



Evolution of host utilization patterns in the seed beetle genus *Mimosestes* Bridwell (Coleoptera: Chrysomelidae: Bruchinae)

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ABSTRACT

The evolutionary history of diet breadth expansion and intergeneric host shifts in the seed beetle genus *Mimosestes* were reconstructed to investigate the process of host range expansion in phytophagous insects. The evolutionary correlation between diet breadth and variation in oviposition behavior of *Mimosestes* was also examined to estimate the process of generalist evolution within the genus. Ancestral state reconstruction based on a molecular phylogeny inferred from three mitochondrial markers (16S rRNA, 12S rRNA, and COI) and one nuclear marker (EF-1 α) revealed that host utilization patterns were shaped by repeated colonizations to novel or pre-adapted host plants. Neither plant genus and species group level host conservatism nor an evolutionary tendency toward specialization was found in the genus, contrary to the expectations of plant–insect co-evolutionary theory. In addition, statistical analyses revealed that diet breadth was significantly correlated with oviposition behavior, suggesting that behavioral factors such as the oviposition preferences of female seed beetles affect the expansion of diet breadth in generalists.

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1. Introduction

The extreme species diversity of phytophagous insects has given rise to one of the most attractive research fields in evolutionary biology (Farrell, 1998; Lopez-Vaamonde et al., 2003; Novotny et al., 2006). Ehrlich and Raven (1964) argued that reciprocal evolution between plant secondary metabolic compounds and the physiological adaptations of insects to those compounds is a main cause of the present high diversity of phytophagous insects. This is one of the adaptive radiation processes by which an insect lineage colonizes novel plants that are phylogenetically unrelated to the ancestral hosts (herein referred to as major host shift). The insect then diversifies, resulting in ecological specialization within these “novel adaptive zones” (Ehrlich and Raven, 1964; Schluter, 2000; Morse and Farrell, 2005). Thus, understanding the process of major host shifts is important for explaining the first step in diversification among phytophagous insects. However, the host expansion process in phytophagous insects remains controversial (Winkler and Mitter, 2008).

Most phytophagous insects use only one or a few related plants as hosts (i.e., specialist species); however, some utilize distantly related plants (i.e., generalist species). One conventional idea of ecological specialization suggests that specialist phytophagous insects are limited in their ability to utilize novel host plants by trade-offs and are thus more prone to extinction than are generalists (Joshi and Thompson, 1995; Kelley and Farrell, 1998; Schluter, 2000; Funk et al., 2002; Stireman, 2005). Therefore, many researchers have suggested that the evolution of diet breadth among phytophagous insects tends to proceed from generalists to specialists (Futuyma and Moreno, 1988; Kelley and Farrell, 1998). However, recent studies based on molecular phylogeny have demonstrated that no obvious general trends toward specialization exist for many phytophagous insects (Janz and Nylin, 1998; Janz et al., 2001; Nosil, 2002; Nosil and Mooers, 2005). Furthermore, such studies have shown the patterns that generalists have arisen from specialized ancestors (Morse and Farrell, 2005; Yotoko et al., 2005; Weingartner et al., 2006; Cho et al., 2008). These data imply that even though the identification of factors causing generalist evolution in phytophagous insects is still controversial (Morse and Farrell, 2005; Yotoko et al., 2005), diet breadth cannot be completely explained by ecological specialization processes such as chemical co-evolution between insects and plants (Ehrlich and Raven, 1964; Futuyma and Moreno, 1988).

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If generalists have evolved from specialists via the addition of novel plants to their host repertoire, one can hypothesize that the major host shift may be related to the evolution of generalist phytophagous insects. Indeed, several recent studies have shown that major host shifts and generalization have occurred simultaneously. For example, Winkler and Mitter (2008) reported that oligophagous insects in clades including at least one polyphagous species more frequently change their host plant family than do species in clades consisting of only oligophagous species. Additionally, Janz et al. (2001), Janz and Nylin (2008), and Weingartner et al. (2006) found that most changes in host utilization appeared to occur during the “expanded phase” of diet breadths in the *Polygonia* butterfly and argued that most major host shifts in the genus have occurred alongside generalization. However, few studies have focused on the relationship between major host shifts and generalization.

Here, we examined generalist evolution and major host shifts in the seed beetle genus *Mimosestes* (Coleoptera: Chrysomelidae: Bruchinae: Acanthoscelidini), whose component species exhibit considerable interspecific variation in diet breadth and host utilization.

1.1. Research target: The genus *Mimosestes* Bridwell, 1946

The genus *Mimosestes* consists of 17 known species from the United States to the Amazonian basin (Kingsolver and Johnson, 1978; Hopkins, 1983, 1984; Johnson, 1983b; Kingsolver, 1985). All species feed on the seeds of the two subfamilies of Leguminosae: the Mimosoideae (*Acacia*, *Enterolobium*, *Parkia*, and *Prosopis*) and the Caesalpinioideae (*Bauhinia*, *Caesalpinia*, and *Parkinsonia*;

Kingsolver and Johnson, 1978; Hopkins, 1983, 1984; Johnson, 1983b; Kingsolver, 1985; Romero Nápoles et al., 2009).

Ten species of *Mimosestes* utilize only the *Acacia* subgenus *Acacia*, and four species are associated exclusively with non-*Acacia* host plants. Three species of *Mimosestes* utilize both *Acacia* and non-*Acacia* plants: *M. insularis* utilizes *Acacia* and *Prosopis*, and *M. amicus* and *M. mimosae* feed on both Mimosoideae and Caesalpinioideae (Table 1).

Host plant utilization patterns of *Mimosestes* exhibit two remarkable features. First, most host plants of the three multi-genera-utilizing species are also used by the specialists (Table 1). Second, differences in host utilization exist among multi-genera-utilizing species. For instance, *M. mimosae* does not use plants in common with hosts of *M. amicus*, except for *Parkinsonia aculeata*, even though these two species have the broadest diet breadths within the genus. These host utilization patterns suggest that multi-genera-utilizing species may represent an intermediate step between *Acacia* specialists and non-*Acacia* specialists and that multiple host expansion events have occurred in the genus. Thus, *Mimosestes* is an appropriate model genus for studying major host shifts and generalization.

As a first step in the comprehensive study of diet breadth evolution within *Mimosestes*, we also focused on the effects of variation in oviposition behavior on diet breadth within the genus. We hypothesized that diet breadth in *Mimosestes* is affected by differences in oviposition behavior. All known *Mimosestes* species, except *M. chrysocosmus*, oviposit on the surface of the seed pods of their host plants (Kingsolver, 1985; Johnson, 1987). Previous studies (Johnson, 1983b, 1987; Traveset, 1990, 1991; Siemens et al., 1992) and our field observations (T. Kato and M. Shimada,

Table 1
Species groups and previously published host plant utilizations of *Mimosestes* spp.

| <i>Mimosestes</i> species group | Host plant group | | |
|--|---|---------------------------------------|---|
| | Species group in <i>Acacia</i> subgen. <i>Acacia</i> | Other Mimosoideae | Caesalpinioideae |
| Enterolobii group | | | |
| <i>Mimosestes enterolobii</i> Kingsolver and Johnson, 1978 | | <i>Enterolobium</i> (1 sp.) | |
| Chrysocosmus group | | | |
| <i>Mimosestes chrysocosmus</i> Kingsolver, 1985 | | <i>Parkia</i> (5 spp.) | |
| Humeralis group | | | |
| <i>Mimosestes humeralis</i> (Gyllenhal, 1873) | Farnesiana (1 sp.) [*] , Macracantha (2 spp.) | | |
| <i>Mimosestes janzeni</i> Kingsolver and Johnson, 1978 | Macracantha (1 sp.), Rigidula (1 sp.) [*] | | |
| Mimosae group | | | |
| <i>Mimosestes acaciastes</i> Kingsolver and Johnson, 1978 | Constricta (2 spp.), Rigidula (2 spp.) | | |
| <i>Mimosestes amicus</i> (Horn, 1873) | Constricta (1 sp.), Farnesiana (2 spp.) [*] , Macracantha (2 spp.) [*] | <i>Prosopis</i> (4 spp.) | <i>Parkinsonia</i> (5 spp.) |
| <i>Mimosestes anomalus</i> Kingsolver and Johnson, 1978 | Ant-acacia (2 spp.) [*] , Macracantha (2 spp.) | | |
| <i>Mimosestes cinerifer</i> (Fähræus, 1839) | Ant-acacia (1 sp.), Macracantha (1 sp.) [*] | | |
| <i>Mimosestes insularis</i> Kingsolver and Johnson, 1978 | Farnesiana (2 spp.), Macracantha (1 sp.) | <i>Prosopis</i> (2 spp.) | |
| <i>Mimosestes mimosae</i> (Fabricius, 1781) | Ant-acacia (4 spp.), Farnesiana (2 spp.), Macracantha (3 spp.), Rigidula (1 sp.) [*] | <i>Prosopis</i> (1 sp.) | <i>Bauhinia</i> (1 sp.) [*] , <i>Caesalpinia</i> (2 spp.), <i>Parkinsonia</i> (3 spp.) |
| <i>Mimosestes nubigens</i> (Motschulsky, 1874) | Ant-acacia (3 spp.) [*] , Farnesiana (3 spp.), Macracantha (1 sp.) [*] | <i>Prosopis</i> (2 spp.) [*] | |
| <i>Mimosestes viduatus</i> (Sharp, 1885) | Ant-acacia (6 spp.), Macracantha (1 sp.) [*] | | |
| Obscuriceps group | | | |
| <i>Mimosestes brevicornis</i> (Sharp, 1885) | Farnesiana (2 spp.), Ant-acacia (1 sp.) | | |
| <i>Mimosestes obscuriceps</i> (Sharp, 1885) | Ant-acacia (2 spp.) | | |
| Protractus group | | | |
| <i>Mimosestes protractus</i> (Horn, 1873) | | <i>Prosopis</i> (2 spp.) | |
| Ulkei group | | | |
| <i>Mimosestes playazul</i> Johnson, 1983 | Ant-acacia (1 sp.) | | |
| <i>Mimosestes ulkei</i> (Horn, 1873) | | | <i>Parkinsonia</i> (2 spp.) |

All data are collected from published literature (Kingsolver and Johnson, 1978; Johnson, 1979, 1983a, 1998; Kingsolver, 1985; Johnson and Siemens, 1996; Romero Nápoles et al., 2009).

Host plants listed by Zacher (1952) were also removed, following Kingsolver and Johnson's (1978) argument.

^{*} Only one emergence record in the literatures.

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