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ORIGINAL ARTICLE

Redescription of *Manicocoris rufipes* (Fabricius 1787), including nymphs I, II, III, and V (Reduviidae: Harpactorinae: Apiomerini), and its association with *Clusia* fruits

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Abstract

The genus *Manicocoris* and its only species, *M. rufipes*, are described and illustrated, including nymphal instars I, II, III, and V. Descriptions nelude morphological and morphometrical characters. This article also provides a new record of an association between *M. rufipes* and the fruits of *Clusia grandiflora* Splitg. In French Guiana, adult specimens and nymphal instars II and III of *M. rufipes* were collected within fallen *C. grandiflora* fruits, where they awaited prey with their raptorial forelegs coated with a sticky fruit-derived substance.

Keywords: Apiomerini, Clusiaceae, Manicocoris rufipes, Reduviidae, resin bug

Introduction

Associations between resin-producing plants and resin-collecting bees are well documented, and sporadic records also document associations between resinous plants and assassin bugs that are specialized predators of resin-collecting bees. Plant resins are sticky, hydrophobic mixtures of terpenoid and/or phenolic compounds that usually are secreted in specialized structures, but wounding may also induce their production. They are widely distributed, especially among tropical woody angiosperms (Langenheim 2003). Resin is considered an essential resource for the bees that use it in nest construction (Roubik 1989), and foraging bees aggressively defend oozing plant exudates (Howard 1985; Bittrich & Amaral 1997).

Floral resins, hypothesized to be derived from biochemically similar defense secretions (Armbruster 1997), are known in only five angiosperm genera: Dalechampia (Euphorbiaceae) and Clusia, Clusiella, Chrysochlamys, and Tovomitopsis (Clusiaceae). Clusia and Dalechampia, the best-known systems, include species in which floral resins are the sole pollinator reward (Armbruster 1993; Gustaffson & Bittrich 2002). In the Neotropics, euglossine (orchid), meliponine (stingless), and megachiline bees have been observed collecting floral resins. Many are considered effective pollinators, although smaller bees sometimes appear to be resin thieves (Tables I and 2 in Armbruster 1984; Mesquita & Franciscon 1995; Bittrich & Amaral 1996; Bittrich & Amaral 1997; Lopes & Machado 1998; Correia et al. 1999; Gonçalves-Alvim 2001). Bee behaviors hypothesized to have "set the stage" for the evolution of floral resin as a pollinator reward include the collection of fragrant floral oils by euglossines, and the collection of latex from plant wounds by meliponines (Armbruster 1984, 1993; Gustaffson & Bittrich 2002). The viscous floral resins have important structural and binding functions in nest building, and are rich in antibacterial compounds that apparently protect bee larvae against pathogens (Armbruster 1984; Lokvam & Braddock 1999). Floral resins may be particularly valuable because they remain malleable much longer than resins that flow from wounds, and flowers are a comparatively predictable resource (Armbruster 1984; Roubik 1989).

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Clusia grandiflora Splitg. is a small dioecious tree that grows to 12 m, often as a hemiepiphyte (Pipoly & Gustaffson 2002). Robust male and female flowers secrete copious resin (up to 700 mg per flower) from specialized staminodia as the pollinator reward (Lokvam & Braddock 1999). Male flowers also secrete chemically distinct floral oils from the connectives of fertile stamens, which may aid in the transfer of pollen to pollinator (de Oliveria et al. 1996; Bittrich & Amaral 1997; Marsaioli et al. 1999). In addition, Clusia tissues are permeated by latex canals; when tissues are ruptured, a hydrophobic exudate oozes from wounds and oxidizes to a yelloworange color (Mori et al. 1997; Lokvam et al. 2000). Biologically active polyisoprenylated benzophenones have been identified from C. grandiflora floral resins, trunk latex, and vegetative organs (de Oliveria et al. 1996; Lovkam et al. 2000), and one Clusia benzophenone was detected from a Trigona nest (Marsaioli et al. 1999). Clusia is pollinated principally by euglossine and meliponine bees (Roubik 1989; Bittrich & Amaral 1996, 1997; Langenheim 2003).

The association between the family Clusiaceae and resin-collecting bees appears to be an ancient one. A Late Cretaceous fossil deposit in New Jersey yielded 90 million year-old fossil flowers of *Paleoclusia*, which forms a monophyletic clade with modern genera *Clusia* and *Garcinia*. *Paleoclusia* flowers appear to have secretory canals similar to those in modern Clusiaceae (Crepet & Nixon 1998; Langenheim 2003). Amber inclusions from nearby, slightly younger deposits show that stingless bees were already meeting a sticky end in their quest for plant resin (Michener & Grimaldi 1988; Crepet & Nixon 1998).

Dominican amber deposits also document a long association between stingless bees and their specialized assassin bug predators, the "resin bugs" (Harpactorinae: Apiomerini). Dominican amber (25-40 million years old) has yielded hundreds of specimens of the stingless bee Proplebeia dominicana (Wille & Chandler) along with several apiomerine nymphs, including one with a clump of resin clearly visible on its front tibiae (Poinar 1992). According to contemporary observations in both the Old World and New World tropics, the diurnal resin bugs wait for prey directly at a resin source with sticky plant resin applied to their raptorial forelegs to aid in the capture of bees, ants, termites, and other insects (China 1932; Johnson 1983; Adis 1984; Plowden 2001). Resin bugs, including Manicocoris rufipes (Fab.), also aggregate at meliponine nests and seize commuting workers: Apiomerus pictipes Herrich-Schaeffer has been documented laying its eggs near a favored nest (Johnson 1983; Adis 1984).

Thus far it appears that Neotropical resin bugs exploit few of the many resin- or latex-producing

plants visited by stingless bees (Armbruster 1984; Roubik 1989). They are associated most frequently with producers of copious exudates such as trees in the families Caesalpiniaceae and Burseraceae (Bérenger & Pluot-Sigwalt 1997; Plowden 2001). The Dominican amber that documents a long-term association between plant resin and assassin bugs is derived from Hymenaea L., a member of the Caesalpiniaceae (Poinar 1992). Bérenger & Pluot-Sigwalt (1997) discuss the unusually high level of plant fidelity noted for predatory apiomerines and other members of the Harpactorinae in French Guiana. Eperua falcata Aubl. and Vouacapoua americana Aubl., both locally abundant members of the Caesalpiniaceae, are considered the primary plant associates of Manicocoris rufipes.

Reported here is the first record of a regular association between *M. rufipes* and fruits of Clusiaceae. During the prolonged rainy season in French Guiana, fruits of hemiepiphytic *C. grandiflora* are common on the forest floor. After flower fertilization and fruit development, the large septicidal capsules open high in the canopy and expose bright orange arillate seeds to passing birds. Once the seeds are dispersed, the woody capsules fall to the ground (Mori et al. 1997). The seeds initially are attached to fleshy septa in the center of the capsule, but after the fruits fall the septa soon senesce to form a viscous resinous mass. The aromatic fallen fruits attract meliponine bees and numerous other insects including nymphs and adults of *Manicocoris rufipes* (Figure 1).

Stål's description of *Manicocoris*, intended to provide characters used to diagnose the Apiomerini genera, is short and incomplete. The genitalia of *M. rufipes* and other representative Apiomerini are illustrated, and their taxonomic utility evaluated, in Gutiérrez (1999). Herein we redescribe the genus and its only species, adding new characters including male and female genitalia, and including descriptions of nymphs I, II, III, and V.



Figure 1. Manicocoris rufipes in fallen Clusia graudiflora fruit, with sticky substance on forelegs.

Materials and methods

The material used in this study consists of specimens collected in French Guiana and specimens from the collections of the American Museum of Natural History (AMNH), New York, USA, and the Max-Plank-Institut Für Limnologie (MPIL), Plön, Germany. Guianan specimens were preserved in 70% ethanol. Terminology for general morphology and genitalia follows Wygodzinsky (1948). Nymphs were described and measured following the terminology of Swadener and Yonke (1973). All measurements are given in millimeters. Field observations of M. rufipes were made in central French Guiana during an extended field study not related to resin bugs (Sept. 95 through Aug. 96, 3°37-39'N, 53°12-13'W, approximately 7 km N of Saül). Additional observations were made of nymphs and adults kept in captivity. Clusia grandiflora was identified using the key and descriptions provided in Pipoly III & Gustafsson (2002). Natural history notes follow the descriptions.

Results

Manicocoris Stål, 1866

Manicocoris Stål 1866, 23: 247-248.

Type of genus *Reduvius rufipes* Fabricius 1787, 2: 309. By monotypy.

Head elongate, shorter than pronotum, slightly curved in lateral view, constricted posteriorly to ocelli into neck; ocelli directed laterally, each on a small tumescence; interocellar distance greater than interocular distance; antennae shorter than body length, segment I extending beyond apex of head. Pronotum with longitudinal suture almost reaching transverse sulcus. Hemelytra brown with whitish areas; scutellum triangular, disc elevated and setose, posterior process not developed. Legs slender; all femora of about same width; foretarsi minute, 2-segmented, fitting into a tibial sulcus above when retracted; middle and hind tarsi 3segmented.

Geographic distribution: Bolivia, Brazil, Colombia, French Guiana, Guyana, and Surinam.

Manicocoris rufipes (Fabricius 1787)

Reduvius rufipes Fabricius 1787, 2: 309 Cimex erythropus Gmelin 1788, 4: 2197. Synonymized by Stål 1872, 2: 94 Reduvius lunatus Fabricius 1803: p. 274. Synonymized by Stål 1868, 1: 114 Apiomerus (Beharus) lunatus: Erichson 1848, 3: 613. Synonymized by Stål 1868, 1: 114 Apiomerus capucinus Herrich-Schaeffer 1848, 8: 76. Synonymized by Stål 1868, 1: 114 Manicocoris rufipes: Stål 1866, 23: 247–248 Trichoschelis rufipes: Walker 1873, 8: 74

Adult (Figure 2) (n = 9)

Total length 26.97-33.17 (mean = 30.06). Head (Figure 3) thin, dark brown almost black, densely covered with erect setae. Length of head 4.30-5.31 (mean = 4.77). Ocelli present, interocellar area slightly swollen, interocellar space 1.01-1.32 (mean = 1.15). Median transverse pit between eves at their posterior margins. Eyes large, hemispherical, width of eyes 0.63 - 0.88 (mean = 0.75). Antennae 4-segmented, length 13.17 - 16.58(mean = 15.14): segment I slightly thickened with several setae shorter than its diameter, sparsely covered with shorter pilosity; segment II with moderately dense setae shorter than its diameter; segments III and IV densely covered with regularly spaced, slightly long setae; segment III longer than segments I, II, or IV; ratio of segment lengths ca. 1:0.95:1.07:1.02. Rostrum straight, 3-segmented, length 4.81-5.95 (mean = 5.38), reaching stridulatory furrow between anterior coxae: segment I short, with numerous short decumbent and long erect setae; segment III short, covered with erect setae; ratio of segment lengths ca. 1:4.03:0.39.

Pronotum bilobed, length 4.93-6.83(mean = 5.76), width 9.62-13.29 (mean = 11.15): anterior lobe convex, appearing trapezoidal from above; dark brown almost black, with setae on raised areas and laterally; posterior lobe brown, anterolateral margins divergent, posterolateral margins straight, humeral angles rounded, disc raised and densely setose. Propleurae glabrous, mesopleurae and metapleurae pilose. Stridulatory furrow striate, with oval glabrous areas on each side, remainder of prosternum covered with short erect setae.

Hemelytra, length 19.75-22.79 (mean = 20.44): usually brown with two whitish spots at apex of corium, surpassing apex of abdomen, corium and clavus sparsely setose.

Forelegs dark brown almost black, middle and hind legs reddish brown. Femora thickened, with abundant setae dorsally. Foretibiae densely setose with a comb-like cleaning device on apex. Middle tibiae with short abundant setae; hind tibiae setose with longitudinal row of thick setae medially. Foretarsi short, segment I as long as segment II, middle and hind tarsi long, segment III longer than I, II combined. Each tarsus with two simple, widely divergent claws.



Figure 2. Manicocoris rufipes, male, dorsal view. Scale line: 1 mm.

Abdomen, length 10.51-13.42 (mean = 11.90), width 6.45-7.97 (mean = 7.26): oval and elongate, setose.

Male: pygophore globose and setose, posterior process reduced (Figure 4); parameres elongate and curved apically, shorter internally with long external setae (Figure 5). Phallus: articulatory apparatus short and curved with pedicel short and *processus capitati* large, basal foramen quadrangular, dorsal phallothecal sclerite triangular and acute apically; lateral view as seen in Figure 6.

Female: gonocoxite VIII subquadrangular with abundant sparse setae, gonapophysis thin with setae apically (Figure 7). Gonocoxite IX with two lateral projections and two internal projections, both with setae (Figure 8). Tergites IX + X densely setose (Figure 9).

Material examined: Brazil, Amazonas, Manaus, 19-XI-1976, B.C. Ratcliffe col., det. Forero 1998 (1 AMNH); Brazil, Amazonas, 26 km N Manaus, 10-XI-76, N. Penny col. (1 AMNH); Brazil, Amazonas, Manaus, I-1968, Alvarenga col. (1 AMNH); Colombia, Río Tacana, selva, 19-X-46, Richber col. Wygodzinsky det. (1 AMNH); Colombia, 12-VII-1989, Wygodzinsky det. (1 AMNH); French Guiana, Les Eaux Claires 7 km N Saül, 24-VII-1996, Berkov col. (in Clusia fruit) (1 AMNH); French Guiana, Saül, IV-1999, Berkov col. (1 AMNH); French Guiana, Les Eaux Claires 7 km N Saül, 9-13-II-96, Berkov col. (in Clusia fruit) (1 AMNH); Surinam, Mapane Creek, 25 Km E SE Joden, Savannah (D.G.), 26-XI-1959, Bergamini col. (1 AMNH); Guyana, Tumatumari, B.G. XIII-13 (1 AMNH); Guyana, Tukeit, B.G., 20-VII-1911 (1 AMNH); Aremu [= Arimu Mine?, WSW of Georgetown, Guyana] (1 AMNH).



Figure 3. M. nufipe head, lateral view. Figs. 4-6. M. nufipes male genitalia. (4) Pygophore, lateral view. (5) Paramere. (6) Phallus, lateral view. Figs. 7-9. M. nufipes female genitalia. (7) Gonocoxite and gonapophysis VIII. (8) Gonocoxite IX. (9) Tergites IX and X. Scale lines: 1 mm.

First instar (Figure 10) (n = 1)

Body oval, total length 5.63. Head, pronotum, and forelegs brown. Head pyriform, granulated, with short abundant setae. Postocular region convex, with transverse sulcus, neck evident. Length of head 1.45, width 1.07. Eyes well developed, dark brown, width of eye 0.31, interocular space 0.75. Ocelli absent. (Antennae missing from specimen). Rostral length 2.21, ratio of segment lengths ca. 1:4.6:1.4. Thorax dark brown; setae and median sulcus present. Pronotum length 1.20, width 1.26. Propleurae dark brown, mesopleurae and metapleurae paler. Wing pads absent. Forelegs dark brown, middle and hind legs reddish brown; foretibiae with abundant long setae, middle and hind tibiae with sparse short setae; tarsi 2-segmented, exposed. Abdomen length 2.59, width 2.02; oval, reddish brown, granulose, with sparse short and long setae; scent glands visible on 3^{rd} , 4^{th} and 5^{th} abdominal terga; connexivum absent.

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Material examined:

Brazil, Belem Station A, 6-VII-1977 (1 MPIL).

Second instar (Figure 11) (n=2)

Body oval, not elongate, total length 6.39-6.58 (mean = 6.48). Head, pronotum, and forelegs brown, almost black. Length of head 1.89-2.08 (mean = 1.99), width 1.23. Width of eve 0.30 - 0.33(mean = 0.31),interocular space 0.40 - 0.50(mean = 0.45). Antennae cylindrical, filiform, setose; dark brown, segment IV paler distally; length 5.33, ratio of segment lengths ca. 1:0.89:0.95:1.65; intersegmental areas also paler. Rostrum dark brown as well as head, segment III slightly paler. Rostral length 1.83-2.26 (mean = 2.05), ratio of segment lengths ca. 1:3.8:0.58. Long setae present, more abundant on segment III. Thorax dark brown almost black. Pronotum length 1.07 - 1.20 (mean = 1.13), width 1.32-1.77 (mean = 1.55). Wing pads developed, length of mesothoracic wing pads 0.25-0.26 (mean = 0.26). Foretarsi shorter fitting on a tibial sulcus. Abdominal length 3.41 - 3.67 (mean = 3.54), width 2.60 - 4.81 (mean = 3.70). Other features same as first instar.

Material examined:

French Guiana, Les Eaux Claires 7 km N Saül, 2-XI-1995, Berkov col. (in *Clusia* fruit with bee) (2 nymphs AMNH).

Third instar (Figure 12) (n = 1)

Total length 9.49. Length of head 2.72, width 1.45. Width of eye 0.37, interocular space 0.50. Antennae segment IV light brown; length of antennae 6.77, ratio of segment lengths ca. 1:0.92:0.87:1.67. Rostral length 2.91, ratio of segment lengths ca. 1:3.37:0.78. Pronotum length 1.77, width 1.83. Propleurae dark brown, mesopleurae darker anteriorly and lighter posteriorly, metapleurae light brown. Length of mesothoracic wing pads 0.94. Abdominal length 5.19, width 3.73. Other features same as second instar.

Material examined:

French Guiana, Les Eaux Claires 7 km N Saül, 29-X-95, Berkov col. (in *Clusia* fruit, with fly) (1 nymph AMNH). Brazil, Belem, 6-VII-1977 (1 MPIL).

Fifth instar (Figure 13) n = 2

Body setose, total length 15.69-19.37 (mean = 17.53). Head brown ventrally, length of head 2.40-4.11 (mean = 3.25), width 2.08-2.34 (mean = 2.21). Eyes surpassing dorsal edge of head

in lateral view, width of eve 0.69 - 0.75 (mean = 0.72), interocular space 0.69 - 0.94 (mean = 0.82). Antennae cylindrical, filiform, setose; dark brown, intersegmental areas brown, segment IV missing; ratio of segment lengths ca. 1:0.85. Rostrum dark brown almost black; abundant setae present on segment I, segments II and III almost glabrous; length 4.87 - 5.06 (mean = 4.96); ratio of segment lengths ca. 1:3.61:0.44. Thorax with anterolateral angles somewhat produced. Pronotum length 2.46 - 4.68(mean = 3.57),widt 1 3.41 - 3.79(mean = 3.60). Propleurae dark brown; mesopleurae darker on anterior and dorsal areas, lighter posteriorly; metapleurae light brown tinged with red. Mesothoracic wing pads well developed, covering metathoracic wing pads, length 5.38-6.33 (mean = 5.85). Forelegs dark brown, middle and hind legs reddish brown. Coxae light brown, forecoxae covered with abundant short setae. Forefemora with long setae, middle and hind femora with sparse short setae. Foretibiae with abundant long setae, middle and hind tibiae with sparse short setae. Abdomen reddish brown dorsally, light brown ventrally; length 7.78-8.73 (mean = 8.26), width 5.25 - 5.69 (mean = 5.47).

Material examined:

Brazil, Res. Ducke, 26 km NE Manaus, XII-17-23-64. R. Thorington (1 nymph AMNH). Brazil, Belem, 6-VII-1977 (4 MPIL).

Remarks: The most important diagnostic characters to distinguish the immature stages of this species are the distinctive colors of the head, pronotum, and legs, which are also found in the adults. To differentiate the immature instars, the most noticeable features are relative body size and relative development of the wing pads. The first instar differs from all others in the lack of wing pads, and subsequent instars show their progressive development.

Natural history notes

Female specimens of *M. rufipes* sometimes have the ventral side of the abdomen covered with a sticky material, and individuals of both genders often have the foretibia covered with resinous material. The source of sticky substances on resin bugs has been the subject of some investigation. Swadener & Yonke (1973) concluded that the "cement" on the ventral side of *Apiomerus crassipes* females was an accumulation of secretions produced during egg deposition. Because specimens were laboratory-reared and lacked access to plant resins, they concluded that secretory glands in the tibiae produced the sticky material on the forelegs. Wygodzinsk (1948) found



F gures 10-11. Manicocoris rufipes nymphs. (10) First instar. (11) Second instar. Scale lines: 1 mm.

that although laboratory-reared first instar nymphs of *Heniartes jaakkoi* Wygodzinsky covered their forelegs with honey prior to hunting, second through fifth instar nymphs produced their own tibial secretions, as did *Apiomerus pictipes* nymphs (Szerlip 1980). Photomicrographs in Adis (1984) show the hairy foretibia of *M. rufipes* (nymph and adult), including the cleaning device and the sulcus into which the tarsus is placed. The possibility that the sticky

substance on the forelegs was endogenous was excluded because no secretory organs were found.

In this study, both nymphs and adults of *M. rufipes* were observed in freshly fallen *C. grandiflora* fruits, with the sticky substance from the center of fruits on their forelegs (Figure 1). This appears to be more than a casual association. Over the course of almost a year (October 1995 through August 1996), individuals were observed in fruits that had fallen from at



Figures 12-13. Manicocoris rufipes nymphs. (12) Third instar. (13) Fifth instar. Scale lines: 1 mm.

least two separat : plants along the Sentier Botanique trail (at approximately 840 m and 940 m from the trail entrance), (see Figure 3 in Mori et al. 1997 for a map) on seven occasions. Nymphs were observed on October 29 1995, November 2 1995 (late dry season, transition), and February 131996 (mid rainy season); and adults were observed on December 191995, Febru: ry 9-191996, and July 241996 (mid and late rainy season). Clusia grandiflora fruits, which take approximately one year to mature (Bittrich & Am ral 1997), appeared to be more abundant during the rainy season. Of the 13 Guianan fruit collections deposited in the Cayenne Herbarium, none was collected during the two driest months of the year (http://www.cayenne.ird.fr/aublet2/Referential.html). Our single most productive observation was in February, when M. rufipes adults, nymphs, and an unidentified adult assassin bug were found in four freshly fallen fruits. Occupied fruits generally housed a single adult, but on one occasion two nymphs shared a single fruit. Because second instar nymphs were found in fruits, it is possible that the adults were laying eggs near to a valuable resin source.

Although both nymphs and adults were exploiting the sticky mass in the center of the Clusia fruit, the exact nature of the substance is not known. Because C. grandiflora produces both floral resin and hydrophobic latex (emulsion), both may occur in a mixture with senescent tissues from the fruit septa. There appear to be qualitative and quantitative differences in the benzophenones present in Clusia resin and latex (de Oliveira et al. 1996; Lokvam et al. 2000). Chemical analysis might provide clues about their relative contributions to the mixture, however results would have to be interpreted with caution given the tendency of plant chemicals to be modified as tissues age (Marsaioli et al. 1999). The substance failed to dissolve when specimens were passively stored in 70% ethanol, and it is the sticky, hydrophobic nature of this mixture tl at makes it of value to resin bugs.

The fallen *C. grandiflora* fruits are fairly persistent on the forest floor due to their large size and woody pericarps. They are extremely aromatic and are visited by a variety of insects including meliponine bees, flies (*Drosophila*, Ceratopogonidae) and beetles (Staphylinidae, Nitidulidae, Curculionidae, Scolytinae). The fragrance of *C. grandiflora's* fruit has not yet been analyzed. Its floral volatiles are rich in fatty acid derivatives, not likely to contribute to the unmistakable spicy scent, and benzenoids including eugenol, which is the main component of clove oil and a more pro nising candidate (Nogueira et al. 2001; Dictionary of Natural Products 1982–2004).

Apiomerines are considered timid or weak predators that may pecialize on hovering bees because they are too slow to catch flies (Johnson 1983; Bérenger & Pluot-Sigwalt 1997). This was not observed in the captive feeding behavior of the robust *M. rufipes*. Both adults and nymphs routinely dispatched flies (mostly Tabanidae), and one fieldcollected nymph had a fly stuck to the sticky substance on its foreleg. Captive adults even subdued smaller assassin bugs, but only the largest individual was able to subdue a large orthopteran. Nevertheless, it seems that *C. grandiflora* fruits attract a broad range of insects likely to satisfy the pickiest predator.

Thus far, casual observations of *Clusia* fruits at other localities have not suggested that the fruit inevitably harbors the bug. Additional observations, field experiments, and additional analyses of resin, oil, latex and fruit aromas are needed to more precisely elucidate the association between *C. grandiflora*, *M. rufipes*, and its prey.

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