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Introduction To
ATTACK AND DEFENSE: BEHAVIORAL ECOLOGY
OF DEFENSE

MEDIEVAL INSECT BEHAVIORAL ECOLOGY, AND CHAOS

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**ABSTRACT**

Behavior of ants and bees was perceived by medieval European writers as virtuous. Singing by crickets and cicadas was perceived as profligate. Medieval writers used these precepts to impart order to human behavior. Aggressive behavior by antlions was noted by a medieval writer, but defensive behavior by insects, the complement of aggression, was overlooked. Crickets were credited with medicinal properties, perhaps by error of transcription. Public perception of insect behavior may have deteriorated in the ensuing centuries. Plants use chemicals in defense against herbivores, and humans use chemicals extracted from plants to defend other plants. Herbivores extract chemicals from plants in defense against predators and parasitoids. Parasitoids use chemical cues to detect herbivores, aided by the plants themselves. The concept of chaos provides an explanation of some complexities, though it seems the antithesis of medieval order.

**RESUMEN**

El comportamiento de hormigas y abejas fue considerado virtuoso por escritores europeos medievales. El canto de grillos y cicadas fue considerado vicioso. Los escritores medievales utilizaron estos preceptos para impartir orden al comportamiento humano. El comportamiento agresivo de la hormiga león fue observado por un escritor medieval, pero el comportamiento defensivo de insectos, el complemento de la agresión, fue olvidado. A los grillos les fueron acreditadas propiedades medicinales, probablemente por error de transcripción. La percepción pública del comportamiento de insectos puede haberse deteriorado en los siglos subsiguientes. Las plantas usan sustancias químicas como defensa en contra de herbívoros, y los humanos utilizan sustancias químicas extraídas de las plantas para defender otras plantas. Los herbívoros extraen los químicos de las plantas como defensa en contra de depredadores y parasitoides. Los parasitoides, ayudados por las plantas, utilizan señales químicas para detectar herbívoros. El concepto de caos provee una explicación de algunas complejidades, aunque ellas lucen como la antítesis del orden medieval.

Our previous introductions to behavioral ecology symposia used citations from early literature to explain the origins of modern concepts (Frank & McCoy 1989, 1990). In this introduction we examine the reductionist concepts of medieval writers to emphasize the hazard of modern reductionism in insect behavioral ecology.
The zoological work of Aristotle was largely neglected in 12th century Europe, and a new category of writings on animal behavior was developing: the bestiary. Bestiaries concerned animals that the writers believed to be real, such as ants, bees and crickets, as contrasted with animals widely perceived to be purely mythical, such as centaurs, mermaids and wyverns. Inclusion of behaviors of dragons, griffins, and unicorns shows that the writers believed and borrowed heavily from folklore, and did not limit the accounts to their own observations.

Antecedents of the medieval bestiary have been traced to a work in Greek but not derived from the work of Aristotle. It was written “before 140 BC” (Cook 1921), “probably... the second century AD” (Clark & McMunn 1989), “in second century Alexandria”... [by an] “anonymous author, Physiologus, or ‘The Natural Historian’... [whose] identity... will probably never be discovered” (Ives & Lehmann-Haupt 1942). It, in turn, had origins in Indian, Hebrew, or Egyptian legends (Curliey 1979). It was translated into Latin before 431 AD and numerous other languages (Cook 1921), but it is from the Latin versions that the various medieval bestiaries descend (Clark & McMunn 1989). The purpose of these bestiaries was not to interpret animal behavior; in fact the behaviors described were often misinterpreted. Instead, bestiaries were written as a means of instruction: to influence the behavior (and thus ecology) of humans.

Under the next four headings we examine the behavior of insects as described in a few of the medieval bestiaries. Generally it is clear how the examples were intended to influence human behavior. In zoology, the common names ant, antlion, bee, cicada and cricket refer not to species, but to families (Formicidae, Myrmecontidae, Apidae, Cicadidae and Gryllidae) of insects. The plurality dictated by the familial reference allows us to write “the ants”, “the antlions”, etc., but does not accord with literary use. By writing “an ant” we can serve the zoological meaning but not the literary, and by writing “the ant” we can serve the literary but not the zoological meaning. So we have chosen to omit the definite article “the” at introduction of ant, antlion, etc. Latin, because it does not use an article “the”, here has an advantage over English and French.

THE BESTIARY OF BISHOP THEOBALD

The author, Theobaldus, was perhaps abbot of Monte Cassino in 1022-1035 AD (Rendell 1928). Whoever he was, he wrote a metrical bestiary in Latin concerning 12 animals. A version of this bestiary (Physiologus Theobaldi Episcopi), printed in Cologne in 1492, has 18 metrical lines followed by almost two pages of interpretive text under the heading formica (ant), the only example drawn on an insect. Below are the 18 lines, separated by virgules, and followed by a translation [a composite of translations by Rendell (1928) and Eden (1972)].

De formica. Exemplum nobis precebt formica laboris/ Quando sua solium portat in ore cibum/ Inque suis faetis res monstrat spirituales/ Quas (quia iudeus non amat), inde reus/ Ut valeat brume fieri secura futura/ Dum calor in terra non requiescat en/ Nosque laboremus fratres, dum tempus habemus/ Securi fieri tempore judiciali/ Hec frumenta legit, si comperit ordea spermit/ Tuque novam legem collige non veterem/ Sed ne de pluvii aspersione germinet udis/ Aut id ne pereat esse quod nequeat/ Granum (quod legit) prudens formica bipertit/ Hoc est quod binas lex habet una vias/ Que terrena sonat simul et celestia donat/ Nunc mentem paseat, et modo corpus alit/ Nos ut lex repleat famis formido recedat/ Tempore judiciali, quod simile est hyemi.

Ant provides us with a model of labor when it carries its food in its mouth. In this it shows spiritual qualities that the Jew does not love, wherefore he stands accused. To be free of worry for the coming winter it does not rest while there is warmth, so let us work, brothers, while we have time, to be free of worry at the judgement. It harvests grain; if it finds barley seeds it rejects them; it harvest the new law, not the old. But
to prevent the grain from germinating, splashed by rain, or to prevent itself from perishing, unable to eat, the ant prudently bisects the harvested grain. That is, one law has dual interpretation; what sounds earthy simultaneously appears heavenly. Now it feeds the mind and so nourishes the body. Would that it fill us so that the terror of hunger recede at the time of judgement, which is like winter.

THE BESTIAIRE DIVIN OF GUILLAUME LE CLERC OF NORMANDY

Greek versions of Physiologus included μυρμικέλοντος which vanished from later, Latin versions perhaps because the mythical nature of this antlion became too much for later writers to accept (White 1958). This antlion (myrmikelon) was supposed to have a carnivorous father with the face of a lion and herbivorous mother with the face of an ant, resulting in an ant-like offspring with the face of a lion. The unfortunate offspring, torn between herbivory and carnivory, was doomed to starve. The moral interpretation given was that it is not proper for the religious to be of two minds (Curley 1979).

Guillaume le Clerc, otherwise known as Guillaume le Normand, compiled his bestiary early in the 13th century; its religious purpose was evident in the title as well as in Guillaume's statement that the examples were "to benefit the soul" (Beer 1986). It was not the first bestiary written in France or in French, but was written in octosyllabic verse and may be the most literary (Curley 1979). Among Guillaume's lengthy and moralizing treatment of formi (ant) in some versions is brief reference to formicaleon (antlion), and these are the only insects represented. Original wording about formicaleon is given below as reproduced by Reinsch (1892, with a translation [based on translations by Druee (1923) and Pierre Jolivet, but rewritten by Howard Frank in the octosyllabic style of the original]. This account of formicaleon is anomalous in the text because it bears no moral message.

Formicaleon. Uncor i a altre formi/ Que nul de eels que jeo vos di/ Qui formicaleon a non/ Des formiz est ell le lion/ Si est li plus petiz de toz/ Li plus hardiz e li plus prou/ Altres formiz het durement/ En la puldrere belement/ Se musce, tant est veziez/ Quant les autres venent chargez/ Sor els de la puldrere salt/ Si les occit, se les assait.

There ss yet another ant/ Different from those I've told you of/ Known by the name of antlion/ Among the ants it is the lion/ It is the smallest of them all/ It is the hardiest and the most wise/ The other ants it hates bitterly/ In the dust quite skilfully/ It conceals itself, so clever it is/ When the others come with loads/ Out of the dust it jumps upon them/ It assails them and it kills them.

THE MONDOVI LIBELLUS DE NATURA ANIMALIUM

The author of this work is unknown, but it was printed in 1508 by Vincenzo Berruerno in Mondovi, Piedmont (Davis 1958, McCulloch 1963). Its Latin prose text includes 2 sections on insects: apis (bee) and cicada (cicada), the latter as follows [translation by Bruce Woods].

De cicada. Natura sive proprietas Cicade talis est quod tantus delectatur suo cantu quod obliviscitur omnium et sic mortitur omnium cibo. Unde illi homines possunt cum cicade suis actibus culparari qui tantus delectatur suo cantu id est vanitatis et delectationibus hulus mondii quod bona omnium sunt oblitae et obmisae cibo id est Christi corpore privati mortuntur id est ad penas damnamurit ietiferas et eternas nam nesciunt nomen nostri regis et duplici consolamentum nec laudabant postquam sunt ab eorum corpora separati luxta illud non mortui laudabant te domine neque omnes qui descendunt in infernum.

The nature or character of cicada is such that it delights in its own song to such an extent that it forgets all and dies for lack of food. Whence those men are able, with the
cicada, to be blamed for their own actions, who delight in their own song, that is [their] vanities and the delights of this world, to such an extent that they have become forgetful and die for lack of food, that is the body of [their] private Christ that is they are condemned to an eternal and death-bringing punishment, for they do not know the name of our king and they, in a two-faced fashion, have praised greatly but they will not praise after they are separated from their bodies. In a like manner the dead will not praise you, Lord, nor those who descend into the underworld.

**The Bestiaire d’Amour of Richard de Fournival.**

Richard de Fournival was born in Amiens in 1201, becoming canon, deacon, and chancellor of Notre Dame of Amiens, where his brother was bishop (Beer 1986). Whereas the bestiaries of Bishop Theobald and of Guillaume le Clerc were collections of self-contained exhortations, Richard de Fournival’s bestiary was written as a flowing, integrated composition. All of the earlier bestiaries had a religious purpose, but Richard’s did not. No doubt this alone was seen as iconoclastic and as a daring act for a clergymen to commit. But Richard’s subject was love; in his bestiary he used the technique of the earlier bestiaries but adapted it to try to persuade his lady-love that she should love him. And he wrote his bestiary not in Latin, but in French, which some have claimed is the language of love. Some versions of the Bestiaire d’amour contain a response, which counters Richard’s arguments. The author of the response is unknown, but Beer (1986) believes that it was written by a woman.

Richard uses behavior of a crisson cricket and of eis (bees) in advancing his cause d’amour. The response argues the irrelevance of Richard’s mention of cricket, and ignores his mention of bees. The following passages in medieval French are from a version examined by Segre (1987), with a translation [modified by Howard Frank after a translation by Beer (1986)].

**Crisson [d’amour].** Et une autre raisons de ce meisme si est prise en la nature del crisson dont je me sui molt pris garde. Car sa nature si est ke li kaitis aime tant sen
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canter k'il se muert en cantant, tant en pert sen mangier et tant s'en laie a pourcaichier. Et por che me sui jou pris garde ke li chanters m'a pau valu ke je m'i puisse tant fier ke j'en perdisse nis moi, si ke ja li chanters ne m'i socourust; nomeement a chou ke je esprova bien ke a l'eure ke je miex cantai et ke je miex dis en cantant, adont me fu il pis. Ausi comme del chine.

And another reason for the same is found in the nature of a cricket of which I took great heed. For such is its nature that the poor beast so loves to sing that it dies in song, goes without food and neglects to look for it. And for that I paid heed because singing has been of so little value to me that I can be so sure that I would lose myself in song, so that song would not save me; especially since I found that at the hour when I sang best and most lyrically, things were worst for me. Just as with the swan.

Crison [response]. Et pour cezt i raison, sire et maiestres, je ne prenderai mie garde au crison dont je vous ai ci parler. Car encore il plaise ses chans tant que il s'en laisse apourcaichier et muire par tel defaute, ne m'est il mie grans mestiers que je prengne warde a vos paroles, qui ont sanlanche de moi mestre a vostre volenté; et me sanle que je no m'i doi me del tout asseurer, selone le nature du cisne.

And for this reason, lord and master, I shall pay no attention to the cricket of which I heard you speak. For though it enjoys its song so much that it lets itself starve and dies as a consequence, it does not help me to pay attention to your words, which are designed to subject me to your will; it seems to me that I must not trust them at all, as is the nature of the swan.

Eis [d'amour]. Et il est esrit es natures ke les eis n'ont mie oie, et neporquant quant uns vaisseaux d'eis est essamés, on les maine a sifle et a cant, ne mie pour che k'eles l'oent, mais il pert bien a leur oevres signories ke leur nature est si noble et si ordnée, selone lor maniere, k'il ne puuet mie estre ke bons ordenemens et parfois les trespast, k'eles ne le sentent. Et cil ki ont leüt et etendu les haute philosophies sevent bien combien musike puuet, et a chiaux ne puuet mie estre chelé qu'en toutes les choses ki sont n'a si parfaite ordenance comme en chant, ne si esquise.

And it is written in books on nature that bees have no ears, and regardless, when a hive of bees has swarmed, they are led by whistle and song, not because they can hear it, but it follows clearly from their signal works that their nature is so noble and so ordered, as is their behavior, that good organization and perfection cannot pass by them without being perceived by them. And those who have read and understood the high philosophies know well how much music can accomplish, and it cannot be doubted that nothing among all things that exist has such a perfect order as a song, nor so exquisite. [there seems to be no response to this].

PSEUDO-BESTIARIES AND PHARMACOPOEIAS

A manuscript written in England about 1100 AD is preserved in the Bodleian Library at Oxford University and is known as the Bodley Herbal and Bestiary (Hassall 1978). It offers medicinal uses for plants and animals, including one insect: grillus (cricket) [with translation by Howard Frank]:

De grille ad qui paralisi temptantur: Grillis adeps remedii afferet his qui paralisi treptant.

De claritatem oculorum: Grillis et sorici combustiones cum melle menseat et inde cotidie mane gustent. Item alter: Adipem de grillo cum melle attico et opobalsamo aequis ponderibus de eo ininguatur.

Ad somnum, qui non dormiunt: Grillis adipe fronte tempora inungues.

From the cricket for those afflicted with paralysis: Cricket fat brings a remedy to those who are paralysed.

For clarity of the eyes: Mix burnt crickets and shrews with honey, and taste every
morning. Alternatively, anoint with cricket fat and Athenian honey in equal parts by weight.

A soporific for those who cannot sleep: Anoint the forehead with cricket fat.

The Bodley Herbal and Bestiary is not descended from Physiologus, but is an abbreviated version of a treatise ascribed to Sextus Placidus (? 4th century AD) and entitled De virtutibus bestiarum in arte medicinae (Hassall 1973). Such works on medicinal arts were copied by hand, and mutations were introduced, deliberately or by error. Some of the variants in works derived from Sextus Placidus use De grille, and others use De gliris (Howald & Sigerist 1927). It seems more probable that the dormouse (glis) rather than the cricket (grillus) would be found to have the fatty tissue (adeps) which would be employed for such medicinal arts as curing paralysis (item 1), clearing the eyes (items 2, 3) and promoting sleep (item 4). Could it be that generations of English, following instruction to use adipem de grillo as transcribed by a dyslexic 12th century cleric, were unable to achieve the sleep that they had been led to expect?

The Bodley Herbal and Bestiary is a herbal and pseudo-bestiary. Although the English word herbal exists to describe a work dealing with medicinal properties of plants, there is no word to describe a work dealing with medicinal properties of animals, leading to misappropriation of the word bestiary. A similar problem occurs in Chinese and Japanese where the word that, because of its context, we have to translate as pharmacopoeia (a work dealing with medicinal materials of plant, animal and mineral origin), incorporates a character meaning plant, but no character meaning animal (Frank & Kanamitsu 1987). Pharmacopoeias in these two cultures are of at least as great antiquity, and were at least as prevalent for at least as wide a range of maladies as in medieval Europe.

Fables

Fables have their place in behavioral ecology (Frank & McCoy 1989). However, the animals playing roles in fables have at least a modicum of human behavior and they communicate with humans and with animals of other species in the lingua franca of the time. In contrast, animal behavior depicted in bestiaries was thought to be factual.

17TH CENTURY, 20TH CENTURY, AND MEDIEVAL ATTITUDES

The demise of bestiaries in England was given impetus by Thomas Browne's (1646) questioning of the facts during the renaissance of science. Not only was Browne outspoken in his criticism of the "commonly received tenents" presented in bestiaries, but he also was an early user of the words autochthon and indigenous which still are employed in ecological writing (Frank & McCoy 1990). Thereafter, books on insects such as Muffet's (1658) Theater of insects were written primarily for secular, not religious, purposes.

Only ant, antlion, bee, cicada and cricket are mentioned in the bestiaries consulted by us, whereas the writers, if not cloistered in scriptoria throughout their lives, must have encountered at least hundreds of species of insects. This emphasizes that bestiaries were not zoological works, but employed imagery from animal behavior to moralize on human behavior. That the behavior attributed to cricket by de Fournival is the same as the behavior attributed to cicada in the Munduvi Libellus (see above) did not matter; the names of the insects were only labels for the ascribed behavior, which was itself only a vehicle to influence human behavior.

If religion was the opiate of the masses in medieval Europe, an opiate in modern North America is organized sports. If animal behavior was used to guide the religious in medieval Europe, so animal symbols are used to foment the support of followers of
football teams, political parties, and even nationalism in the modern USA. The proponents are less inventive on the subject of animals, and only the symbolism remains. Lacking other explanations for the few insects in bestiaries, we suppose attitudes toward insects have changed little since the middle ages: "... insects, if they get anywhere near you ... whomp them with a hard-cover work of fiction at least the size of Moby Dick" (Barry 1990).

If the public was no more enlightened about insects in 12th century Europe than in 20th century North America, observational powers of the artists who illustrated the bestiaries were not acute. Even the 10th century illustration of a cicada in the Monodia Libellus (Fig. 1) shows this animal to have 12 legs. Did the writers, too, ignore the real world to concentrate on their compositions, and did they prefer to use the religious materials available to them in libraries as opposed to drawing from worldly events outside the confines of religious fraternities?

We were surprised to find no mention of mantis, whose symbolism is apparent in the name "praying mantis", nor of gnat, nor of demoiselle. Absence of their mention is not because medieval scribes were too fastidious to write about behavior equivalent to that of the feeding habits of female mosquitoes, mating habits of damselflies and mantis, or defensive behavior of bombardier beetles. After all, female dragons [origin: large serpent] were credited with devouring the heads of their mates during copulation, and bison [origin: bison] with using flatulence for defense (White 1990, Clark 1975). The reader is referred to Eisner & Aneshansley (1982) and Zinner (1989) for accounts of defensive behavior of bombardier beetles. Defense is the topic of this symposium. Contributions include defense of plants against insects and of insects against other insects.

**THIS SYMPOSIUM**

Medieval observers sought explanations for the natural things around them. They saw within the behavior of insects and other beasts moral guidance for the actions of man. Never mind that the observations were, in hindsight, often badly flawed or even contrived; these early observers were operating within the bounds of the "natural history" of their time. Their world was a simple place compared to ours, and its lessons were obvious. Surely, we could never be accused by later generations of scientists of the same short-sightedness as we have accused the authors of bestiaries. We are indeed vulnerable to such criticism, however, because of the reductionist nature of modern science. Reductionism compels us to see the natural world in a simple way: complex natural phenomena are thought to be reducible to a series of straightforward and relatively easily-comprehended processes. One potential trap in the reductionist method, when employed in disciplines such as ecology and ethology, however, is to assume that processes uncovered by reduction in one case can be used to explain all other similar instances. In other words, the trap is in assuming that such processes are general, and thus akin to physical "laws."

This trap is nowhere more evident than in the field of plant-insect-interactions. It once seemed that pressures brought by herbivores on plants could cause the plants to evolve defensive mechanisms against herbivory, and that if a particular kind of herbivore were dependent upon a particular kind of plant, then the plant's defensive mechanisms could cause the herbivore to evolve some way to overcome them. Direct reciprocal evolution ("co-evolution") thus could explain the plant-insect relationships we see all around us. But, for a number of reasons, this ready explanation must be viewed with caution (see Janzen 1980). Furthermore, co-evolution, even if it could be demonstrated to be operating in a particular case, may be a far more complex process than envisaged originally. On this note, we turn to the contributions to this symposium,
which show in exquisite detail some of the complexities involved in the relationships between plants and insects.

At least three important themes are evident in the contributions. The first is that plant-insect relationships may be manifested in a variety of ways. That is, potential defensive avenues open to plants are many, and simple, predictable responses of herbivores to plant defenses apparently are few. For example, defensive chemicals need not be "toxic" in the common sense of the term. Toxicity may derive more subtly, by means of, say, regulation of insect feeding behavior (Klocke & Kubo) or regulation of growth and long-term survival (Shea & Romeo). In either case, the chemicals involved seem to be but a part of the plant's defensive repertoire.

The second theme is that plant-insect relationships often cannot be viewed profitably outside their natural context. It seems likely, for instance, that the outcomes of many relationships are altered in the presence of predators, parasitoids, and perhaps even competitors of herbivorous insects (ecologists refer to relationships that change in this way as "higher-order relationships"). Chemicals released by plants in response to herbivory may be used by parasitoids to locate hosts (Turlinge & Tumlinson). Recruitment of parasitoids by plants may provide them with defensive capabilities beyond those conveyed by the chemicals alone. Yet, one should not leap too quickly to the assumption that it is necessarily to the plant's advantage, evolutionarily, to involve parasitoids as much as possible in the defensive option available to it. Such findings have obvious implications for IPM programs.

The final theme dealing with the complexity of plant-insect relationships involves the idea of co-evolution itself. An implicit assumption in one's positing evolution as the basis for a particular relationship may be that the co-evolutionary interaction is stable. A simple, phenomenological model demonstrates that co-evolution is not a stabilizing force a priori, however (Allen). Once more, the particular circumstances of the relationship are important, in that they determine whether co-evolution will work for or against chaotic dynamics of the populations.

We must conclude that our notions of plant-insect relationships indeed have been short-sighted. The world in which these relationships reside is not as simple as we might have supposed, or hoped. Like the medieval observers of nature, we have been operating within the bounds of what we perceive to be right, and, also like them, when our perceptions are limited, we must suffer the criticisms of more sophisticated observers. The difference between then and now seems largely to involve the rapidity with which such criticisms are levied.

ENDNOTES

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