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BRIEF COMMUNICATION

Aristotle's *Historia Animalium* and *Apis* reproduction

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Abstract. The details of observations and accounts recorded in Aristotle's *Historia Animalium* have been cataloged by scholars for decades. The degree to which his interpretations and accounts are accurate and demonstrate an actual understanding of honey bee biology have been debated. Throughout these discussions, however, it appears that one observation dutifully recorded has escaped notice. Aristotle made note of the direct product of the haplodiploid sex determination system, attesting to the power of his accounts, although he made no attempt to interpret it.

The ancient Greek philosopher Aristotle (384–322 BC) is widely regarded as the father of scientific inquiry. His body of work covering topics from logic to natural history formed the foundation of Western thought and inquiry for more than a millennium before being more rigorously questioned. Classical scholars have scoured his works and examined in great detail what observations and accounts Aristotle made or recorded, whether or not they were correct by our present understanding, and the degree to which his interpretations of these observations were accurate. Modern authors are interested in knowing not only what Aristotle and his contemporaries knew and understood, but also what was perhaps based on original observation versus hearsay, rumor, and myth but naïvely taken as fact. Owing to the popularity and importance of the genus *Apis* Linnaeus it is no wonder that scholars have examined the accounts of bees in antiquity (*e.g.*, Cook, 1895; Ransome, 1937; Davies & Kathirithamby, 1986) and that numerous studies have focused some of this attention on Aristotle's accounts of the biology, behavior, and management of honey bees. For instance, one of Aristotle's observations on honey bee biology from *Historia Animalium* that has received notable attention is his account of the waggle dance (Haldane, 1955) [Bekker reference 624b6: note that these are the standard reference numbers to textual sections of the Corpus

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Aristotelicum as developed from August Immanuel Bekker's (1785–1871) Greek compilation of these texts titled *Aristotelis Opera edidit Academia Regia Borussica* published between 1831 and 1870]. It does appear that Aristotle had observed the waggle dance but, as was noted by Whitfield (1958), his interpretation was that of simply relieving the worker of its load and not of a communication system [as first demonstrated by Nobel Laureate Karl von Frisch (1965)]. Nonetheless, the observation of a dance was faithfully recorded by Aristotle millennia before its modern interpretation and understanding.

Among the misconceptions taken from antiquity and perpetuated by early scholars (not all from Aristotle, though), the two most widely known were those concerning the spontaneous generation of bees from the carcasses of oxen and that their societies were ruled by a male monarch. The spontaneous generation of bees, most commonly taken from Constantine's *Geoponica* (Niclas, 1781), was still debated in the 17th Century [even with 'experimental' evidence demonstrating their purported generation from bulls (Hartlib, 1655)] as was the sex of the 'ruler-bee' [some authors did correctly discern the gender of the queen (Butler, 1609), an issue eventually put to rest by the publication of Swammerdam's work (1737)]. With respect to this latter issue, authors have enjoyed debating whether or not Aristotle, among the authors of antiquity, had correctly identified the sex of the 'ruler-bee' since some statements in his *Historia Animalium* suggest that he knew, or at least suspected, the correct gender of this 'monarch'. In particular, the following passage is oft quoted in this debate [Bekker reference 553a28: translation from Barnes (1984)]:

"These rulers [queens] have the part below the waist half as large again, and they are called by some the 'mothers' from an idea that they generate the bees [workers]; and, as proof they declare that the brood of the drones appears even when there is no ruler-bee [queen] in the hive, but that the bees [workers] do not appear in their absence. Others, again, assert that these insects copulate, and that the drones are male and the bees female."

It is fascinating that tied into this passage is another interesting aspect of *Apis* biology recorded by Aristotle; one that has been overlooked by those scholars who have attempted to make note of all of his observations. This omission is perhaps due to the intimate intertwining of the reference with the discussion concerning the gender of the 'ruler-bee'. Although Aristotle was most certainly unaware of the haplodiploid sex determination system of hymenopterous insects, his above statement records observations of the direct product of this genetic mechanism. Haplodiploidy, whereby diploid eggs produce females and males are haploid (resulting from unfertilized eggs), is a distinctive feature of Hymenoptera and has powerful implications for understanding social dynamics, mating, and evolution in *Apis* (not to mention other bees, ants, and wasps as a whole). Aristotle notes that when the queen is removed from the colony a preponderance of drones is produced and no new workers appear. In queenless colonies of *Apis* where queen cells were not already present or where emergency gyne cells were not produced, workers will begin laying unfertilized eggs and nearly all will produce drones (except in *Apis mellifera capensis* Eschscholtz). Such colonies will perish after the standing worker population has expired.

Thus, Aristotle, although oblivious to the mechanism, faithfully records a direct product of the honey bee sex determination system just as he had recorded the waggle dance and other fascinating aspects of honey bee biology over two thousand years ago.

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