Religious Supplicant, Seductive Cannibal, or Reflex Machine? In Search of the Praying Mantis

FREDERICK R. PRETE AND M. MELISSA WOLFE

Department of Psychology
Youngstown State University
Youngstown, Ohio 44555

INTRODUCTION

Adrian Wenner recently published a thought-provoking article in which he argued that the inevitable scientific controversies that arise from time to time are exacerbated when allegiances to traditional theories or established hypotheses prevent the thoughtful consideration of newly discovered, apparently contradictory data.[1] Targeting the broad field of organismal biology, Wenner pointed out that "it is with studies of whole organisms that the relationship between theory and research can become most apparent."[2] The rhetorical question used as the unifying theme for his paper asks: Are organisms necessary in the resolution of biological controversies? Wenner, of course, answered that they are: the organism itself must be the final criterion by which conflicts between disparate perceptions of its nature are resolved.

As straightforward as this point seems to be, Wenner sketched several interesting examples of controversies in which appeals to the actual organisms in question did not (or do not) play a role. For instance, in 1926, two papers published in the *Scientific Monthly* were instrumental in promulgating the belief that male deer flies (*Cephenemyia*) can fly at 818 mph, and females at 614 mph.[3] Early attempts to criticize these beliefs were resisted, and

1. Adrian M. Wenner, "Concept-Centered *versus* Organism-Centered Biology," *Amer. Zool., 29* (1989), 1177–97. Wenner's argument is expanded in Adrian M. Wenner and Patrick H. Wells, *Anatomy of a Controversy: The Question of a "Language" among Bees* (New York: Columbia University Press, 1990).

2. Wenner, "Concept-Centered *versus* Organism-Centered Biology," p. 1186.

3. H. V. Haight, "Around the World in Twenty-four Hours," *Sci. Monthly,*

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the ideas persisted for more than a decade. The initial controversy over the veracity of these claims did not involve appeals to the flies themselves; proponents and opponents presented mathematical calculations and rhetoric, but neither provided data on actual flight speeds of the flies. A similar example involves the putative ability of worker ants to orient by the sun. Several studies have presented results that have been interpreted as demonstrating that desert ants collected at remote points from their nest, and then released at opposite locations, can use a "sun compass ability" to find their way home.[4] Again, attempts by some to point out the ambiguities in the data, and possible alternate interpretations, have been strongly resisted.

Wenner offered several other interesting examples of biological controversies in which the confirming evidence collected in support of a particular hypothesis has evolved into what T. C. Chamberlin termed a "ruling theory."[5] When this occurs, the ruling theory is often defended against emerging, contradictory findings by the use of impassioned rhetoric born of strong loyalty, including at times ad hoc accommodation of the original hypothesis to the extent that it is no longer vulnerable to the new data. Of the remaining controversies presented by Wenner as examples of this phenomenon, one is particularly interesting, both inherently and because the ruling theory is still strongly adhered to by many scientists and nonscientists alike. The controversy revolves around whether cannibalism of the male praying mantis by the female is a regular, perhaps even necessary part of this insect's mating behavior.

The belief that female mantids regularly cannibalize the males just prior to, or during, mating first came to our attention in a graduate course on the biology of behavior. It was explained that the female bites off the head of the male in order to release the male's copulatory reflex from the inhibitory influences imposed by the insect's cerebral ganglia (i.e., "brain"). Recently, several students heard the story from yet another professor and came to us

22 (1926), 468—472; C. T. H. Towsend, "Around the World in a Daylight Day: A Problem in Flight," *Sci. Monthly, 22* (1926), 309—311.

4. R. Wehner, "Polarized Light Navigation by Insects," *Sci. Amer., 235* (1976), 106—115; R. Wehner and P. Duelli, "The Spatial Orientation of Ants, *Cataglyphis bicolor*, before and after Sunrise," *Experimentia, 27* (1971), 1364—66; R. Wehner and R. Menzel, "Homing in the Ant, *Cataglyphis bicolor*," *Science, 164* (1969), 192—194.

5. See T. C. Chamberlin, "The Method of Multiple Working Hypotheses," *J. Geol., 5* (1897), 837—848, reprinted in *Science, 148* (1965), 754—759; John R. Platt, "Strong Inference," *Science, 146* (1964), 347—353.

to ask if it is really true. Additional informal inquiries revealed that, indeed, most academics with whom we spoke believed in the phenomenon. Further, when we asked 149 university students on two campuses to indicate any one fact that they knew about the praying mantis, the most frequent response was that the female cannibalizes her mate.[6] The degree to which the belief is generally held is evidenced by the recent appearance of a *Far Side* cartoon in which two praying mantis housewives are pictured standing on one's front porch, having a bit of an argument. The caption reads, "I don't know what you're insinuating, Jane, but I haven't seen your Harold all day — besides, surely you know I would only devour my *own* husband!"[7]

People continue to believe in the regularity of mating-related cannibalism of male mantids in spite of many recent challenges in both the scientific and popular literature. Previous attempts to explain why this belief is so strongly held have invariably traced the origin of the story (at least in its modern form) to a brief but graphic anecdote written by Leland O. Howard and published in the prestigious journal *Science* in 1886.[8] The various reasons suggested for the story's persistence include these: that there is ubiquitous misunderstanding of Darwinian evolution;[9] that there is a general failure to recognize disconfirming empirical data (especially those gathered by the biologist Ken Roeder in the

6. The questionnaire consisted of a picture of a mantis perched on some foliage, under which appeared the following: "At the top of this page is a picture of a praying mantis. Will you please indicate below one thing that you know about this insect." The questionnaires were given to 149 psychology students (74 females and 75 males, ranging in age from 17 to 43 years) in various classes at the University of Chicago and at Roosevelt University (Chicago). The categories into which responses were subsequently grouped and the number in each group are as follows: Female eats her mate, 57; Is predacious or eats bugs, 27; Is camouflaged or cryptic in appearance, 12; I do not know, 11; Assumes an attitude or posture resembling praying, 7; Nonsense answers (e.g., "It goes to church"), 7; Makes noise by rubbing legs or wings together, 6; Other miscellaneous answers, 22. The response "Female eats her mate" occurred significantly more often than can be accounted for by chance ($\chi^2 = 112.01, p \leqslant 0.01$).

7. The cartoon was originally copyrighted in 1986. It appears in Gary Larson, *The PreHistory of the Far Side: A 10th Anniversary Exhibit* (Kansas City, Missouri: Andrews and McMeel, 1989), p. 220. Also to the point is the line, "It devours its mate during the act of love," which appears on the videocassette package of the recently rereleased science fiction film *Praying Mantis* (Portman Productions, distributed by Karl-Lorimar, Irving, Calif., 1983).

8. L. O. Howard, "The Excessive Voracity of the Female Mantis," *Science, 8* (1886), 326.

9. Stephen J. Gould, "Only His Wings Remained," *Nat. Hist., 93* (1984), 10—18.

1930s);[10] that the myth is "ghoulish, kinky, and bizarre" and "appeals to the human imagination";[11] and that "all men are afraid of women."[12]

These rather simple accounts of the story's origin and persistence raise two interesting historical questions. The first, and most obvious, is: Can these simple explanations adequately account for such a long-standing, widely held belief? For instance, with regard to the argument that the myth stems from a misunderstanding of Darwinian evolution, one can argue both that the story was already well established at least half a century prior to publication of the *Origin*, and that one of the story's most influential proponents (Jean Henri Fabre, 1823—1915) was a lifelong opponent of evolutionary theory. To the contention that it stems from men's fear of women (or some other gender-based explanation), one can argue that the story was, and still is, promulgated by scientists and lay writers of both genders. In fact, we first heard the story from a woman scientist. The second interesting historical question is: How could Howard's 500-word anecdote stand six decades against the putatively disconfirming evidence collected by a scientist as influential as Ken Roeder, considered by many the father of American neuroethology? These questions led us to believe that there was more to the story, and we set out to find what other forces may have been involved in the myth's creation and persistence. The journey took us back four millennia.

ORIENTAL VERSUS OCCIDENTIAL MANTIDS

Insects have occupied a more prominent place in Chinese culture, and have done so for a longer period of time, than in cultures of most other countries.[13] In particular, the praying

10. Sharon May Brown, "Of Mantises and Myths," *BioScience, 36* (1986), 431—423; Wenner, "Concept-Centered *versus* Organism-Centered Biology" (above, n. 1).

11. Brown, "Of Mantises and Myths," p. 423.

12. This explanation was suggested to us by a biologist at a recent meeting of the American Society of Zoologists. Originally, we too mistakenly thought that gender role considerations might play a part in shaping conceptualizations about mantids, as they did, for instance, in the case of the honey bees; see Frederick R. Prete, "Can Females Rule the Hive? The Controversy over Honey Bee Gender Roles in British Beekeeping Texts of the Sixteenth—Eighteenth Centuries," *J. Hist. Biol., 24* (1991), 113—144.

13. For instance, sericulture and silk technology began in China some 4500—7000 years ago, commerical beekeeping was prospering 1800 years ago, the first official pest control officer was installed 2230 years ago, and insects have been used for medicine, entertainment, and aesthetic reasons for at least

mantids, being indigenous to China, have been subjects of scientific study, frequent subjects of art and literature, and objects of entertainment for at least 1000 years.[14]

Perhaps due to their long-developed observational skills, the mantid's seemingly pious demeanor did not deceive observers in the Far East as it did those in western Asia, Africa, and Europe. In China (and, later, Japan) the mantid became a symbol of strength, courage, and boldness, extending sometimes to foolhardiness. This conceptualization, based on the mantis's willingness to attack creatures as large as or larger than itself, was popularized in a Chinese proverb that states that the mantis is not strong enough to stop a bullock cart, although, the accompanying folktale goes, one actually thought it could do so.

As early as the ninth century, the mantid was used as a metaphor for boldness in Chinese poetry, and it later served the same literary purpose in Japanese poetry.[15] Typical are the following two poems. The first, "The Praying Mantis Also Gets a Warning," was written by the Chinese poet Liu Yü-Hsi in the ninth century; the second, entitled "Mantis," was written by the Japanese poet Kinoshita Choshoshi in the seventeenth century:

Your neck indeed, my friend looks strong;
Armed with huge battle axes you convey a fierce expression.
But do not presume on your arrogant ways and swallow up your kind;
Be on your guard for the yellow bird, as he may open his mouth and finish you![16]

The promised night
Has come and gone;

2000 years. See Robert W. Pemberton, "The Selling of *Gampsocleis gratiosa*, Brunner (Orthoptera: Tettigoniidae) as Singing Pets in China," *Pan-Pacif. Entomol., 66* (1990), 93; James H. Tsai, "Entomology in the People's Republic of China," *N.Y. Entomol. Soc., 90* (1982), 186–212; Gaines Liu, "Some Extracts from the History of Entomology in China," *Psyche, 46* (1939), 23–28.

14. See, e.g., Tsai, "Entomology," 187–191; D. Keith McE. Kevan, "The Land of the Locusts: Being Some Further Verses on Grigs and Cicadas," Part 2, *Mem. Lyman Entomol. Mus. Res. Lab., 10* (1983), 1–554.

15. The poem by Wei Juang (836–910 A.D.), "Thoughts of Autumn Days with Mr. Cheng Shih — A Poem in One Hundred Verses," discusses the horrors of the civil war that preceded the period of the Five Dynasties (907–960 A.D.). Also see F. S. Bodenheimer, *Materialien zur Geschichte der Entomologie bis Linne* (Berlin: Junk, 1928), I, 20–23.

16. Liu Yü-Hsi (ca. 810), "The Praying Mantis Also Gets a Warning," cited in Kevan, "Land of the Locusts," p. 455.

In place of me,
Who can have stopped
Your bullock cart?[17]

The mantid's audacity was put to use by the Chinese in the gaming arena. Beginning in the tenth century A.D., several species of orthopteroid insects, including crickets and mantids, were captured or bred for fighting. The sport of insect fighting became quite widespread in China, giving rise to several monographs on the topic and supporting an extensive trade in specially made equipment for acquiring and caring for the insects.[18] Tales of the mantid's pugnacity in and out of the sporting arena as recounted by European explorers were quite shocking when considered in juxtaposition to the traditional Western beliefs about the insect. In contrast to the harsh (but more realistic) light in which the mantids were viewed in the Far East, in the Middle East, Africa, and Europe they were, and in some cases still are, regarded as benign, magical, or divine.

Insects have always been an integral part of the daily lives of the people of the Middle East and Africa, as attested to by the earliest written histories from these regions. Insects are, of course, unrelenting competitors for space and resources, often preying upon both crops and people.[19] However, in addition to their practical and economic import, insects have also played a vital symbolic role in the Middle East and Africa. For example, in Egypt the sign of the oriental hornet was associated with the titles of kings from at least the First Dynasty,[20] and the scarab beetle is

17. Kinoshita Choshoshi (ca. 1630), "Mantis," cited in D. Keith McE. Kevan, "The Land of the Locusts: Being Some Further Verses on Grigs and Cicadas," Part 3, *Mem. Lyman Entomol. Mus. Res. Lab., 16* (1985), 295.

18. Tsai, "Entomology," p. 189; J. Linsley Gressitt, "Entomology in China," *Entomol. Soc. Amer., 39* (1946), 154; Berthold Daufer, "Insect-Musicians and Cricket Champions of China," *Field Mus. Nat. Hist., Chicago, Anthro. Leaf., 22* (1927), 1–28.

19. See, e.g., W. G. Bruce, "Bible References to Insects and Other Arthropods," *Bull. Entomol. Soc. Amer., 4* (1958), 75–78; R. P. Dow, "Studies in the Old Testament," *Bull. Brooklyn Entomol. Soc., 12* (1917), 1–13, 64–69; R. P. Dow, "Studies in the Old Testament," *Bull. Brooklyn Entomol. Soc., 13* (1918), 90–93.

20. F. S. Bodenheimer, *Animal and Man in Bible Lands* (Leiden: Brill, 1960), p. 74, cited in Isaac Harpaz, "Early Entomology in the Middle East," in *History of Entomology*, ed. Ray F. Smith, Thomas E. Mittler, and Carrroll N. Smith (Palo Alto, Calif.: Annual Reviews, 1973), p. 23. Other authors consider the symbol to be that of a bee (e.g., H. Malcolm Fraser, *Beekeeping in Antiquity* [London: University of London Press, 1931], pp. 1–2).

so common in the artifacts of Egyptian civilization that it has been referred to as "almost the personification of ancient Egypt."[21] Praying mantids, too, played a symbolic role in Egypt, appearing first in the Eighteenth Dynasty (1555—1350 B.C.) in what has become known in the West as *The Book of the Dead.* In this text, the mantis appears as a minor deity whose function it is to conduct the souls of the dead into the netherworld to meet the greater divine spirits:

> I have made my way into the Royal Palace, and it was the Bird-fly [i.e., mantis] who brought me thither.
> Hail to thee, who fliest up to Heaven, to give light to the stars and protect the White Crown which falleth to me.
> Stable art thou, O mighty god, for even, Make thou for me a path upon which I may pursue my course.[22]

Mantids also appear with supernatural powers in what may be the first book on zoology.[23] A collection of cuneiform texts assembled by the Assyrian king Ashurbanipal (669—626 B.C.), and stored in the royal library of Nineveh, includes a Sumero-Akkadian lexicographical dictionary in cuneiform script known as Har-ra=Hubulla. Compiled during the ninth century B.C., the text contains systematically organized lists of Sumerian names with

21. Harpaz, "Early Entomology," p. 23. Worship of the coprophagous Scarabaeidae antedates most, if not all, recorded history. It has been suggested that the worship of these fascinating beetles predates the first Egyptian king, Menes (ca. 6000 B.C.) (R. P. Dow, "The Testimony of the Tombs," *Bull. Brooklyn Entomol. Soc., 11* [1916], 26, 29; T. R. E. Southwood, "Entomology and Mankind," *Proc. Int. Congr. Entomol., 15* [1977], 36—51).

22. From the *Book of the Dead*, ca. 1550—1450 B.C.: Le Page Renouf, "Book of the Dead, 3," *Proc. Soc. Biblical Archeol., 16* (1894), 218—224, cited in D. Keith McE. Kevan, "The Land of the Locusts: Being Some Further Verses on Grigs and Cicadas," Part 1, *Mem. Lyman Entomol. Mus. Res. Lab., 6* (1978), 391; see also C. H. S. Davis, *The Egyptian Book of the Dead* (New York, London: G. P. Putnam, 1985). Further, the Kalahari Bushmen of southern Africa consider the mantis a manifestation of the creator and supreme deity Kaggen; see Kevan, "Land of the Locusts," Part 3 (above, n. 16), p. 310; Erwin Von Schmitschek, "Mantis in Kult und Mythe der Buschmänner," *Z. ang. Entomol., 76* (1974), 337—347. The mantis (*Orthodera ministralis*) also figures in one of the several creation myths of the Maori of New Zealand; see David Miller, "The Insect People of the Maori," *J. Polynesian Soc., 61* (1952), 1—61.

23. The following comments on the Har-ra=Hubulla are based on B. Landsberger, *Die Fauna des alten Mesopotamian nach der 14. Tafel der Serie Har-ra=Hubulla* (Leipzig: Hirzel, 1934), and F. S. Bodenheimer, *Animals in Bible Lands*, Vol. I (Jerusalem: Bialik Foundation, 1949), as explained in Harpaz, "Early Entomology," pp. 26—29.

their corresponding Akkadian translation. In those portions of the text which list animals, the names are arranged in related zoological groups, each group characterized by a common prefix. Numbered among the group corresponding to the modern taxon Orthoptera (Sumerian prefix *buru*) are, of course, the locusts, and two Sumerian terms for mantis, *buru.EN.ME.LI.* and *buru.EN.ME.LI.a sha(g).ga*, which translate, respectively, to "necromancer" (i.e., a foreteller of the future by communicating with the dead, a wizard, or a conjurer) and "soothsayer of the field." The taxonomic groups of the Har-ra=Hubulla are similar to those used by Pliny, and were maintained for some time in the Middle East, being used as the basis for much of the zoology in the Talmud, and for some medieval Arab writings.[24] Certainly, in the case of the Orthoptera, the Sumerian classification was quite influential, given that mantids would continue to be classified with locusts even in Linnaeus's early writings.

Although there are a number of references to "*μαντις*" (mantis) in ancient Greek literature, most mean simply "prophet" or "soothsayer," and do not refer to the insect. However, the insect did, after a time, come to acquire the name "mantis" due to its seemingly pious demeanor and its purported ability to point the way home to lost travelers. Of the references to the mantis in early Greek writings, one is particularly noteworthy because it would later appear in the two most influential entomology texts of the seventeenth century. The reference is an allusion, in the tenth idyll of Theocritus (ca. 270 B.C.), to the mantid's raptorial forelegs. In lines 17 and 18, Theocritus draws an analogy between the arms of a young woman and those of a mantid:

> Lord! thy sin hath found thee out. Thou'dst wished and wished, and now, 'faith, thou'st won.
> There'll be a mantis to clasp thee all night long.[25]

COMPENDIA AND BESTIARIES

Indian, Hebrew, and Egyptian legends and folklore were absorbed into Greek and Roman folklore, poetry, and art, ultimately being included in Alexandrian handbooks of paradoxology and medical-magical treatises. From there, ancient writers such as

24. Harpaz, "Early Entomology," p. 29.

25. Theocritus, "The Reapers," in John Maxwell Edmonds, *The Greek Bucolic Poets*, Loeb Classical Series (London: Heinemann, 1912), p. 133, cited in Kevan, "Land of the Locusts," Part 1, pp. 397—398.

Pliny and Aelian passed these legends to the Christian world. The legends, now infused with religious and moral teachings, were collected by an unknown author into a popular zoological text known as the *Physiologus*, the original Greek text dating from the fourth century. This collection of Christian allegories revolving around a number of animals, stones, and trees was the most widely distributed zoological work of the time, marking the transition, some have argued, from antiquity to the Middle Ages.[26]

The *Physiologus* along with a few other uncritical compendia constituted the bulk of the zoological and, of course, entomological literature in Europe during the Middle Ages.[27] However, by the end of the twelfth century the natural history compendium had begun to evolve into a new genre of popular nature book that would come to be known generically as the "bestiary." These texts could be voluminous, and grew to absorb all extant animal legends and lore, including those contained in the various versions of the *Physiologus*.[28] Arguably, the three most important of the

26. Michael J. Curley, trans., *Physiologus* (Austin: University of Texas Press, 1979), pp. i—xxxiii; Albert Cook, *The Old English Elene, Phoenix and Physiologus* (New Haven: Yale University Press, 1919), p. lvii—lviii; Florence McCulloch, *Mediaeval Latin and French Bestiaries* (Chapel Hill: University of North Carolina Press, 1960); Günter Morge, "Entomology in the Western World in Antiguity and in Medieval Times," in *History of Entomology* (above, n. 20), p. 58. The *Physiologus* became the most widely read work on zoology during the Middle Ages. In fact, a popular version, the *Theobaldus-physiologus*, was used as a school book; a recent translation of the latter is P. T. Eden, *Theobaldi "Physiologus"* (Leiden: E. J. Brill, 1972). The mantis seems not to have been included in any version of the *Physiologus* of which we are aware. However, the suggestion has been made that the myth behind the use of the locust as a symbol representing conversion to Christianity (or triumph over evil) may actually have originated in observations of mantids subduing their prey. This seems possible in that the myth involves a locust (of which mantids were considered a type) seizing a snake (which represents Satan, or opposition to the church) and killing it by biting its neck. If this story does indeed have an empirical basis, it is unlikely that the original observation(s) could have been of any orthopteran other than a mantid (D. Keith McE. Kevan, "The Mantis and the Serpent," *The Entomologist's Monthly Magazine, 121* [1985], 2). One such account of an orthopteroid eating a snake appears in the imprint *Discorso sopra il nvovo apparir delle cavalette*, dated October 1, 1542, and printed by Francesco Rossi of Ferrara; the original is held by the Michigan State University Library (R. S. Wilkinson, "An Anonymous Sixteenth-Century Treatise on Locusts," *Entomol. Rec. J. Var., 96* [1984], 34—35).

27. These other compendia include *Origines sive etymologiae* by Isidorus, Bishop of Seville; *De visione naturae* by Johannes Scotus Erigena; *Nutura rerum* by Bede; and *De universo* by Rhabanus Maurus (776—856), Bishop of Mainz. These works reflect a general decline in zoological knowledge, as compared to the ancients, that would last until about the beginning of the sixteenth century.

28. Curley, *Physiologus*, p. xxx.

early natural history texts are *Liber de natura rerum* by Thomas Cantipratanus (1201—between 1263 and 1293), *De animalibus* by Albertus Magnus (1193—1280), and a codex of animals written about 1460 by Petrus Candidus Decembrus (1399—1477). Although each author included some information about locusts, Thomas Cantipratanus and Petrus Candidus Decembrus mentioned the mantis (*Brucus*) specifically,[29] and Albertus Magnus described a mysterious snake-killing orthopteroid, the opimacus, that may have been a large mantis.[30]

Until about the mid-sixteenth century, entomology was concerned primarily with practical considerations, and was frequently included in medical texts, many students of medicine being also avid students of entomology.[31] After mid-century, however, entomology took a significant step forward. This was made possible both by a growing independence of the natural scientist/philosophers from the ancient authorities, and by a reorganization in the universities such that medical/zoological studies were no longer restricted to purely pragmatic concerns. The first of the two most influential entomologists of this period was the philosopher/physician Ulisse Aldrovandi (1522—1605).[32] Among the hundreds of manuscripts he produced is *De animalibus insectis libri VII*, first published in 1602.[33] This work is considered the first European text devoted solely to entomology, and the beginning of modern entomological science.

29. See Bodenheimer, *Geschichte der Entomologie* (above, n. 15), I, 182—183, and II, 330—331; S. Killermann, "Das Tierbuch des Petrus Candidus," *Zool. Ann., 6* (1914), 113—122 (Cited in Bodenheimer, *ibid.*, I, 183).

30. The opimacus "can fight and conquer a snake, not by its strength but by its fearless spirit and skill" (James J. Scanlan, trans., *Albert the Great: Man and the Beasts, de Animalibus* [Binghamton, N.Y.: Medieval and Renaissance Texts and Studies, 1987], p. 436). If the opimacus (or ophiomachus, in the Vulgate version) is really a mantid, this characterization is quite similar to those in the early oriental literature.

31. Among these physician/entomologists was the English doctor Edward Wotton (1492—1555). Wotton is known primarily for his work *De differentiis animalium libri decem*, published in Paris in 1552. The work is divided into ten books, the ninth dealing with insects. However, it contains no new information; its strength is that it is an early objective summary of the ancient Graeco-Roman entomological literature. Although Wotton's book did not see a second printing, it is considered to be the beginning of the Aristotelian Renaissance in Zoology. Many popular, secular, and theologically oriented works appeared during the period, but, like Wotton's text, none offered any new, or even much accurate, information about insects. See Max Beier, "The Early Naturalists and Anatomists during the Renaissance and Sevententh Century," in Smith Miller, and Smith, *History of Entomology* (above, n. 20), pp. 82—85.

33. Ulisse Aldrovandi, *De animalibus insectis libri VII* (Bologna, 1602 and 1638; Frankfurt am Main, 1618 and 1623).

As had others, Aldrovandi considered mantids to be large grasshoppers.[34] Although it seems to be the case that he had some first hand knowledge of these insects, many of his facts are confused. For instance, he claimed that mantids can deliver a painful bite, and that they feed on vegetation as do other grasshoppers. The reason that mantids have such large front legs (rather than large hind legs, as do grasshoppers) is that they fly more than they jump, and their scissor-like forelegs allow them to grasp and hang onto their perch as they alight. The mantids differ from other species of grasshoppers only in their general appearance, one of the most noticeable differences being the triangular shape of their head.

Although Aldrovandi's work was generally influential, historically it did not fare as well as did that of his contemporary Konrad Gesner (1516—1565), whose work served as a model for much of Aldrovandi's.[35] Upon his death, Gesner left an unfinished manuscript dealing with the natural history of insects. This manuscript was sold to Thomas Penny, who had worked on Gesner's collection of insects and had also acquired the entomological notes of his friend and fellow physician, Edward Wotton. Penny died in 1589, after accomplishing some amalgamation of the materials, and the work passed into the hands of Thomas Moffett (Moufet, Muffet; 1553—1604). Moffett added both descriptions and drawings to the text but was unable to find a publisher prior to his death. The manuscript was finally purchased by Sir Theodore de Mayerne, court physician to James I and Charles I, who (with difficulty) found a publisher in London; it appeared in 1634 under Moffett's name, as *Insectorvm sive minimorum animalium theatrvm*, and was the first book devoted to entomology to appear in England.[36] It was subsequently translated from Latin into English, and in 1658 was issued as part

34. The following comments on Aldrovandi's understanding of mantids are based on Bodenheimer, *Geschichte der Entomologie*, (above, n. 15), I, 265—266.

35. Aldrovandi studied Gesner's work diligently but is thought by some to have been neither as criticial nor as good a stylist as was Gesner (Erik Nordenskiöld, *The History of Biology* [New York: Tudor, 1928], p. 95). Aldrovandi came to be seen simply as a compiler, for which he has been harshly (and perhaps undeservedly) criticized. For instance, the naturalist Georges—Louis Leclerc, Comte de Buffon (1707—88), said that nine-tenths of Aldrovandi's work is useless and untrue, and Cuvier (1769—1832) referred to it as "an undigested and wearisome compilation" (cited in James Wilson, *A Treatise on Insects* [Edinburgh: Adam and Charles Black, 1835], p. 5). On the other hand, Max Beier has argue that Aldrovandi was the superior entomologist (Beier, "Early Naturalists," p. 86).

36. See *Dict. Sci. Biog.*, *5*: 378—379, *9*: 440—441, and *14*: 507—508.

of the second edition of Edward Topsell's bestiary, *The History of Four-Footed Beasts and Serpents* (which was also based on Gesner's work).[37]

Moffett's book is important in that it introduced to a broad readership the accumulated information about a wide range of insects, including Western beliefs about mantid behavior. In chapter 16, Moffett described the locusts, which he divided into two broad groups, the winged and the wingless; the former he again divided into two groups, the ordinary and the rare, the latter including the mantids. Moffett claimed to have seen but three kinds of these most rare "locusts" in the meadows and pastures of France and Britanny: "*i.e., Italian, Greek*, and *African*: They are called *Mantes, foretellers*, either because by their coming . . . they do shew the Spring to be at hand, So *Anacreon* the Poet sang; or else they foretell death and famine, as . . . *Theocratus* observed. Or lastly, because it alwaies holds up its forefeet like hands praying." Moffett went on, recounting the myth that if a traveler is lost, the kindly mantis will point the way home: "So divine a creature is this esteemed, that if a childe aske the way to such a place, she will stretch out one of her feet, and shew him the right way, and seldome or never misse."[38]

TALES OF VORACIOUS CANNIBALISM

Moffett's characterization notwithstanding, dark clouds were on the horizon for the mantis. Its reputation for pious helpfulness was about to be sullied by tales from continental Europe and the Far East. The earliest of these unflattering accounts was offered by the well-known German painter/naturalist August Johann Rösel von Rosenhof (1705—1795).[39] In attempting to study the

37. Edward Topsell, *The Historie of Four-footed Beasts, Serpents and Insects* . . . (London: E. Cotes for G. Sawbridge, T. Williams, and T. Johnson, 1658). The first edition appeared as *The Historie of Four-footed Beasts and Serpents* . . . (London: William Jaggard, 1608).

38. Thomas Moffett, *The Theatre of Insects*, in Topsell, *Historie of Four-footed Beasts*, 98, (1658 ed.), vol. III, pp. 982—3 (italics in original).

39. August Johann Rösel von Rosenhof (sometimes referred to as Roesel) was a successful portrait painter who became enthralled with painting insects and describing their habits after seeing the work of Maria Slbylla Merian (1647—1717). Merian was the first person to undertake an expedition solely for the purpose of entomological research. She produced several volumes of work containing beautiful plates of insects and their habitats. Her best-known works are *Metamorphosis Insectorum Surinamensis* (Amsterdam, 1705) and *Histoire des Insectes de l'Europe* (Amsterdam: Jean Frederic Bernard, 1730); in the former she depicted two species of mantid in plate 27. Rösel von Rosenhof

habits of these creatures, Rösel placed several in a glass jar for observation. To his amazement, he found that both young and old specimens battled viciously with each other, the victor always devouring the vanquished. Rösel likened these ferocious battles to those of vicious hussars, fighting to the death with razor-sharp sabers. However, more important than the fact that his young mantids devoured one another was Rösel's claim that they did not cease to attack, kill, and eat each other even when their hunger had been satisfied by an abundant supply of other, nourishing food![40]

The second important, unflattering account of mantid behavior appeared in a widely read travel documentary about China written by John Barrow (1764—1848), and published in London in 1804.[41] In his discussion of Chinese gaming practices, Barrow recounted seeing gamblers wager their wives and children on the final toss of a die: "It may easily be conceived that where a man can sell his children into slavery, there can be little remorse, in the breast of a gamester reduced to his last stake, to risk the loss of what the law has sanctioned him to dispose of."[42] To Barrow's eye, this lack of remorse was equally evident in the "cruel and unmanly amusement" of animal fights. Such fights — shamefully, he noted — were also practiced in Europe; however, in China the sport included not just the cock and the quail, but extended even "into the insect tribe, in which they have discovered a species of gryllus, or locust that will attack each other with such ferocity as seldom to quit their hold without bringing away at the same time a limb of their antagonist." The sport, Barrow recounted, "is so common that, during the summer months, scarcely a boy is seen without his cage and his grasshoppers [i.e., mantids]."[43]

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produced the finely illustrated, four-volume entomological work *Insecten Belustigungen* (Nürnberg, 1746—61). A fifth, supplementary volume, *Beytraege zur Natur oder Insecten Geschichte* (Nürnberg, 1761) was brought to publication by his son-in-law, F. C. Christian Kleeman (1735—89).

40. This account of Rösel's findings is based on several translations including (but not limited to) those in *The Natural History of Insects* (London: John Murray, 1835), II, 165—169; Baron Cuvier, *Animal Kingdom*, (London: Gilbert and Rivington, 1832), XV, 189; and Philip Henry Gosse, *Zoology*, 2nd ed. (London: Society for Promoting Christian Knowledge, 1857), II, 331—333.

41. John Barrow, *Travels in China* (London: T. Cadwell and W. Davis, 1804, 1806). Several translated editions of this widely read book were also published in France between 1804 and 1896, and in Germany in 1805. We have relied on the American edition of the text (Philadelphia: W. F. McLaughlin, 1805), pp. 106—108.

42. Ibid., p. 107.

43. Ibid. Although Barrow does not identify the species of insects he saw

An equally shocking account of mantid ferocity was given in James Smith's popular travelogue, *A Sketch of a Tour on the Continent*, published in London in 1807. In describing the unusual plants and animals around Montpellier, Smith included that "singular" insect, *Mantis religiosa*, which gets its name from the "perpetual erection of its fore-paws," and will, according to Moffett, point the way home to lost travelers; however, Smith's accompanying entomologist, a Mr. Dorthes, offered a contradictory characterization, "which savors little of divinity."[44] After having put a captured male and female together in a bottle, Dorthes witnessed events not unlike those reported by Rösel: First, the pair mated, after which "the larger and stronger [female] . . . devoured the head and upper part of the body of her companion. But the most wonderful circumstance is, that a subsequent union took place; the life and vigor of the male being unimpaired by the loss of his head, as that part is not in insects the seat of the brain: this was no sooner concluded than his insatiable mate ate up the rest of his body!"[45]

The tales of voraciousness offered by Rösel, Barrow, and Smith rapidly found their way into popular natural history, and into the general scientific literature as well. They were repeated by virtually everyone who wrote about mantids, often being placed in juxtaposition to other, kinder characterizations.[46] For instance, in 1806 in

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fighting, all subsequent commentators believed them to be mantids. As noted earlier, mantids were originally thought to be a type of locust. Insect fighting in China was also recounted in *Travels in Kamtschatka* by Dobell, which is cited in A. H. Swinton, *Insect Variety: Its Propagation and Distribution* (London: Cassell, Petter, Galpin, 1880), pp. 48—49.

44. James E. Smith, *A Sketch of a Tour on the Continent* (London: for Longman, Hurst, Rees, and Orme, 1807), I, 168—169.

45. Ibid., p. 170.

46. The juxtaposition of these two opposing views of the mantis — one charming or beneficial, the other frightening or evil — occurs throughout popular literature extending through the nineteenth and twentieth centuries. Consider the following three examples. In the article "A Queer Pet," Elizabeth Bellamy wrote, regarding a pet mantid: "Once, for ten summer days, I had the pleasure of entertaining a strange and most interesting guest" — but she also admitted, "I have a horror of the creature, and prefer not to touch it" (*Pop. Sci. Mon.*, *37* [1890], 528—529). A century later, on May 13, 1990, the Arlington Heights, Ill., *Daily Herald* ran a story written by Carolyn Hill for the *Christian Science Monitor* News Service entitled, "Is Bug-Eyed Praying Mantis a Sentry or Mini-Monster?" The author related, on the one hand, her infatuation with the mantids in her garden ("My husband and I both developed a real fascination for our new friends"), but she also admitted her fear of the creatures ("neither would admit to the other we weren't interested in doing any hand feeding"). Finally, consider these lines from the poem "The Praying Mants Visits a Penthouse" by Oscar

George Shaw's *General Zoology* one reads the following: A stranger to the British Isles, this creature holds its forelegs in the attitude of prayer, for which "the vulgar [have] conferred upon it the reputation of a sacred animal." Some believe that it will point the way home to a lost traveler or child, and the Hottentots venerate it as an idol, believing that the person on whom the mantis alights is blessed by the gods. On the other hand, Shaw continued, the mantis's real disposition is "far from sanctity": it is pugnacious, and when kept with others in captivity will "attack its neighbors with the utmost violence, till one or the other is destroyed." Citing both Barrow and Rösel, Shaw explained that mantids fight like hussars with sabers, sometimes cleaving the opponent through with a single stroke, severing head from body, and then devouring the antagonist.[47]

The general distaste with which mantid cannibalism was viewed is evident in the widely read and influential *Introduction to Entomology* written by the natural theologians William Kirby (1759—1850) and William Spence (1783—1860).[48] Among the indirect benefits derived from insects, Kirby and Spence included the fact that many insects, by feeding on others, keep the total number of insects in check: "I cannot doubt that you will recognize the goodness of the Great Parent in providing such an army

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Williams: "The praying mantis with its legs of straw / Out of nowhere's forehead born full armed / Engages the sentry at my terrace door. / Focused at inches the dinosaur insect sends / Broadsides of epic stillness at my eye, / . . . / My love who fears the thunder of its poise, / Has seen it and cries out . . . / I strike, the stick whistles, shearing off two legs / Which run off by themselves . . . / All sinews doubtless screaming insect death. / . . . / I search my mind for possible wounds and feel / The victim's body heavy on the visitor's heart" (*A Little Treasury of Modern Poetry* [New York: Scribners, 1950], p. 416).

47. George Shaw, *General Zoology* (London: for G. Kearley, 1806), pp. 117—121. Having raised several species of mantid ourselves, we must say that we have never seen a mantis cleave another through, as Rösel suggests. An account similar to Shaw's appears in Thomas Smith, *The Naturalist's Cabinet* (London: James Cundee, 1807), VI, 288—290. In addition to the information gleaned from Moffett and from James Smith's *Tour on the Continent*, Thomas Smith elaborated an additional characteristic, stealth: "If it see an insect a little beyond its reach, over its head, it slowly erects its long thorax . . . then resting on its posterior legs, it gradually raises the anterior part also. . . . Should the insect go from the spot, it flies or crawls after it slowly on the ground like a cat; and, when the insect stops, erects itself as before" (pp. 289—290).

48. William Kirby and William Spence, *An Introduction to Entomology*, 4 vols. (London: for Longman, Hurst, Rees, Orme, and Brown, 1815—26). Subsequent editions were published in London (the seventh appearing in 1858), and in Germany (Stuttgart: Cotta, 1823—33). It has been said that this book "[was] the chief means of producing whatever may exist of a *general* taste for Entomology in Britain" (Wilson, *Treatise on Insects* [above, n. 35], p. 14 [italics in original]).

of counterchecks to the natural tendency of almost all insects to incalculable increase." But as good as it is to eat the excessive numbers of unrelated insects, it is bad, indeed, to eat your conspecifics: "But before I quit this subject I may call your attention to what may be denominated Cannibal Insects, since in spite of those disclaimers who would persuade us that man is the only animal that preys upon his own species, a large number of insects are guilty of the same offence." Here the authors include several insects and insect larvae, including the "cowardly and cruel" mantis, who seems to engage in the practice of cannibalism out of sheer wantonness, even "when in no need of other food."[49]

The famous French naturalist Georges Cuvier (1769—1832), in the fifteenth volume of his *Animal Kingdom*, reiterated the reports of Shaw, Moffett, Aldrovandi, and Rösel, and an account of mating-related cannibalism written by the French naturalist Poiret. Curiver embellished his own description with three important comments that accurately reflected the general opinion on mantid behavior. The first comment is that the mantis is in some sense an abnormal insect: "The mantes may be called truly anomalous insects. . . ." The second is that the mantis has a basically evil disposition: "The mantis is as cowardly as it is cruel, for it will fly away from the ant, though it will destroy abundance of helpless flies." Third, and perhaps most critical, is Cuvier's reiteration of Rösel's claim that mantid cannibalism is a product of the insect's disposition, *not* a part of its normal eating behavior: "They are so cruel and carnivorous that (even as hatchlings) they kill and eat one another, *without being compelled to do so by hunger.*"[50]

By the time Cuvier's comments were published, mantid eating behavior had come to be seen not just as unusual, but as actually consisting of two separate components, each corresponding to one of the two sides of the mantid's character. Due to the commonplace juxtaposition of pious helpfulness versus cruel voraciousness, the mantis had come to be conceptualized as an animal that eats small prey for nutrition (a manifestation of its

49. Kirby and Spence, *Introduction to Entomology*, I, 267—270 (in the 1828 edition of vol. I, see pp. 275—278; in the 1858 edition of vol. I, see pp. 158—160). The authors cite Rösel and Barrow as their sources of information on mantid cannibalism and fighting behavior. Similar sentiments were voiced in 1893: in an article entitled "Cannibalism among Insects," Carl Berg noted several species of insect that "become addicted to a flesh diet, and what is still more strange . . . feed on their own kind" (*Natural Science: A Monthly Review of Scientific Progress, 2* [1893], 444).

50. Baron Cuvier, *The Class Insecta* (London: Whittaker, Treacher, 1832), II, 188—190 (italics added).

good-natured, or normal, side) and also cannibalizes conspecifics, not out of hunger, but out of wanton voraciousness (a manifestation of its cruel, or abnormal, side). As explained in *The Natural History of Insects* (1835), when the prey is of *appropriate* size, such as a bluebottle fly that "is not too large, it is curious to remark how cunningly [the mantis] endeavors to entrap its prey." However, *even when well fed*, "They never ceased to attack, kill, and eat each other when they met."[51] The nature of these cannibalistic attacks appeared particularly heinous when considered in juxtaposition to the mantid's pretensions to divinity. *The Penny Magazine* reported that "A more pugnacious and rapacious little creature does not live, and its cannibal propensities . . . have been established without a doubt. . . . Several experiments have proved that they will devour each other *less from hunger than from savage wantonness*."[52] In *The Naturalist's Library*, one reads that mantids have a "peculiar instinct and mode of life. [They are] . . . fierce, cruel, gormandizing creatures . . . continually seeking what they may devour."[53] And, finally, from the popular book *Insect Life*: "Some of the tribe of Mantis — treacherous and cruel creatures, with long, desiccate, skeleton limbs — are like spectral anatomies of vegetable death — yet living and locomotive."[54]

51. A recounting of Rösel's comments in *Natural History of Insects* (above, n. 40), II, 168 and 166, respectively. Among the usual citations on mantis behavior is numbered Barrow's account of mantis fighting in China.

52. "The Mantis," *The Penny Magazine of the Society for the Diffusion of Useful Knowlege* (London: Charles Knight, 1841), p. 436 (italics added). In this article, the author notes that myths of mantid divinity are prevalent among the rural French, the Turks, the Muslims, the Africans, and the South Americans. In contrast to these beliefs, the remarks of Barrow, Smith, and Rösel are presented.

53. James Duncan, *Entomology*, vol. XXXI of William Jardine, ed., *The Naturalist's Library* (Edinburgh: W. H. Lizars, 1843), p. 229. Of interest is the fact that a strange mistake about mantis behavior appears in this volume, attributed originally to the seventh edition of the *Encyclopedia Britannica*; the mistaken claim is that mantids "are perpetually moving their arms or forelegs in the air, and closing one armed joint upon another, so that whatever insect prey comes within reach, is immediately transfixed and consumed" (p. 229). This and several other comments suggest that the author has never himself observed a living specimen. An interesting article of similar tone entitled "Insect Appetite" appeared in the British magazine *Once A Week, 4* (1861), 300—301; although mantids are not mentioned specifically, the general impression that many insects are insatiable eaters is clearly indicated: "Some insects are endowed with an appetite so keen . . . that they eat incessantly. . . . Their existence is a feast, without a change of plates, or a pause between the courses. . . . Breakfast commences with infancy, and their only after-dinner nap is a passage to another state of existence."

54. Acheta Domestica (Rev. J. G. Wood), *Insect Life* (London: Bell and Daldy, 1867), p. 265.

WHAT DO MANTIDS REALLY EAT?

The belief that the mantis eats small, "soft bodied" insects for nutritional reasons, and engages in cannibalism for reasons other than hunger, rests on the belief that mantids actually do maintain themselves on the former — if not exclusively, at least with rare exception. And, indeed, the belief that mantids live primarily on flies or flylike prey did become firmly entrenched in people's minds, but not because mantids in the wild were observed to do so. Actually, the belief became a commonplace for two other reasons. The first is the frequent repetition of Rösel's claim that mantids "will destroy [an] abundance of helpless flies." This line, or words to its effect, was regularly included in accounts of mantid behavior. The second reason is the fact flies came to be the food of choice (i.e., of convenience) for those keeping mantids in captivity.[55]

However, in contradiction to the popular notion that small

55. Because this is a critical point for our overall argument, we wish to offer several corroborative examples: "Not being aware if there is any instance on record of the hatching of any species of *Mantis* in England, I beg to inform you that . . . I was much gratified by the sight of a very lively little specimen in a tumbler glass . . . in pursuit of small flies . . . [upon which] . . . it fed readily for about fifteen days. . . . [In Melbourne] it is a common practice to place specimens of the *Mantis* on the window blinds, where they keep the room clear of flies" (Henry Denny, "Hatching of the *Mantis* in England," *Mag. Nat. Hist., 19* [1867], 144); Fig. 465 in William B. Carpenter, *Zoology* (London: Bell and Daldy, 1867), p. 146, depicts a "Mantis, in the act of seizing a fly . . ."; "But only let an imprudent fly come within reach of our devotee, and you will see it stealthily approach it, like a cat who is watching a mouse" (Louis Figuier, *The Insect World* [New York: Appleton, 1869], pp. 288—289); "This perfect quietude does not raise any suspicions . . . but if an unfortunate fly comes too close the *Mantis* extends its foot rapidly and too surely" (P. Martin Duncan, *The Transformations [or Metamorphoses] of Insects* [Philadelphia: Claxton, Remsen, and Haffelfinger, 1870], p. 338); "Mr. Charles O. Waterhouse sent for exhibition a living specimen of a Mantid. . . . The captor stated that he had supplied it with flies, &c., in the hope of ascertaining the mode in which it seized them" (Edward Newman, ed., "A Living Mantid Exhibited," *Entomologist, 7* [1874], 188); ". . . our fastidious captive had his meals served *au naturel.* The living fly was simply turned loose in his cage, and instantly the devil's-riding-horse was on alert" (Bellamy, "Queer Pet" [above, n. 46], p. 530); "The food of this tribe of insects [i.e., mantids] being flies of any kind" (Mrs. Brighton, *Inmates of My House and Garden* [New York: Macmillan, 1895], p. 204); "This is the way the house-flies rightfully take the mantis's attitude. Watch an unwary bluebottle crawl or buzz into the fatal corner" (Vernon J. Kellogg, *American Insects* [New York: Henry Holt, 1905], p. 129); "[Trimen] also describes its mode of feeding, and says that it was fond of house-flies, and would eat 'blue-bottles,' i.e., *Musca vomitoria*" (S. F. Harmer and A. E. Shipley, eds., *The Cambridge Natural History*, vol. V [London: Macmillan, 1922], p. 274). As we will explain, the belief that mantid predation is

insects are the mantid's sole diet, there began to appear reports that mantids are actually opportunistic predators that will eat a wide range of prey, including small vertebrates larger than themselves. These reports first appeared around the mid-eighteenth century and they continued into the late twentieth century, but they either were not cited in articles on mantid predatory behavior or were dismissed as so unusual as not to be of general importance. Had these studies been integrated into the literature, it would have been impossible to maintain the belief that the mantids' capturing of same-sized conspecifics is a unique eating behavior.

The earliest observation of a mantis eating a vertebrate seems to have been made by C. A. Zimmermann, and was first reported in 1838 in the German literature by his colleague, the well-known entomologist H. C. C. Burmeister (1807—1892): "It devoured as before, several dozen flies daily, sometimes also robust grasshoppers, then some young frogs and even a lizard . . . three times as long as the insect."[56] Zimmermann's report appeared again in German in 1843,[57] and then in English in *The Annals and Magazine of Natural History* in 1844. The fact that mantid eating behavior was thought to be limited to small insects is evidenced by the fact that the latter report was a replication of Zimmermann's first account in an attempt to refute the skepticism of the

limited to fly-sized insects would eventually come to play a critical role in shaping both experimental paradigms using the mantis, and interpretations of the results derived from those experiments.

56. (Again note the reliance on flies as the primary food for the captive mantis.) H. C. C. Burmeister, "Kaukerfe. *Gymnognatha.* Ersta Hälfe; *vulgo* Orthoptera," in *Handbuch der Entomologie* (Berlin, 1838), pp. 397—756; cited in Kevan, "The Mantis and the Serpent," (above, n. 26), p. 3. These early accounts were cited in many popular books (e.g., A. S. Packard, *Guide to the Study of Insects* [Salem: Naturalist's Book Agency; and London: Trübner, 1869], p. 575; *Cambridge Natural History*, V, 250), and articles on mantids (e.g., "Mantidae," *Sci. Amer., 66* [1892], 375). Most of the literature on mantid predation on vertebrates is reviewed in Kevan's article, but also see John S. Kingsley, ed., *The Standard Natural History* (Boston: S. E. Cassino, 1884), p. 176; M. D. Johnson, "Concerning the Feeding Habits of the Praying Mantis, *Tenodera aridifolia sinensis*, Saussure," *J. Kans. Entomol. Soc., 49* (1976), 164; M. G. Ridpath, "Predation of Frogs and Small Birds by *Herodula Werneri*, Mantidae in Tropical Australia," *J. Austral. Entomol. Soc., 16* (1977), 153—154; D. A. Nickle, "Predation on a Mouse by the Chinese Mantid *Tenodera aridifolia sinensis*, Saussure (Dictyoptera: Mantoidea)," *Proc. Entomol. Soc. Wash., 83* (1981), 802—803.

57. W. F. Erichson, ed., "Zur Naturgeschichte der *Mantis Carolina*: aus einem Schreiben des Dr. Zimmermann," *Arch. Naturgesch., 9* (1843), 390—392; cited in Kevan, "The Mantis and the Serpent," (above, n. 26), p. 3.

editor who originally published it: "Instead of the striped lizard . . . I made use of a species of newt. . . . One newt after the other was seized, and to a greater or less extent devoured. I send you the very specimen of mantis with which these experiments were performed."[58] Reports such as Zimmermann's continued to appear periodically, and included instances of mantids catching and/or eating small birds, lizards, frogs, mice, snakes, and turtles. The original reports, and numerous references to them in articles and textbooks, appeared in English, German, and French from the mid-eighteenth century on, with virtually no impact on subsequent accounts of mantid predatory behavior.

The basic understanding of mantid predatory behavior changed little from the mid-nineteenth century to the first quarter of the twentieth century. Mantids continued to be seen as engaging in basically two types of eating behavior: predation on small insects for nutrition, and predation on (large) conspecifics for other reasons. The latter continued to be viewed as distinct from normal eating behavior, primarily because reports of mantids capturing other large prey were ignored and this omission dramatically constrained the way in which mantid behavior could be understood. Consider, instead, the following scenario: Let us assume for a moment that mantids are generalized, opportunistic predators that will capture and eat any prey that they are strong enough to hold. This is the most parsimonious explanation of all the information on mantid predation that had been collected to this point. The reason that smaller insects are the mantid's usual fare is simply that mantids come into contact with small insects more frequently than they do with other, large creatures. However, if one holds this alternate interpretation of manted predation, then what is so unusual about one mantid capturing and eating another? Under this alternative explanation, capturing a conspecific is no more unusual than capturing a large grasshopper, a small bird, or a newt.

The interesting historical question is, of course, why was this type of alternate explanation never effectively promoted, especially in light of the evidence suggesting that mantids are generalized predators that will eat anything they can hold onto, relative or not? There are, we believe, three reasons for this omission. The first has been revealed by the history presented so far. In the Far East, people had long observed mantids; perhaps due to their prevalence, certainly due to the ancient sport of insect fighting, it

58. Alfred Tulk, "Habits of the Mantis," *Ann. Mag. Nat. Hist., 14* (1844), 78.

was generally recognized that mantids are quite bold, ready to challenge a variety of other creatures. However, in Africa, Western Asia, and Europe an ignorance about mantid behavior allowed the development and entrenchment of myths based on assumptions of gentle piousness. When a general interest in nature was rekindled, and the sciences began to evolve, people turned their attention away from ancient authority and toward nature itself. The apparent cruelty and insatiable voracity of living mantids clashed both with the established myths of gentle piousness, and with a general distaste for animal cannibalism.

THE HORROR OF CANNIBALIZING A MATE

Much of the scientific literature on mantids published from the mid-eighteenth to the early twentieth century had a narrow focus, concentrating on unembellished taxonomy, and descriptions of species, habitats, and the like. However, there were a few notable exceptions to this trend that would be critical in maintaining the conceptual dichotomy between normal mantid eating behavior and mantid cannibalism. Of these exceptions, the most popular and arguably the most influential voice was that of Jean Henri Fabre (1823—1915). After a period as a physics teacher, Fabre earned his doctorate in the natural sciences at Paris in 1854, after which he devoted himself to the biology and behavior of insects. His widely read, major work, the ten-volume *Souvenirs entomologiques* (1879—1907), presents a considerable number of significant original discoveries about insect (and arachnid) behavior — including, of course, Fabre's observations on mantids.[59]

In spite of Fabre's gift of careful observation, his poetic style, while wonderful to read, contributed to some errors of interpretation in the case of mantid behavior. Unlike many others, Fabre seems to have reconized correctly that mantids will regularly capture and eat prey as large as or larger than themselves.[60]

59. J. H. Fabre, *Souvenirs entomologiques*, 10 vols. (Paris: Librairie Ch. Delagrave, 1879—1907). The praying mantids are discussed in vol. V, pp. 287—355. The work was translated into English by A. Teixiera de Mattos as *The Works of J. Henri Fabre* (London, 1912). In addition, various popular condensations of Fabre's work were published, such as Mrs. Rodolph Stawell, *Fabre's Book of Insects* (New York: Tudor, 1921 and 1936), and Edwin Way Teale, *The Insect World of J. Henri Fabre* (New York: Dodd, Mead, 1949).

60. "These particular captures are destined to show me just how far the vigor and audacity of the Mantis will lead it. They include the large grey cricket . . . which is larger than the creature that devours it" (J. H. Fabre [Bernard Miall, trans.], *Social Life in the Insect World* [London and Leipzig: T. Fisher Unwin,

However, he also believed that the defensive display sometimes adopted by a mantid when faced with a large prey is intended to mesmerize the victim: "The wing-covers open, and are thrust obliquely aside . . . parallel screens of transparent gauze, forming a pyramidal prominence which dominates the back; the end of the abdomen curls upwards. . . . The murderous forelimbs . . . open to their full extent, forming a cross with the body. . . . The object of this mimicry is evident; the Mantis wishes to terrorize its powerful prey, to paralyse it with fright; for if not demoralized with fear the quarry might prove too dangerous."[61]

Although Fabre recognized the range of prey sizes that mantids will consume, he never made the connection to the capture of same-sized conspecifics. Like many of his predecessors, he attributed mantid cannibalism to less than noble causes. To Fabre's mind, the first of these causes is the quick temper of gravid females.[62] He described the results of caging several females together as follows: "At the outset matters did not go badly. . . . But this period of concord was of brief duration. . . . The swelling of the ovaries perverted my flock, and infected them with an insane desire to devour one another. . . . Ferocious creatures! It is said that even wolves do not eat one another. The mantis is not so scrupulous; she will eat her fellows when her favorite quarry, the cricket, is attainable and abundant."[63]

But even worse, in Fabre's eyes, is cannibalism associated with the act of mating:

These observations reach yet a more revolting extreme . . . [for

1912], p. 73). Similar anecdotal accounts of the mantid's catholic tastes appeared in the early twentieth-century entomological literature. For instance: "Full grown adults if hungry ate almost any living thing . . . [even] huge cockroaches and grasshoppers as large as themselves" (Mary Didlake, "Observations on Life-Histories of Two Species of Praying Mantis [Orthopt.: Mantidae]," *Entomol. News, 37* [1926], 170).

61. Fabre, *Social Life*, pp. 74—75. "With the smaller crickets . . . the Mantis rarely employs her means of intimidation; she merely seizes the heedless passer-by as she lies in wait" (ibid, p. 76).

62. This is the only instance of which we are aware that mantid cannibalism is linked to a mantid's gender. Fabre's observations, that adult females are more likely to eat conspecifics than are adult males, are supported by other observations; for instance, ". . . never yet have I seen an adult male attack either a female or another of its own sex" (Phil Rau and Nellie Rau, "The Biology of *Stagmomantis Carolina*," *Trans. Acad. Sci. St. Louis, 22* [1913], 19). The reason for the difference in behaviors is that adult females are usually larger and stronger, and eat more than adult males. However, we have seen male *Sphodromantis lineola*, (Burr.) eat male conspecifics.

63. Fabre, *Social Life*, p. 81.

> which there is not] the excuse of hunger. . . . The male Mantis, a slender and elegant lover, . . . throws himself timidly on the back of his corpulent companion. . . . Finally the two separate, but they are soon to be made one flesh in a much more intimate fashion. . . . Here we have no case of jealousy, but simply a depraved taste. . . . I have seen the same Mantis treat seven husbands in this fashion. She admitted all to her embraces, and all paid for the nuptial ecstacy with their lives.

The worst instances of this behavior are those which actually occur during copulation: "The custom of eating the lover after the consummation of the nuptials, of making a meal of the exhausted pigmy, who is henceforth good for nothing, is not so difficult to understand . . . but to devour him during the act surpasses anything that the most morbid mind could imagine. I have seen the thing with my own eyes, and I have not yet recovered from my surprise."[64]

Fabre saw these latter, distasteful acts of cannibalism as being the product of primitive, undeveloped, instincts:

> I do not deny that the limited area of the cage may favor the massacre of the males; [they have nowhere to flee], but the cause of such butchering must be sought elsewhere. It is perhaps a reminiscence of the carboniferous period. . . . The Orthoptera . . . are the firstborn of the insect world. Uncouth, incomplete in their transformation, they wandered amidst the arborescent foliage, already flourishing when none . . . sprung of more complex forms of metamorphosis were as yet in existence. . . . Manners were not gentle in those epochs, which were full of lust to destroy in order to produce; and the Mantis, a feeble memory of those ancient ghosts, might well preserve the customs of an earlier age.[65]

As we have discussed, the dichotomy between normal eating behavior and cannibalism was maintained because reports of mantids capturing large prey were never completely integrated into people's understanding of mantid predation. As Fabre so

64. Ibid., p. 84. Similarly, the well-known Swedish entomologist Charles de Geer (1720—78) reported being filled with "horror and indignation" at the sight of a male spider being captured and eaten "in the midst of his preparatory caresses" (Charles de Geer, *Mémoires pour servir à l'histoire des insectes* [Stockholm: 1758], VII, 335; cited in Kirby and Spence, *Introduction to Entomology* [above, n. 48], I, 272).

65. Fabre, *Social Life*, pp. 84—85.

eloquently described it, the attack on conspecifics represents the dark, undeveloped side of the mantis — its innate wantonness, greed, and unbridled voracity. However, if a belief in the existence of these anthropomorphic traits in mantids was the only force maintaining the idea that the insect has two separate predatory strategies, then the latter should have disappeared along with the ascription of the traits to the mantid. That is, after Fabre, mantids should have come to be seen as generalized predators that regularly eat large prey including conspecifics. However, this did not occur.

The belief that cannibalism is a regular part of mantid mating behavior, on the one hand, and that mantids have evolved to be the perfect fly-catching machines, on the other hand, has persisted long past the time when cannibalism could be explained as a product of wantonness, cruelty, or an insane desire to devour one another. The first of the two remaining reasons for the persistence of the belief in the dichotomy in mantid predation is that as anthropomorphic excuses for cannibalism faded from the literature another alibi immediately took their place.

THE DISSOCIATION OF MANTID BEHAVIORS

Fabre marked the last important attempt to claim that mantid cannibalism is distinct from other predatory behaviors due to the mantid's innate, despicable character. However, without the alibi of ill-temperedness, how might one account for the behavior? This question is best answered, we believe, by asking a more fundamental question: Why does one need to account for the behavior? The answer to this second question is that when the male's head, and even most of its prothorax, is eaten by the female just prior to or during copulation, he still manages to mate for quite some time after the decapitation. If the headless male simply ran around for a few moments as does a chicken prior to dropping dead, the whole scenario would be of little interest, scientifically or otherwise. (To our knowledge, no one has sought to determine the biological advantage to the headless chicken's undignified display.) But the headless mantid does extraordinary things, including that most important evolutionary task. Surely this could not be the case by chance; surely, the most important act this creature must perform cannot be analogous to the frenetic, undirected behavior of the headless chicken.[66]

66. This analogy is borrowed from the following articles, to which the reader should turn for a thorough experimental analysis of courtship behavior in one

To understand how the behavior of the headless mantid came to be seen as so special, one must consider the following. Contemporary ideas about mantid behavior were shaped by two basic notions. As explained, the first is that they eat flies, or flylike insects. The second has to do with the functional organization of the insect's central nervous system (CNS). The general plan of the insect CNS is that there is a series of discrete ganglia (groups of functionally related nerve cells) along the length of the insect, connected by two parallel, ventral nerve cords (or longitudinal connectives). The largest aggregation of nerve cells is in the insect's head and is sometimes referred to as a "brain" (although this term is somewhat misleading). Ventral to the brain, and also in the head, is the subesophageal ganglion (SEG), with which we will be concerned in a moment. Thereafter follows a series of ganglia, the number of which varies from species to species. In most insects, including mantids, the three thoracic ganglia remain separate, each innervating the muscles and sense organs of the segment in which it is located. Likewise, a varying number of abdominal ganglia innervate the structures in the abdomen.[67] What is important to note is the fact that because each ganglion contains motor neurons, sensory neurons, and some capacity to integrate information, all of the necessary neural machinery to emit a complex behavior may be present in a single ganglion — for instance, the ability to learn has been demonstrated in a single, isolated cockroach ganglion and its corresponding metameric leg.[68] Functionally, this means that an insect may be able to walk or mate seemingly normally, even without a head, if the motor and sensory neurons necessary to control the behavior are contained within an undamaged ganglion in another part of the insect.

The understanding that mantid behaviors are to a greater or lesser extent both discretely organized in, and controlled by, individual ganglia was first derived from anecdotal observations of damaged mantids emitting complex, seemingly normal behaviors. Of particular influence was a brief observation made in 1784 by the French naturalist Poiret, which was subsequently confirmed

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species of mantid: E. Liske and W. J. Davis, "Sexual Behavior of the Chinese Praying Mantis," *Anim. Behav., 32* (1984), 916—917; E. Liske and W. J. Davis, "Courtship and Mating Behavior of the Chinese Praying Mantis, *Tenodera aridifolia sinensis*," *Anim, Behav., 35* (1987), 1524—37.

67. R. F. Chapman, *The Insects* (Cambridge, Mass.: Harvard University Press, 1982), pp. 607—641; Cedric Gillott, *Entomology* (New York: Plenum, 1980), pp. 361—420.

68. E. M. Einstein amd M. J. Cohen, "Learning in an Isolated Prothoracic Insect Ganglion," *Anim. Behav., 13* (1965), 104—108.

and elaborated in four quasi-experimental reports published in French in 1893, 1914, and 1916.[69] As had others, Poiret noted that a male mantis will still mate if partially cannibalized. The implications of this observation — that mantid behaviors must be discretely organized in order to allow their continuation after decaptitation — were explored in the four subsequent articles; their importance requires citing several lines from three. From the first:

> Duges has seen that the [separated] posterior section of the body of the praying mantis . . . could still stand . . . resist impulses, raise itself, and regain its balance when overturned. . . . Duges concluded that this single thoracic ganglion senses the fingers which apply pressure . . . recognizes the point at which it is grasped, wishes to disencumber itself, and directs the appendages which it animates. . . . [My confirmation of these facts have revealed behaviors] as well coordinated as prior to the removal of the head.[70]

From the second:

> On Thursday November 2, [1911], in order to study the mouthparts, I had decapitated a female [mantis]. The next day I found . . . the insect still alive, . . . her posture had remained remarkably similar to that of normal individuals. [On] November 6, . . . the insect fashioned a perfectly constructed ootheca, of entirely normal shape. . . . This fact demonstrates that,

69. Poiret's observation, published originally in *Journal de Physique* in 1784, is cited in L. F. Henneguy, *Les insectes* (Paris: Masson, 1904), p. 263. In turn, this reference is cited in Étienne Rabaud, "Accouplement d'un mâle décapité de *Mantis religiosa*, L. (Orth.)," *Bull. Soc. Entomol., 21* (1916), 57. The other two articles are Raphel Dubois, "Sur l'innervation réflexe chez la mante religieuse," *Prés. Soc. Linn. Lyon, 40* (1893), 205—207 (in which an article by Duges appearing in the same volume of the journal is cited); and L. Chopard, "Sur la vitalité de *Mantis religiosa*, L. (Orth. Mantidae); ponte après décapitation," *Bull. Soc. Entomol. Fr., 19* (1914), 481—482. It is noteworthy that Chopard cited the Dubois article, and Rabaud cited both Dubois and Chopard. Although, to the best of our knowledge, these articles were never published in English, they were well known and frequently cited in scientific and popular literature, as will be explained. Translations of these articles from French into English have been done especially for this paper by Ms. Cathryn Easterbrook.

70. Dubois, "Sur l'innervation réflexe," pp. 205, 206. One reads a similar item in N. Hudson Moore, "The Mantis Religiosa in Rochester, N.Y.," *Sci. Amer., 84* 1901), 105—106: "The loss of head, or a leg or two, or even a portion of the body does not quench the fiery nature of a fighting Mantid, but they may go on battling in this condition for hours" (p. 106).

> despite the suppression of the nerve centers, insects can accomplish certain actions which are in appearance very complicated. . . . [My] assistant at the laboratory informed me that she died only on November 21.[71]

From the third:

> Having introduced a male into a cage where a female had resided for several days, the latter immediately seized the former . . . after a few moments the decapitation was complete. The remainder of the body was nevertheless not reduced to immobility and, . . . the abdomen executed a series of movements exactly comparable to those which a male executes during the preliminaries to mating . . . does not the important phenomenon lie in the execution of complex movements in the absence of cerebral ganglions?

To this account Étienne Rabaud added the following theoretical note:

> Under normal conditions, attraction as a result of sensory influences, and coplation as a result of sensory excitation, form a whole. In all probability, the cerebral ganglions directly influence the copulatory reflex, by exercising an inhibitory action on them, to such an extent that a male may remain on a female for hours without making the slightest movement. Liberated from this influence, the reflex undergoes no modification in form or rapidity, but it occurs under the most singular conditions.[72]

In contrast to these rather sophisticated analyses, we now consider the brief report by L. O. Howard mentioned in the introduction in this essay, and generally thought to be the beginning of "the modern version of the decapitation myth."[73] Certainly, Howard's account contains nothing that is new. In fact, he cited three well-known English-language texts that had already reported mating-associated cannibalism by mantids.[74] Howard

71. Chopard, "Sur la vitalité de *Mantis religiosa*," pp. 481—482.

72. Rabaud, "Accouplement d'un mâle décapité," pp. 57—59.

73. Brown, "Of Mantises and Myths," (above, n. 10), p. 421. Also note, for instance, "[Howard's article] represents the first account I know of an all-time favorite among nature's curious facts" (Gould, "Only His Wings Remained" [above, n. 9], p. 10).

74. "Westwood quoted from the *Journal de Physique*, 1784, an instance in

briefly recounted the all-too-familiar events that take place after caging male and female together, and echoed the long-held belief that female cannibalism is independent of hunger:

> Not until she had eaten all of his thorax except about three millimeters, did she stop to rest. All this while the male had continued his vain attempts to obtain entrance . . . and he now succeeded. . . . The female was apparently full-fed when the male was placed with her, and had always been plentifully supplied with food. The extraordinary vitality of the species which permits a fragment of the male to perform the act of impregnation is necessary on account of the rapacity of the female, and it seems to be only by accident that a male even escapes alive from the embraces of his partner.[75]

Six years later, in a brief (half-page) secondhand account, Charles Valentine Riley and Howard modified Howard's original claim only slightly. A colleague had written to them, describing a pair of *Stagmomantis carolina* that began copulation without injury to the male. However, Riley and Howard explained that as their owner watched, "the female turned her head and began to rapidly devour the head of the male . . . [who] made no effort to escape." The observer then killed the female by applying cloroform to her head, and permanently pinned the pair *in copulo*. Thus pinned, the specimens were shipped to Riley and Howard. "The nonchalance with which the male devoted himself to the sacrifice . . . indicated [to the letter writer] that the male has no serious objection to this method of suicide."[76]

Having now placed Howard's original anecdote in a historical context, we have come to a partial answer to the first broad

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which the female of the European species . . . decapitated the male before mating. . . . Riley in his 'First Monthly report,' p. 151. wrote, 'The female being the strongest and most voracious, the male in making his advances, has to risk his life many times, and only succeeds in grasping her by slyly and suddenly surprising her; and even then he frequently gets remorselessly devoured,' In Packard's 'Guide,' p. 575, we find, 'Professor Sandborn Tenny tells me he has observed the female after sexual union devour the male" (Howard, "Excessive Voracity" [above, n. 8], p. 326).

75. Ibid.

76. C. Riley and L. Howard, "The Female Rear-Horse versus the Male," *Insect Life, 5* (1892), 145. This article was translated into Swedish as S. Lampa, "Engendomliga vanir hos Mantidernas honor," *Entomol. Tidskr., 15* (1894), 118. It should also be noted that another account of a female *S. carolina* devouring a male *in copulo* appeared shortly thereafter in W. S. Baltchley, "Miscellaneous Notes," *Can. Entomol., 28* (1896), 210–215.

historical question that we posed in the introduction to this essay (i.e., Can one adequately account for the origin and persistence of the long-standing, widely held belief in the regularity of mating-related cannibalism by mantids with any of the explanations previously suggested?). First, it seems clear that Howard's account of mantid cannibalism is not the beginning of the story; Howard only echoed the well-established fact that cannibalism does occur, and the long-engrained belief that it is not the product of normal mantid hunger.

Further, the evolution of the idea that cannibalism is a part of the mating ritual appears not to have stemmed from Howard's account per se, but rather from the belief that cannibalism is not a part of the mantid's normal eating behavior and, consequently, needs a special explanation. When the ascription to the mantis of qualities such as "wanton voraciousness" could no longer serve as that special explanation, the claim that cannibalism is a part of the mating ritual was a ready substitute. This transition from the former to the latter excuse is clearly evidenced in the fact that as anthropomorphisms faded from the literature so did discussions regarding the cannibalism of same-sex conspecifics, which were the terms in which cannibalism had been discussed for centuries. That is, if one considers mantid cannibalism to be a manifestation of a general voraciousness, then male-on-male, female-on-female, and gender-neutral accounts of immature mantids engaged in cannibalism are of great interest (e.g., Rösel's or Fabre's accounts). On the other hand, if one considers cannibalism to be a product of the idiosyncrasies of mantid mating behavior, then only instances of adult, female-on-male or male-on-female cannibalism are of potential interest. However, because the adult female mantis is generally larger and stronger, and eats more than the male, male-on-female cannibalism rarely if ever occurs among adults. Hence, one is left with only one story to tell, that of the adult female cannibalizing the adult male. All other stories, especially those concerning gender-indifferent cannibalism among sexually immature mantids, become uninteresting.[77]

The second broad historical question we posed at the beginning of this essay asked how it could be that the disconfirming evidence presented by a researcher of Ken Roeder's status had virtually no impact on the belief that cannibalism is a regular part

77. If male-on-female cannibalism occurred with any frequency, we are sure that a story would have sprung up claiming that the female has evolved such that decapitation releases the egg-laying response from cerebral inhibition (recall Chopard's account).

of mantid mating behavior. The answer to this question also becomes clear once it is place in a historical context. When Roeder wrote his classic paper on mantis sexual behavior, he was, of course, aware of most (if not all) of the literature that we have presented here. In his references he listed, for instance, Aoki and Takeishi,[78] Chopard, Fabre, Howard, Riley and Howard, and Rabaud. In addition, however, he also cited a fascinating article, the historical importance of which has not been considered in previous discussions of the topic at hand. This article, which appeared in *Transactions of the Academy of Science, St. Louis* in 1913, is neither poetic nor anecdotal (as were Fabre's accounts), nor is it based on single observations (as were the accounts of Chopard, Howard, Howard and Riley, and Rabaud). It is an extensive, modern study undertaken by Phil and Nellie Rau on the biology of *Stagmomantis carolina.*

The Raus began by admitting explicitly the fascination that the act of mantid cannibalism holds for people: "The fact that the female mantis *almost always* devours her mate while the pair are *in copulo*, and the male unresistingly clings while he is slowly being eaten, makes the mating habits of this species arouse more than ordinary interest."[79] Indeed, the Raus' fascination with this event is evident in both their text and the accompanying photos. However, as the article progresses, one comes to a realization that would have been impossible when reading accounts of mantid behavior based on single observations. For the first time, one sees that the extensive observations reported by the Raus are being filtered through the authors' admitted fascination with the act of cannibalism itself. That is, any reasonable explanation of mantid behavior that is based on a *single* observation can be made to sound plausible (e.g., Howard's account) — but the Raus' belief in the regularity of mating-related cannibalism is not supported by

78. B. Aoki and S. Takeishi, "On the Copulatory Behavior of the Japanese Mantis (*Tenodera aridifolia*, Stoll.), and the Seat of Its Nerve Center," *Dobutsu-gaku Zasshi, 39* (1927), 114—129. The authors demonstrated that males will copulate when their heads are "killed" or severed, and (as Chopard indicated) that females will continue to lay egg cases after decapitation. The authors concluded that "this peculiarity [on the part of the males] is adaptive . . . in view of the fact that the male is often eaten up by the female while approaching its mate or even during copulation" (p. 128). In support of the latter contention, the authors included two photographs of several headless males mating. Ironically, the captions read "*Natural* copulation" (p. 127, italics added). It is of note that no evolutionary significance is attached to the decapitated female's egg-laying abilities.

79. Rau and Rau, "Biology of *Stagmomantis carolina*" (above, n. 62), p. 29 (italics added).

the behaviors of the many mantids they observed. In seeming contradiction to the lines cited above ("the female ... almost always devours her mate"), in all but three of the more than thirty *matings* that the Raus described, males were not cannibalized! Yet in spite of this, they concluded: "The practice of the female devouring her mate may be one of the little economical devices of Nature. ... Why should he not go to help nourish the female while she goes through the function of egg-laying?"[80] To dramatize the point, the Raus included a full-page photograph of half-devoured males, still *in copulo*, pinned with their mates, like the specimens sent to Riley and Howard.[81]

In spite of these inconsistencies in the Raus' presentation, the belief that the "female generally devours the male after copulation"[82] appeared even more frequently in popular and scientific literature, and cannibalism came to be seen not as a product of the mantis's pugnacious character, but as a regular part of the mating ritual. As the Harvard entomologist William Wheeler explained, "the nutritive meaning of the male to the female is clearly revealed, for both Fabre, Howard and the Raus have shown that he himself is actually devoured piecemeal by his spouse after copulation."[83] Even popular articles that presented well-balanced accounts of the mantids' eating behaviors could not resist the inevitable comment: ". . . the female almost invariably devours her mate."[84]

Two decades after the Raus published their report, Ken Roeder wrote his classic article on mantis sexual behavior, mentioned above.[85] In the article, he argued against the view that male mantids are regularly cannibalized by females during mating and claimed instead that the event is strictly fortuitous, most males remaining unscathed. Further, he reiterated Fabre's claims that males are captured as are other large insects, and that cannibalism is exacerbated by the close quarters of captivity. This has led

80. Ibid., p. 39.

81. Ibid., plate III. The Raus had read Riley and Howard's work, including the pertinent article.

82. H. Maxwell Lefroy, *Manual of Entomology* (New York: Longmans, Green; and London: Edward Arnold, 1923), p. 49.

83. William Morris Wheeler, *Foibles of Insects and Men* (New York: Knopf, 1928), p. 160.

84. Edwin Way Teale, "Dinosaur of the Insect World," *Travel, 64*: 4 (1935), 25.

85. K. D. Roeder, "An Experimental Analysis of the Sexual Behavior of the Praying Mantis (*Mantis religiosa*, L.)," *Biol. Bull., 69* (1935), 203–220. Roeder's findings were also explained in his popular *Nerve Cells and Insect Behavior* (Cambridge, Mass.: Harvard University Press, 1963), pp. 129–170.

some to argue that Roeder's findings should have sounded the death knell for the belief in the regularity of mating-associated cannibalism among mantids. However, it did not do so — for two important reasons. First, as in the Raus' paper, there are critical inconsistencies in Roeder's portrayal of mantis predatory behavior. Secondly, Roeder offered sophisticated experimental evidence supporting the hypothesis suggested by Rabaud, among others, that decapitation releases the copulatory reflex from the inhibitory influences of the mantid's cerebral ganglia.

In the first case, although Roeder claimed that males are eaten simply because their movements attract the female's attention (i.e., there is nothing unusual about a female capturing an almost-same-sized insect), and he cited a case of a mantis eating a lizard,[86] he also claimed that mantids will only eat insects that are "not too large."[87] He attempted to reconcile these contradictory claims about the size of prey that mantids will capture by reiterating the old beliefs that overcorwding, or an unusually high level of hunger, will bring about the capture of these large-sized prey. Hence, even Roeder's elegant (for the time) experimental analysis begins with the long-standing assumption that cannibalism (i.e., the capture of large prey) is an unusual behavior that is outside the mantids' normal repertoire of predatory behaviors and is in need of special explanation.

In the second case, and of utmost importance, are the facts that Roeder not only offered experimental evidence that removal of the male's head disinhibits the copulatory reflex, he also proposed a plausible model of mantid brain organization that explains why the phenomenon occurs.[88] Without going into unnecessary detail, Roeder's experiments demonstrated that removal of the subesophageal ganglion (SEG), either through decapitation or by severing the ventral nerve cords between the SEG and the first thoracic ganglion, yields copulatory movements that appear normal even in sexually immature adults (which would not normally perform them).[89] Based on these findings, and following the suggestions of

86. Roeder cited M. Morgue, "Un reptile chassé et tué par un insecte," *Feuille Jeunes Nat.*, (1909), 87.

87. Roeder, "Experimental Analysis," p. 205.

88. Also see K. D. Roeder, "The Control of Tonus and Locomotor Activity in the Praying Mantis (*Mantis religiosa*, L.)," *J. Exp. Zool., 76* (1937), 353—374.

89. In addition, Roeder found that removal of the SEG yields a general drop in muscle tone, spontaneous locomotor movements (occurring simultaneously with the copulatory movements), and immediate grasping of any rounded object accompanied by "violent attempts" at copulation ("Experimental Analysis," pp. 212—213).

several of his predecessors, Roeder hypothesized that "the nerve center responsible for . . . copulatory reflexes, is situated in the last abdominal ganglion."[90] The SEG contains a "center which is antagonistic to the last abdominal center, inhibiting copulatory movements except when the male is in contact with the female."[91] Hence, either contact with a female or extirpation of the SEG removes the inhibitory influences to the last abdominal ganglion, and copulatory behavior is released.

On the one hand, Roeder argued that mantid cannibalism is simply a fortuitous event, a normal part of mantid predation, and he described several scenarios in which courting males might be detected and consumed, without having had an opportunity to mate.[92] On the other hand, however, he also claimed: "The head and prothorax of an approaching male are naturally most exposed to the female's attack, and are therefore eaten first."[93] This claim, in conjunction with his neurological explanation of the release of the copulatory reflex, made an irresistable combination. So, although Roeder argued against the idea that cannibalism occurs

90. This was indicated to Roeder by the fact that when "the nerve cord in the abdomen is . . . cut at various levels, the movements of the cerci and claspers continue while [only] the last abdominal ganglion is intact" (ibid., p. 216). The idea that complex behaviors were organized within individual ganglia was already an accepted belief among entomologists. See, for instance, E. Baldi, "Studi sulla fisiologia del sistema nervoso negli insetti," *J. Exp. Zool., 36* (1922), 211—288; A. Bethe, "Nervous System of Arthropods," *J. Comp. Neur., 8* (1898), 232—238; W. von Buddenbrock, "Rythmus des Schreitbewegungen der Stabheuschrecke, *Dixippus morosus*," *Biol. Zentralbl., 41* (1921), 41—48; H. Z. Ewing, "The Functions of the Nervous System with Special Regard to Respiration in Acrididae," *Univ. Kans. Sci. Bull., 2* (1904), 305—319; S. Kopec, "Über die Funktionen des Nervensystems der Schmitterlinge während sukzessiven Stadien ihrer Metamorphose," *Zool. Anz., 40* (1912), 353—360.

91. Roeder, "Experimental Analysis," pp. 217—218.

92. "Insects up to the size of the mantis may be caught and eaten, including other mantids of the same species. This fortuitous cannibalism is probably minimized in nature by the inactive and cryptic habits of mantids. . . . [A] cannibalistic attack may take place during the male's [courtship] approach, directly after mounting, or as the couple separates. . . . It is not inevitable, and appears to depend upon the female's state of nutrition, and upon her detection of the male's movements during the final phase of his approach" (Roeder, *Nerve Cells* [above, n. 85], pp. 132—134; and see Roeder, "Experimental Analysis," pp. 204—209).

93. Roeder, *Nerve Cells*, p. 136. Again, note the inconsistency in Roeder's claims. The statement cited is much stronger than that made in the conclusion of the original paper: "When the male is attacked by the female he is usually seized by the raptorial arms or the head, and these are devoured first" ("Experimental Analysis," p. 218). However, Roeder makes an equally strong claim in the summary section of the same paper: "Since the head *is* attacked first . . ." ("Experimental Analysis," p. 219; italics added).

with any frequency among mantids in the wild, he ended his article with the comment: "Taken together, the continuous copulatory and lateral locomotor movements constitute a very beautiful means for securing fertilization of the female, should the preliminary courtship [i.e., careful approach of the male] be unsuccessful and the male captured."[94]

Roeder's data notwithstanding, his ambiguous interpretation did little damage to the prevailing theory about mantid cannibalism. His seeming ambivalence, in conjunction with a state-of-the-art explanation of the decapitated male's behavior, actually became the most important factor in *maintaining* the claim that cannibalism is a regular, even necessary, part of mantid mating behavior! One could cite Roeder and still argue for the regularity of mating-related cannibalism, and subsequent authors did just that.[95] By quoting Roeder selectively, one could argue for the regularity (or necessity) of mating-related cannibalism, without obviously contradicting or challenging Roeder's work (this was important, given Roeder's status within the scientific community). For instance, Roeder's findings are presented in some detail in the textbook by Peter Marler and William Hamilton, *Mechanisms of Animal Behavior*, published in 1967. In this text, the reader is left with the unmistakable impression that decapitation of the male, if not absolutely necessary, certainly "facilitate[s] the occurrence of sexual behavior."[96] Similarly, in a 1980 symposium on Orthopteran mating systems, it was suggested that male mantids may be engaging in a "strategy of 'investing all' in the female and/or offspring by being eaten . . . (especially if the female is undernourished)." Here, one of Roeder's strongest claims is used ("the male's head is eaten first"), and it is suggested that this may be "an evolved tactic by which the male ensures copulation . . . if the female begins feeding on him."[97] From this hypothesis it is a short

94. Roeder, "Experimental Analysis," p. 218.

95. As an example of the extent to which the belief in the inevitability of mating-related cannibalism remained embedded in the literature, consider the report on mating in the Trinidad mantis, *Acontiothespis multicolor*, published in 1967. Although the author found no instances of mating-related cannibalism in this species, he stated that his original purpose was "to see whether or not the female habitually devours the male after mating as is apparently the case with the European mantis" (V. C. Quesnel, "Observations on the Reproductive Behavior of the Mantis, *Acontiothespis multicolor*," *Trinidad Field Nat. Club.*, [1967], 53).

96. Peter Marler and William Hamilton, *Mechanisms of Animal Behavior* (New York: Wiley, 1967), pp. 208–210.

97. Darryl T. Gwynne, "Male Nutritional Investment and the Evolution of Sexual Differences in Tettigoniidae and Other Orthoptera," in *Orthopteran Mating Systems*, ed. Darryl T. Gwynne and Glenn K. Morris (Boulder, Col.: Westview Press, 1983), p. 346.

step to the following claim made in a recently published ethology textbook: "In some species of mantis the males are themselves the food offering. . . . In the grisly ceremony . . . the male's head . . . [is] eaten . . . [and] the remainder of his body mates. . . . After mating . . . the female will consume the remainder of the male."[98]

We have now come to a more thorough answer to the first historical question posed at the beginning of this essay, as well the answer to the second. First, it seems clear that one cannot account for the persistence of the belief in the regularity of mating-related cannibalism by any of the explanations previously suggested. The theories of mantid cannibalism and its cause, or its functional role, do not stem from observations of mating behavior per se, questions of evolutionary fitness, or gender-related issues.[99] Further, although it is certainly true, as one biologist put it, that mating-related cannibalism has a ghoulish appeal, this by itself seems insufficient to have maintained the story within the scientific and nonscientific communities for so long.

In place of these simpler explanations, we suggest that the fascination with and the need to explain away mantid cannibalism was (and is) driven by three other, complex forces. The first, as we have noted, was a general repulsion to, or incredulity about, cannibalism in general. That is, it was seen as evil, strange, or maladaptive, and in need of special explanation. Second is the fact that a half-eaten male mantis still mates. The performance of a behavior as complex and important as copulation by just a portion of a male is not easily fathomed as a fluke of nature, especially when a seductively straightforward neurological explanation such as that of Rabaud or Roeder can be mustered.

However, as powerful as they are, these two forces alone would

98. J. L. Gould, *Ethology* (New York: W. W. Norton, 1982), p. 365. Also note: "Females commonly attack and devour males either before or after copulation. . . . Destruction of the [subesophogeal] ganglion allows copulation to proceed" (Vernon Vickery and D. Keith McE. Kevan, *The Insects and Arachnids of Canada* [Canada: Agriculture Canada, 1985], p. 89).

99. As we have noted, the earliest accounts of cannibalism refer only to mantid pugnaciousness, not to gender. Nor did gender enter into subsequent, popular accounts of mantid cannibalism. Characteristic is this description: "If two of these insects be shut up together . . . they deal each other blows with their front legs, and do not leave off fighting until the stronger has succeeded in eating off the other's head" ("The Mantis or Praying Insect," *Pop. Sci. Mon., 4* [1874], 711). Virtually the same account appears in Figuier, *Insect World* (above, n. 55), p. 290; the latter account simply adds as a matter of fact that "The male being smaller than the female, is often its victim." In fact, voraciousness was attributed equally to both sexes: "The winner, that is to say the survivor, generally consummates his victory by devouring the body of his slaughtered foe" (J. G. Wood, *The Illustrated Natural History* [London: Routledge, 1871], p. 485).

not have carried the weight that they have for so many centuries had not one additional factor come into play to prevent the development of a general, integrated model of mantid predation. This third force was, and still is, the belief that the mantis is designed to be the perfect fly-catching machine. Obviously, this belief supports the long-held contention that predation on large organisms is both anomalous and in need of a special explanation — and, like the latter belief, it is long-ingrained in the scientific literature, in the popular literature, and in people's minds. It, too, has become what Chamberlin called a ruling theory, little influenced by the disconfirming evidence of mantids' regularly eating same-sized conspecifics and other large prey.

BORN TO CATCH FLIES

As we have discussed, the mantids were introduced to a broad readership through the works of Aldrovandi and Moffett, and during the eighteenth century authors continued to rely on these sources for their information on the unusual "locusts."[100] However, natural history expeditions, the collecting and trading of specimens, and an array of often beautifully illustrated natural history texts led to the dissemination of information about mantids and their behaviors.[101] One outcome of this dissemination was the recognition of the mantids' strikingly diverse morphologies. Because they often resemble the phasmids (i.e., the walking sticks and leaf insects), the mantids were eventually placed in the same taxonomic group with them, rather than with the locusts; however, it was quickly realized that there are two critical differences between mantids and phasmids, which led to yet another taxonomic reclassification.

In 1797 a paper by Anthony A. H. Lichtenstein, read before the Linnean Society of London, proposed that the praying mantids be separated from the phasmids and placed in their own genus.[102] In characterizing the morphological and behavioral traits

100. See, e.g., John Ray, *Historia insectorum* (London: A. & J. Churchill, 1710).

101. In addition to those texts already mentioned, see: Dru Dury, *Illustrations of Natural History*, vols. I—III (London: B. White, 1770—82), in which species of mantids from Jamaca, India, and America are described in each volume; Hans Sloane, *A Voyage to the Islands . . . and Jamaca*, vol. II (London: for the author, 1725); and George Shaw, *Naturalist's Miscellany* (London: Nodder, 1789—1813).

102. Anthony A. H. Lichtenstein (translated from the German by Thomas Young), "A Dissertation on Two Natural Genera Hitherto Confounded under

that set the mantids apart, Lichtenstein captured much of what would remain the defining characteristics of the group for the next two centuries. Two of the unique, morphological traits he cited are those that were (and are) responsible for eliciting the wave of anthropomorphism that rushes from virtually everyone who observes this unique creature. In tandem, the power of these two traits lies in the fact that they are two of the cardinal characteristics that make us human: our keen eyes set in a highly mobile head, and our dexterous hands.[103] The critical behavioral trait that Lichtenstein cited is, of course, that mantids prey on living creatures. Historically, this latter trait has elicited as much approbation and moral condemnation as the former characteristics have elicited identification. Indeed, it is the "human-like" qualities of the mantis that make its "uncivilized behavior" so appalling to so many.

"The *head*," Lichtenstein wrote, "[is] nodding, heart-shaped, with . . . Two large prominent *eyes*."[104] But unlike other insects,

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the Name of Mantis," *Trans. Linn. Soc., 6* (1802), 1—39. As Lichtenstein noted (p. 2), his argument had been mounted earlier by Casper Stoll in *Natuurlyke, en naar't leeven nauwkeurig gekleurde Afbeeldingen, en Beschryyingen der Spooken, Wandelnde Bladen, Zabelspringhanen, Krekels, Trekspringhaanen en Kakkerlakken* (Amsterdam: J. C. Sepp, 1797), the publication of which was interrupted by the author's death.

103. Note this example of the charm of the human-like qualities of the mantis's gaze: "A dignitary of the Natal Church . . . was, one warm summer evening . . . preaching by candle light . . . when a huge green mantis . . . perched himself upon the preacher's white neckerchief . . . first folding his arms into the prayerful attitude, he raised his chest and shoulders into rapt attention, turning his goggles from side to side, and following responsively. . . . He remained fixed in this convenient position until properly dismissed with the rest of the congregation" (an account by a Dr. Mann, cited in "The Mantis or Praying Insect" [above, n. 99], p. 713). Also note the comment that "[the mantis] is the only insect which appears to see man as an individual" Lefroy, *Manual of Entomology* [above, n. 82], p. 48).

104. The fully articulated head and neck are unique among the insects. Of note also is the fact that as the observer moves in relation to the insect's head, the mantis appears to be following the observer with its gaze: "These animals have a small black pupil or sight, which moves in all directions within the parts that we usually term eyes" (T. Smith, *Naturalist's Cabinet* [above, n. 47], VI, 290). The reason for the illusion has to do with the construction of the insect's compound eyes. The compound eye is made up of individual ommatidia or columns of cells each capped with a lens. Together the lenses form the mosaic of facets covering the convex outer surface of the eye. From any given position, then, one is looking directly into one or several ommatidia, which (because no light is reflected back out) appear as a black spot, similar to the pupil in a person's eye. As one moves in relation to the insect's eye, the pseudopupil moves too, giving the impression that the mantid is following with its gaze. This, in

"The *Mantes* have, instead of fore legs, arms, with nearly scissor-formed hands."[105] As to their behavior, unlike the phytophagous phasmids, "the *Mantes* . . . confine themselves entirely to food taken from the animal kingdom; their falciform hands serving them to catch and carry to their mouths flies and other insects, which they devour."[106] This final line is critical in that it is indicative of the early, general acceptance of the belief that small insects, particularly flies, are the mantid's "preferred" prey.

Given the consensus that mantids feed on flies or flylike prey, and observations of the amazing speed and accuracy with which they capture their prey, it was inevitable that late nineteenth- and early twentieth-century observers of this insect would conclude that their forelegs were remarkably well evolved for the task of capturing flylike prey: "the peculiar structure of their fore-legs [is] . . . marvelously adapted for seizing flies and other insects on which they feed," and "Their wonderful raptorial forelegs . . . are amazingly rapid and dexterous, often capturing an insect as it flies past."[107] The belief that the mantid's forelegs are specifically adapted to capture fly-sized prey was able to develop, of course, precisely because of the fact that observations of mantids capturing larger (even vertebrate) prey were seen as highly anomalous. Certainly, mantids could not have evolved to capture fly-sized prey if, in fact, they regularly fed on much larger prey. Hence, from this perspective, too, the fact that mantids capture (large) conspecifics had to be accounted for by a special explanation.[108]

The convenient separation of mantid predatory behavior into two categories (normal eating versus cannibalism) in the early twentieth century was simply the continuation of a century-old dichotomy. In the light of continued (though sporadic) reports of mantids eating large prey, the dichotomy might have finally disappeared had it not been for the fact that mantids were used as

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conjunction with the mantid's almost human-like head movements (which may, indeed, follow the passer by), make the mantid's gaze quite captivating.

105. Lichtenstein, "Dissertation," p. 7. Earlier, Lichtenstein described the raptorial forelegs as "falciform hands, and a thumb" (p. 4).

106. Ibid., pp. 4—5.

107. "Notes from the Zoo — The Praying Mantis," *Saturday Rev., 69* (1890), 735; Harold Bateson, *Insects Their Life-Histories and Habits* (London: T. C. and E. C. Jack, 1913), p. 174. This idea was carried to its logical extreme in several accounts that suggested that the forelegs were so highly adapted for predation that they could no longer be used for locomotion! See "Mantidae," *Sci. Amer., 66* [1892], 375; Bateson, *Insects*, p. 63; Harmer and Shipley, *Cambridge Natural History* (above, n. 55), p. 251.

108. In addition to the references already cited, see O. W. Richards, "Sexual Selection and Allied Problems in the Insects," *Biol. Rev., 2* (1927), 331.

an experimental model system by a very influential group of behavioral biologists, or ethologists.[109] The early ethologists focused their attentions on innate, or instinctive, behaviors, the assumption being that even the most complex of these behaviors could be broken down into discrete components or subroutines, each of which could, in theory, be acted upon by natural selection. This way of viewing innate behavior fit well with the prevailing belief that invertebrate (including insect) behavior was in the greatest degree (if not entirely) mechanistic.[110] As luck would have it, several of the mantid's behaviors made it an appealing experimental animal on which to test these assumptions.

The ability to conceptualize and explain many seemingly complex behaviors in terms of chains of simpler, discrete comoponents was aided by ethology's timely convergence with control theory, or cybernetics. An insightful and creative pioneer in this early merger, who was also a student of insect behavior, was Horst Mittelstaedt.[111] As a student, Mittelstaedt had been included by his mentor — Europe's premier biologist, Erich von Holst — in the small, close-knit group that would become the kernel of the modern ethological movement.[112] Mittelstaedt's early work included the enthusiastic application of cybernetics to the visual tracking behavior of the mantis.[113] However, of critical

109. Ethology, with its roots in central European biology, is best known through the works of Konrad Lorenz, Niko Tinbergen, and Karl von Frisch, who were jointly awarded the Nobel Prize for physiology or medicine in 1973. Of these three, Lorenz was the key figure in establishing the discipline of ethology in continental Europe. For a general account see W. H. Thorpe, *The Origins and Rise of Ethology* (London: Heinemann, 1979).

110. See, e.g., Jacob von Uexküll, *Umvelt und Innenwelt* (Berlin, 1909); Konrad Lorenz, "The Comparative Method in Studying Innate Behavior Patterns," *Symp. Soc. Exp. Biol., 4* (1950), 421—468; idem, *The Foundations of Ethology* (New York: Springer-Verlag, 1981); and Niko Tinbergen, *The Study of Instinct* (Oxford: Oxford University Press, 1951).

111. See Norbert Wiener, *Cybernetics* (Cambridge, Mass.: MIT Press, 1948). Also see Graham Hoyle, "The Scope of Neuroethology," *Behav. Brain Sci., 7* (1984), 368.

112. In 1950 von Holst invited a group of the Continent's outstanding ethologists to his Max Plank Institut für Verhaltensphysiologie (founded at Seewiesen) for an informal ten-day conference. The group included Konrad Lorenz, Otto Koehler, Gustav Kramer, Wolfgang Metzger, Ursula von Saint Paul, Laura Schoen, Niko Tinbergen, William Thorpe, and two of von Holst's students, Bernard Hassenstein and Horst Mittelstaedt. The meetings of this group of scientists were the forerunners of the long-standing, biannual International Ethological Conferences (Thorpe, *Origins and Rise of Ethology*, pp. 82—84).

113. For an overview, see Horst Mittelstaedt: "Prey Capture in Mantids," in *Recent Advances in Invertebrate Physiology*, ed. B. T. Scheer (Eugene: University

importance here is the experimental set-up that Mittelstaedt devised, not his theories pertaining to mantid tracking behavior. His ingenious procedure fixed the experimental mantis upside down, in such a way that only its head and forelegs could move. Due to Mittelstaedt's influence in the field of ethology, this setup was widely used internationally. The preparation, and a few minor variations of it, became the standard paradigms by which mantid behavior was studied in Europe, the United States, and South America.[114]

While it was extremely well suited to the types of analyses for which Mittelstaedt originally intended it, the inverted, immobilized mantis came to be used in investigations of other mantid behaviors, including prey recognition and capture, for which it was less well suited. In spite of the obvious limitations on movement imposed by the setup, the results obtained through its use by other investigators were given broad interpretations. These interpretations were invariably extended to freely moving mantids in general, and were never confined to the particular species under investigation. The consistent underlying assumption in these studies was that the results derived from immobilized or movement-

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of Oregon Publications, 1957), pp. 51—71; and "Control Systems of Orientation in Insects," *Ann. Rev. Entomol.,* 7 (1962), 177—198. Although Konrad Lorenz worked with vertebrates, Tinbergen and Berends did important work on insects, and von Holst and his students were particularly interested in the endogenous generation of motor patterns in invertebrates, including insects. The suggestion has been made that the attraction of invertebrates for many early ethologists lay in the putative simplicity of these animals (as compared to vertebrates), giving the impression that their central nervous systems are more "transparent" and are amenable to analysis via behavioral experimentation (Dr. Richard Burkhart, University of Illionis, Champaign-Urbana, pers. comm.).

114. See, for example, in Europe: P. Lässig and W. Krimse, "Optimotor Tracking Movements of Mantis Religiosa," in *Biocybernetics,* ed. H. Drischel and P. Dettmar (Jena: Gustav Fischer, 1971), IV, 242—246; E. Liske, "Proprioceptive Control of Head Position and Head Movement in the Praying Mantis," *Naturwissenschaften, 69* (1982), 452—453; E. Liske and W. Mohren, "Saccadic Head Movements of the Praying Mantis, with Particular Reference to Visual and Proprioceptive Information," *Physiol. Entomol., 9* (1984), 29—38. In the United States; J. Y. Lea and C. G. Mueller, "Saccadic Head Movements in Mantids," *J. Comp. Physiol., 114* (1977), 115—128; Susan Rilling, H. Mittelstaedt, and K. D. Roeder, "Prey Recognition in the Praying Mantis," *Behav., 14* (1959), 164—184. In South America: H. Maldonado and J. C. Barros-Pita, "A Fovea in the Praying Mantis Eye. I. Estimation of the Catching Distance," *Z. vergl. Physiol., 67* (1970), 58—78; H. Maldonado, M. Benko, and M. Isern, "A Study of the Role of the Binocular Vision in Mantids to Estimate Long Distances, Using the Deimatic Reaction as Experimental Situation," *Z. verg. Physiol., 68* (1970), 72—83; H. Maldonado, L. Levin, and J. C. Barros-Pita, "Hit Distance and the Predatory Strike of the Praying Mantis," *Z. vergl. Physiol., 56* (1967), 237—257.

restricted preparations accurately reflect both the behaviors of freely moving mantids and, by implication, the neural underpinnings of those behaviors.[115] Put simply, the setup made the mantids appear to behave as if they were but simple reflex machines.

In order to pursue his interest in the neural underpinnings of visual tracking in mantids, Mittelstaedt collaborated with the well-known American ethologist Ken Roeder, considered the expert on mantid neurophysiology at the time. As an aid to their studies one of Roeder's graduate students, Susan Rilling, made a series of paper lures that were used to elicit tracking and striking behavior by the mantids. Although they were not central to the senior investigators' project, Rilling pressed for publication of her findings on the effects of various lure configurations on mantid predatory behavior; this first systematic analysis of mantid prey recognition, coauthored by Rilling, Mittelstaedt, and Roeder, was published in 1959, well after Roeder's work on mantid sexual behavior.[116]

Using Mittelstaedt's tethered preparation, mantids were presented with both flies and a series of paper dummies hanging on strings which were twisted and/or swung in front of the mantids. The results of the series of experiments led Rilling to the following conclusions: First, the strongest eliciting stimuli for prey-catching behavior were the paper dummies that mimicked the movements of flies (i.e., moved irregularly or were "jerky") and had more artificial "wings" affixed to them.[117] Similarly, intact live flies were more appealing than flies with missing appendages. As to overall size, mantids most frequently attempted to capture

115. This misunderstanding seems to have happened for several reasons. The first is the basic assumption that mantid behavior can be adequately described as a hierarchy of simple reflexes. The second is the somewhat limited explanatory power of control theory itself, which does not (nor does it pretend to) mirror the actual biological units that make up the organism. Third, by the time that control theory gave way to newer models that recast animal behavior as more variable, plastic, and context dependent, mantid behavior had already been (it seemed) pretty thoroughly described, and the insect was seldom used in behavioral studies. Finally, experimental paradigms using a tethered, inverted mantis (and a more recent variant involving an inverted mantid restricted to a small platform) constrain the mantid's prey-catching behaviors, thereby giving the impression that the behaviors are more limited than they really are. For a comparison of the behavior of freely moving versus movement-restricted mantids of one species, see F. R. Prete, C. A. Klimek, and S. P. Grossman, "The Predatory Strike of the Praying Mantis, *Tenodera aridifolia sinensis*," *J. Insect Physiol., 36* (1990), 561–565.

116. Rilling, Mittelstaedt, and Roeder, "Prey Recognition."

117. It is of great interest that, as usual, the investigators maintained their mantids on a diet of flies.

approximately fly-sized, oval dummies ranging from 0.3 to 0.8 cm^2. Lures larger than 1.0 cm^2 elicited no responses. What is critical here is that Rilling constructed no dummies that were other than flylike. That is, all were small ovals or rectangles with legs or wings affixed, and were dangled in the air; none resembled conspecifics, caterpillars, worms, or the like (i.e., elongated shapes moving along the ground). The assumption behind Rilling's choice of lures was most probably (and understandably) that the releasing stimulus (or "sign stimulus") for prey capture would turn out to be flylike.

Rilling's article became the final word on mantid prey recognition for three decades — this, in spite of the fact that five years later a study was published indicating that at least one species of mantid struck most frequently at elongated lures almost twice as large as Rilling's.[118] The impact of Rilling's article led to a general orientation in subsequent experimental studies toward the gathering of supporting evidence for the argument that both mantid behavior and mantid morphology have evolved specifically to capture flies or flylike prey.[119]

The experimental results reported by Rilling et al. completed the picture of mantid predatory behavior begun two centuries earlier. Her results, in combination with previous findings on

118. This rarely cited study found that *Hierodula crassa*, (G.-Tos.) responds most strongly to a 8 × 24 mm (1.92 cm^2) lure rotating around its long axis (C. S. Holling, "The Analysis of Complex Population Processes," *Can. Entomol., 96* [1964], 335—347). It has recently been demonstrated that one species of mantis responds with predatory behaviors both to compact lures (such as those used by Rilling) and to large lures which are elongated parallel to their direction of movement (such as those used by Holling). This pattern of responding is similar to that seen in other terrestrial predators, such as toads (e.g., *Bufo bufo*) (F. R. Prete, "Configural Prey Recognition by the Praying Mantis, *Sphodromantis lineola*, [Burr.]; Effects of Size and Direction of Movement," *Bran Behav. Evol., 36* [1990], 300—306).

119. In addition to studies previously mentioned, see C. S. Holling, "The Functional Response of Invertebrate Predators to Prey Density," *Mem. Entomol. Soc. Can., 48* (1966), 3—47; and R. G. Loxton and I. Nicholls, "The Functional Morphology of the Praying Mantis Forelimb (Dictyoptera: Mantodea)," *Zool. J. Linn. Soc., 66* (1979), 185—203. Note also the assumption that the mantis's visual system is specifically evolved to locate prey of "typical size" (read: "fly-sized") in S. Rossel, "Foveal Fixation and Tracking in the Praying Mantis," and "Binocular Spacial Localization in the Praying Mantis," *J. Exp. Biol., 120* (1986), 265—281. And note the exclusive use of flies as lures, and the assumption that the mantis's eyes have evolved to best localize flies when they are at the "optimum" catching distance in the following three studies: H. Maldonado and J. C. Barros-Pita, J. C. Barros-Pita and H. Maldonado, and L. Levin and H. Maldonado, "A Fovea in the Praying Mantis Eye," Parts 1, 2, and 3, *Z. vergl. Physiol., 67* (1970), 58—78, 79—92, and 93—101.

mating behavior, appeared to support the general belief that mantids have two separate predatory strategies. The strongest eliciting stimulus for prey capture (i.e., the eliciting stimulus to which hungry mantids respond innately) appeared to be a fly, or flylike object. The fact that same-sized (or near-same-sized) conspecifics are sometimes eaten is a product of something other than normal eating behavior: it is due either to overcrowing, or to an abnormally high hunger level (Roeder's position), or to a special mantid reproductive strategy (e.g., an investment strategy by the male, or the decapitation-induced release of inhibitory controls over the male's copulatory reflex by the female).

CONCLUSION

The original, prescientific Western belief that the mantis is a pious, helpful creature became a widely held explanation for the mantid's unique resting (apparently prayerful) posture, and for one of its cryptic displays (extending the forelegs straight out). This belief was a characteristic part of a broader discourse about nature in which ancient authority, religious beliefs, and superstition, but few original observations, mixed freely. Gradually, the belief in mantid gentleness and piousness became a commonplace through the continual retelling of the myths and superstitions surrounding this fascinating insect.

By the seventeenth century, a growing interest in observation had begun to replace blind reliance on established wisdom and ancient authority. However, the various young sciences to which the period gave rise did not progress equally, and neither did the subdisciplines within each scientific field; biology, especially entomology, was particularly slow to free itself from past beliefs and contemporary superstitions.[120] In the specific case of the praying mantis, the situation may have been at its worst.

Early observers of nature found evidence that seemed, at first, to disconfirm the well-established belief that mantids are gentle creatures. These few observers, faced with startling firsthand information about mantid voraciousness, created a new characterization of mantids as merciless predators and then often juxtaposed the two images in their descriptions. However, it was not until the beginning of the nineteenth century that the two characterizations — gentleness versus cruelty — became reconciled.

120. A. Wolf, *A History of Science, Technology and Philosophy in the 16th & 17th Centuries* (Gloucester, Mass.: Peter Smith, 1968), II, 394—424; Beier, "Early Naturalists" (above, n. 31), pp. 81—94.

An amalgamation of these seemingly mutually exclusive characterizations was achieved by an interesting accommodation of each to the other. That is, while it could no longer be maintained that mantids are simply gentle insects, neither could it be accepted that they are all cruelty and viciousness. The melding of the two characterizations yielded a hybrid explanation which claimed that the praying mantis actually has *two* sides to its character! On the one hand, and like other creatures, mantids must nourish themselves, and do so quite reasonably by capturing small insects for food. However, even when "well nourished," and without "the excuse of hunger," their other, vicious side may surface; when this happens, the darkest of behaviors, cannibalism, is the result.

To understand the remainder of the story one must pause to consider what had happened in the other sciences up to this point. In the mid-seventeenth century, professional scientific societies (such as the Royal Society of London, the Académic Royale des Sciences in France, and the Accademia del Cimento in Florence) were established throughout Europe. The societies, and the various journals and periodicals that they produced or encouraged, represented an institutionalization of both science and its special, structured discourse.[121] However, as we have stated, entomology lagged behind; and in the case of some insects, superstitions and anthropomorphisms did not fade from descriptions of their behavior for centuries to come.

By the time the new scientific discourse was applied to mantids the creatures were already firmly shackled with a dual personality, and this assumption was never challenged. In fact, it was functionally impossible to disconfirm. Captures of small prey were considered part of the mantid's normal side; captures of large prey (including conspecifics) were considered part of the mantid's abnormal side. There was no alternative explanation.

As luck would have it, by the time that the strictures of scientific discourse had tightened sufficiently to disallow the use of anthropomorphisms in the explanation of insect behavior, another acceptable explanation of mantid cannibalism became immediately available: cannibalism became part of mantid mating behavior. That is, the fundamental explanatory model remained unchanged; it was merely couched in more appropriate terms.

121. The society's preference was for "the language of artisans, countrymen and merchants, before that of wits or scholars" (T. Sprat, *The History of the Royal Society of London* . . . [London, 1667], p. 113; cited in Collin Russell, *Science and Social Change in Britain and Europe 1700—1900* [New York: St. Martin Press, 1983], p. 14). Also see Wolf, *History*, I, 59—63.

The acceptance of this new explanation for cannibalism was virtually immediate and complete. For instance, no one ever asked the following questions: If the headless male remains able to mate as a putative precaution against female cannibalism, for what reason does the headless female remain able to fashion "a perfectly constructed ootheca"? Or: If female-on-male cannibalism plays a role in mating behavior, what role is played by gender-indifferent cannibalism, especially that among immature mantids? The latter phenomena were simply ignored — they were just uninteresting artifacts of insect life. However, the grand logic of nature was immediately apparent in the headless male's ability to mate. The ruling theory, to use Chamberlin's term, had been able to accommodate itself to, and assimilate, the new scientific discourse. It remained unscathed.

A persistent question posed by several historians of this particular topic has been, Why did not the results of Ken Roeder's experiments debunk the myth that males are regularly cannibalized by the females with which they mate? The reason, which we hope is now clear, is that there were (and are) two interdependent ruling theories operating here. If one accepts the argument that mantids' cannibalism is simply a normal part of their prey-catching behavior, then one attacks not only the theory that mantids have two separate predatory strategies, but also the more recent theory that mantids have evolved to be the ideal fly-catching machines. This second theory found its first confirming support in the centuries-old (fortuitous) practice of feeding flies to captive mantids. Again, the disconfirming evidence of mantids eating prey of various sizes had no impact on the theory. Confirming observations were accepted: disconfirming observations were seen as anomalies.

Additional confirmation of both ruling theories was garnered in experiments done in the mid-twentieth century. These experiments were based on the assumption that the original conceptualizations were correct, and consequently they did not test other hypotheses. The combined strength of the two theories is evidenced especially in the Raus' failure to account for the fact that their empirical observations were at odds with many of the conclusions that they drew, and in the fact that Roeder's work is still used to support the belief in the regularity (or necessity) of mating-related cannibalism despite the fact that Roeder, himself, argued the opposite.[122] with both theories well entrenched, it is

122. See Wenner and Wells, *Anatomy of a Controversy* (above, n. 1), pp. 189–205, for a discussion of social forces in science.

virtually impossible to promote an alternative theory of mantid behavior: namely, that mantids are generalized, opportunistic predators that manage to survive *in spite of* the fact that cannibalism sometimes occurs.[123]

Acknowledgments

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123. It is of note that some investigators did present evidence the mantids are opportunistic, generalized predators that will capture any potential prey that happens by, not just flies or fly-sized insects. However, these reports remained sequestered in the ecological literature, and were never integrated into the literature on mantid prey capture per se. See, e.g., J. A. Bartley, "Prey Selection and Capture by the Chinese Mantid *Tenodera sinensis*, Saussure," Ph.D. diss., University of Delaware, 1983; E. M. Barrows, "Perch Sites and Food of Adult Chinese Mantids (Dictyoptera: Mantidae)," *Proc. Entomol. Soc. Wash, 86* (1984), 898–901; L. E. Hurd and R. M. Eisenbergh, "Experimental Density Manipulations of the Predator *Tenodera sinensis* (Orthoptera: Mantidae) in an Old-Field Community. II. The Influence of Mantids on Arthropod Community Structure," *J. Anim. Ecol., 53* (1984), 955–967. Of special interest is the fact that these are the same ecologists who are quoted by Sharon May Brown in "Of Mantis and Myths" as saying that mating-related cannibalism rarely occurs in the field!