report of a mantis killing and eating apparent nestlings is the one by Morse (1922) from Australia relating to the Yellow-rumped Thornbill. Birds >6 g were captured in Australia, South Africa, Spain, and the USA, with some species up to 20 g. However, captures of larger bird species in Europe occurred when the birds were ensnared in mist-nets (e.g., *Erithacus rubecula*, *Ficedula hypoleuca*), which reduce the birds’ defensive and escape abilities. Additionally, the birds’ body mass was likely borne by the net, thereby allowing the mantids to feed on the heavier birds without actually holding them. Some large mantids, however, are capable of capturing larger birds outside of mist-nets. For example, Lauro (1976) reported that a mantid captured a Blue-headed Vireo (*Vireo solitarius*), a bird with a body mass of 14–19 g (Table 2). The mantid, holding the bird with a firm grip, was attempting to chew on the bird’s wing, but the observers separated the mantis from the bird, which flew away apparently unharmed. Similarly, Ridpath (1977) reported the large mantid *Hierodula werner*i capturing a 25-g green treefrog (*Litoria caerulea*).



FIG. 1. Predation of birds by mantids at hummingbird feeder locations in the USA. (A) *Tenodera sinensis* eating a Ruby-throated Hummingbird (*Archilochus colubris*) in Green Castle, Missouri (Photographer: Jeanne A. Scott); (B) *Stagmomantis limbata* eating Allen's Hummingbird (*Selasphorus sasin*) in San Juan Capistrano, California (Photographer: Kris Okamoto); and (C) *Mantis religiosa* eating a Black-chinned Hummingbird (*Archilochus alexandri*) in Millwood, Colorado (Photographer: Tom Vaughan).

The preponderance of predation events of hummingbirds in North America can be explained by several factors. First, North America is inhabited by some of the world's smallest birds,

hummingbirds, which can be overpowered by the larger mantid species in the genera *Mantis*, *Tenodera*, and *Stagmomantis*. Second, the popular practices of maintaining hummingbird feeders and

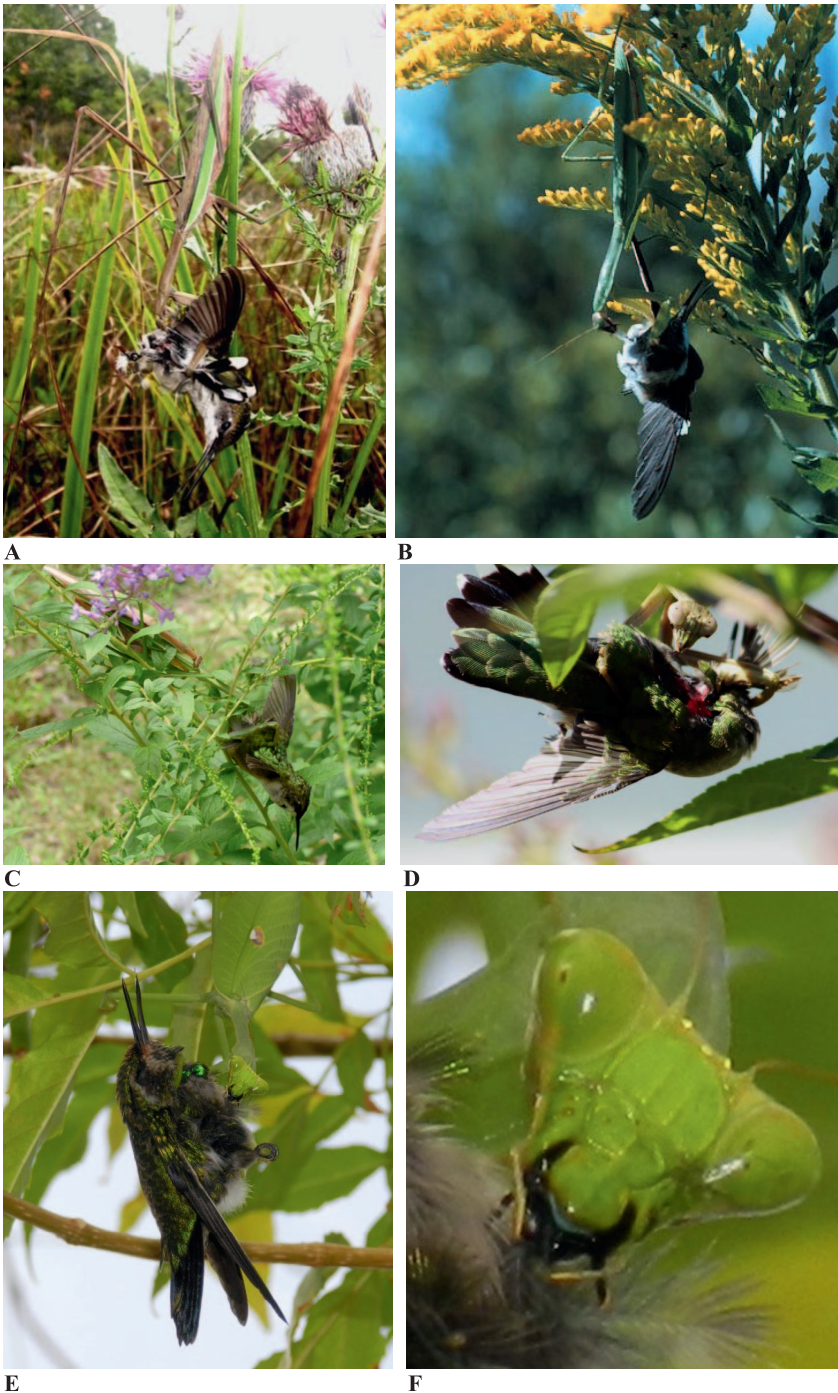


FIG. 2. Predation of birds by mantids on vegetation at locations in North America. (A) *Tenodera sinensis* eating a female Ruby-throated Hummingbird (*Archilochus colubris*) in Benton Harbor, Michigan (Photographer: Chris McCarthy); (B) *Tenodera sinensis* eating a Ruby-throated Hummingbird (*Archilochus colubris*) in Dare County, North Carolina (Photographer: Randy Emmitt); (C) *Tenodera sinensis* eating an immature male Ruby-throated Hummingbird (*Archilochus colubris*) in Clermont, New Jersey (Photographer: Todd Klein); (D) *Tenodera sinensis* eating a Ruby-throated Hummingbird



A



B

FIG. 3. Predation of birds by mantids on nets or fences. (A) *Mantis religiosa* eating a European Pied Flycatcher (*Ficedula hypoleuca*) trapped in a mist-net in the Ebro Delta, Spain (Photographer: David Bigas); (B) *Stagmomantis limbata* eating an Anna's Hummingbird (*Calypte anna*) in the Sierra foothills, California (Photographer: Megan Ralph). The bird first became impaled on barbed wire. After a while, the mantid was seen feeding on the carcass.

←
(*Archilochus colubris*) in Biggsville, Illinois (courtesy from 'What's That Bug'; photographer: Randy Anderson); (E–F) *Stagmatoptera septentrionalis* eating a Garden Emerald (*Chlorostilbon assimilis*) in the Punta Culebra Nature Center, Panama (Photographer: Alvaro Gonzalez).

planting nectar-rich “hummingbird plants” bring these birds close to humans, so that documenting their capture is more likely than for other bird groups. Third, the large mantids *Mantis religiosa* and *Tenodera* spp. were released across North America for biological control purposes in the 1900s (Davis 1918, Gurney 1950, Vickery and Kevan 1983). These mantids have become established and are relatively abundant in parts of the eastern half of the USA (Bromley 1932, Gurney 1950, Hurd 1999, Arnett 2000, Snyder and Evans 2006).

Mechanisms of Bird Capture by Mantids.—Species within the order Mantodea, particularly those within the family Mantidae, are ambush predators (Svenson and Whiting 2004), including four genera in our compilation: *Mantis*, *Sphodromantis*, *Stagmomantis*, *Tenodera* (Svenson and Whiting 2004). When a bird comes within strike distance, usually 5–10 cm, the mantid quickly strikes with its two raptorial front legs, while holding to its perch with its four other legs (Fisher 1994, Schwetman 1995, Prete et al. 1999). Once the bird is seized, the mantid holds it firmly and begins to feed. Birds have been observed to die within one to a few minutes after capture (Dale 2005).

The majority of attacks resulted in the capture and eating of the birds (115 of 147 total attacks, including one case of some type of scavenging [see the following material]). Birds still alive when in the grasp of a mantid were usually trying to escape by vigorous wing beating accompanied by distress calls, but they were able to escape through their own efforts in only three attacks (Ridpath 1977; Anonymous 2009, 2010). In the remaining 26 cases, humans rescued the birds when alerted by the birds’ distress calls or wing noise (e.g., Hildebrand 1949, Williams 1974, Lauro 1976, Mahler 1977, Dale 2005, Richman 2013). In one instance a Brown Creeper (*Certhia americana*) hanging defenseless in a mist-net was attacked by a mantid (Prescott 1968). Prescott (1968:59) noted:

The mantis had reached through the net mesh and firmly grasped the creeper who remained strangely motionless while the mantis fed on its right wing. The ulna was partially exposed and some flesh had been removed although there was very little bleeding along the approximately inch-long opening on the outer side of the wing.

After a while the insect ceased feeding, released the bird, and left the mist-net. The injured bird survived the attack and was later released by the banders. In two other cases, mantids injured birds hanging in mist-nets without killing them (D. Bigas, pers. comm.).

In about two-thirds of the cases, the birds were bitten in the head, neck, or throat (e.g., Carignan 1988, Kesterson and Kesterson 1999, Bigas et al. 2006, Lorenz 2007). In several cases, a hole was chewed in the victim’s head through which its brains were extracted (Morse 1922; Bigas et al. 2006; K. Okamoto, pers. comm.). Direct observations of the capture event will be required to determine whether the mantises are programmed to attack the head and neck (rather than to just begin chewing the area closest to the mouth parts upon capture) and to quantify whether mantises have specific bird-handling techniques, and whether this varies among mantis species. Occasionally, birds were scalped or decapitated, and in a few cases they were defeathered by their captors (see Browne 1899, Dale 2005, Bigas et al. 2006, Shackelford et al. 2009).

One incident was a form of scavenging. An Anna’s Hummingbird (*Calypte anna*) died after becoming impaled on barbed wire (Fig. 3B; M. Ralph, pers. comm.), and a female *Stagmomantis limbata* was then seen feeding on the carcass. Presumably, the bird was still moving after becoming impaled, because *S. limbata* does not attack non-moving items (MRM, pers. obs.), similar to other mantid species (Rau and Rau 1913).

Mantids as Food for Birds.—Large mantises are themselves also eaten by birds. For example, in France, a praying mantis *Mantis religiosa* of 3 g weight was detected in the pellet of an Iberian Grey Shrike *Lanius meridionalis* (Lepley et al. 2004). Tergou et al. (2014) found 46 large mantises (including 41 *Sphodromantis viridis*, four *Mantis religiosa*, and 1 *Iris oratoria*) in the regurgitated pellets of the Tawny Owl *Strix aluco* in Algeria. In Australia, a Black-faced Cuckoo-shrike (*Coracina novaehollandiae*) was repeatedly seen catching and eating the large mantid *Hierodula wernerii* (Ridpath 1977). In Singapore, a *Hierodula* sp., 6.5 cm in length, was found in the stomach of a White-breasted Kingfisher *Halcyon smyrnensis* (Gibson-Hill 1948). In Taiwan, the Besra *Accipiter virgatus* has been reported feeding

its young with the large mantis *Hierodula patellifera* (Huang et al. 2006), and according to a Japanese study the oothecae of this same mantis species are often devoured by the Large-billed Crow *Corvus macrorhynchos* (Kurosawa et al. 2003). These examples of predation on large mantids are all by birds with >50 g body mass (see del Hoyo et al. 2016). Gurney (1950) listed 34 species of North American birds that feed on mantids of unknown sizes.

Ecological Implications.—Some have suggested that North American hummingbirds might be largely immune to predation (Stiles 1978, Miller and Gass 1985, Hixon and Carpenter 1988, Zenzal et al. 2013). Nonetheless, in North America, a diverse array of vertebrate predators feed at least occasionally on hummingbirds, including raptors, other birds, frogs, lizards, snakes, and cats (Miller and Gass 1985, True 1993). However, reports on hummingbird predation in North America to date remain mostly anecdotal (Lockwood 1922, Lowery 1938, Norris-Elye 1944, Monroe 1957, Grant 1959, Wright 1962, Mayr 1966, Spofford 1976, Gamboa 1977, Hofslund 1977, Graves 1978, Seutin and Apanius 1995, Robinson 2003, García-C. and Zahawi 2006), and so the frequency of occurrence has yet to be quantified.

As for invertebrates, the main predators other than mantids on North American hummingbirds and other small birds are large orb-weaving spiders in the genera *Nephila* and *Argiope* (Kirkham 1925, Mackay 1929, Abbott 1931, Woods 1934, Stott 1951, McKenzie 1991, Graham 1997, Heck and Heck 2001, Sakai 2007, Martin and Platt 2011, Brooks 2012, Martínez-Sánchez et al. 2013). Brooks (2012) documented 69 incidents of bird capture by large orb-weaving spiders and found, as in our study, that hummingbirds were the most frequently captured birds and that Ruby-throated Hummingbirds were the most frequently reported victims. The diversity of bird species captured by spiders was more than twice that of the mantids (54 versus 24 bird species). Mantids took a higher percentage of small birds (>70% in the ≤6 g body mass range) compared to spiders (<50% in the ≤6 g body mass range; mean = 11 g). Both these trends make sense because the web-building spiders do not use their own body mass to subdue prey (see Nyffeler and Knörnschild 2013).

Analysis of photos from various parts of the USA that depict bird predation by mantids (see

Methods section) shows that both introduced and native mantids kill birds (Figs. 1, 2A–D). Based on these records, 25 (58%) of the bird captures were by non-native mantids (*Tenodera sinensis* and *Mantis religiosa*), and 18 (42%) were by native mantids (*Stagmomantis* spp.). In the eastern USA, most incidents involved introduced mantis species, whereas native mantids usually were the predators in the western USA. Thus, bird predation by mantises in the USA is not solely because of the introduction of non-native mantid species; in fact observations of bird predation by mantids (Alexander 1888) predate the first record of a non-native mantid in North America.

For many years, the oothecae of non-native mantids have been released in gardens in the USA as a tool for controlling garden insect pests (Hurd 2008). However, the beneficial effect of these predators has been questioned (Antonelli and Glass 2004, Meyer 2010). A meta-analysis of predation by mantids on arthropod community structure reveals mixed effects (Fagan et al. 2002), with the addition of mantids enhancing arthropod herbivores in some cases (e.g., beetles and hemipteran bugs) while suppressing others (e.g., dipteran flies). Additionally, mantids feed on beneficial pollinating insects such as honey bees in addition to pests (Bromley 1948, Maxwell and Eitan 1998, Hurd 2008, Maxwell and Frinchaboy 2014). Also, non-native mantids engage in intra-guild predation, i.e., predation on other predators such as native mantids and spiders, which may enhance pest densities (Hurd 2008). The spread of non-native mantids may even result in the loss of native species (Fea et al. 2013). At least one of the large non-native North American mantids (i.e., the Chinese mantis *Tenodera sinensis*) has since reached the status of an invasive species (Snyder and Evans 2006). These ecological considerations, together with the predation risk that mantids pose to some bird species, particularly hummingbirds, lead us to recommend caution in the release of mantids into North American gardens.

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