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A Comparison of Antlions, Bees, Darkling Beetles and Velvet Ants Across Sand Dune and Non-Sand Dune Habitats at Ash Meadows National Wildlife Refuge

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A COMPARISON OF ANTLIONS, BEES, DARKLING BEETLES AND VELVET
ANTS ACROSS SAND DUNE AND NON-SAND DUNE HABITATS AT ASH
MEADOWS NATIONAL WILDLIFE REFUGE

by

Nicole F. Boehme

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Biology

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Logan, Utah

2014

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ABSTRACT

A Comparison of Antlions, Bees, Darkling Beetles and Velvet ants across Sand Dune and Non-sand Dune Habitats at Ash Meadows National Wildlife Refuge

by

Nicole F. Boehme, Master of Science

Utah State University, 2014

Major Professor: Dr. James P. Pitts
Department: Biology

Insects fulfill important roles within all ecosystems, including deserts, and interact directly and indirectly with the endemic and endangered species at the Ash Meadows National Wildlife Refuge (AMNWR). Here I investigate the variability of species richness, diversity, abundance and community composition of four insect groups between stabilized sand dune habitats, unstabilized sand dune habitats and non-sand dune habitats. The insects examined in this thesis include antlions (Myrmeleontidae), bees (Apiformes), darkling beetles (Tenebrionidae) and velvet ants (Mutillidae). As the impact and interactions of two of the insect groups, antlions and velvet ants, are largely unknown within any ecosystem, this thesis also includes a faunal study of velvet ants at AMNWR and their spatial and temporal variation at the refuge. Generalized linear mixed models were used to identify significant differences in richness, diversity and abundance for each insect group between the stabilized sand dune, unstabilized sand dune and non-sand dune

habitats. Species richness differed between habitats for antlions, beetles and velvet ants over the study period. Diversity differed between habitats for antlions and beetles, and abundance differed between habitats for all groups over the study period. Nearly every habitat supported some unique species. The faunal survey of velvet ants revealed minor variation in flight times between species and a unique pattern of temporal niche partitioning in one species. Habitat preferences were observed for seven of 42 velvet ant species at AMNWR. In a comparison of the diversity of velvet ants between AMNWR and the Nevada Test Site (NTS), six velvet ant species that occurred at the NTS were not found at AMNWR. Diagnoses and a key are provided for the velvet ants of AMNWR. This thesis increases the number of known terrestrial invertebrates at the refuge and provides a comparison of terrestrial insect distribution and habitat use at AMNWR. These investigations contribute to the goals and objectives of the U. S. Fish and Wildlife Service to obtain basic inventories and understand the terrestrial habitat use of invertebrates at AMNWR.

(212 pages)

PUBLIC ABSTRACT

A Comparison of Antlions, Bees, Darkling Beetles and Velvet ants across Sand Dune and
Non-sand Dune Habitats at Ash Meadows National Wildlife Refuge

Nicole F. Boehme

Ash Meadows National Wildlife Refuge (AMNWR) supports nearly 30 organisms found nowhere else in the world. Most of these species are aquatic, dwelling in more than 50 seeps and springs within the over 24,000 acres of the refuge. Much of the research at AMNWR has centered on these unique and abundant springfed pools across the desert landscape. Many of the terrestrial habitats and species at the refuge have not been as well studied. In 2008, Bio-West, Inc. in Logan, Utah was contracted to inventory the terrestrial organisms present on the refuge. To investigate the terrestrial invertebrate fauna, with special interest for pollinators, Bio-West, Inc. recruited graduate students in the Department of Biology at Utah State University.

The goals of the refuge for the inventory of terrestrial insects included identifying pollinators for ten of their endemic and endangered plant species, obtaining basic inventories of terrestrial invertebrates, and understanding habitat use by the terrestrial invertebrates that occur at AMNWR. To contribute to the goals of the refuge, this thesis provides inventories of multiple insect groups and compares the distributions of those groups between desert habitats. These inventories will not only contribute to the goals of the refuge, but will also contribute to the basic knowledge needed for most terrestrial insect groups in all desert environments. Velvet ants are investigated in detail because

their impact within a community is poorly understood. Velvet ants are very abundant in some desert habitats and some species are known to prey upon pollinators. Hence, their impact on pollinator abundance could potentially be very important.

FRONTISPIECE



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Nicole F. Boehme

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CHAPTER 1

INTRODUCTION

Thesis Description

Ash Meadows National Wildlife Refuge (AMNWR) was created to protect multiple endemic and endangered species (U.S. Fish and Wildlife Service 2009). Many insects, especially bees, are likely important to the survival of some of the plant species of concern at AMNWR. However, the impact of most terrestrial insect communities at AMNWR is unknown. The aim of this thesis is: 1) to determine if sand dune habitats with varying plant diversity and soil stability differ from each other and from non-sand dune habitats in the richness, diversity and abundance of their insect communities, and 2) to obtain a baseline of the species richness, diversity, and abundance of four insect groups, antlions (Neuroptera: Myrmeleontidae), bees (Hymenoptera: Apoidea), darkling beetles (Coleoptera: Tenebrionidae), and velvet ants (Hymenoptera: Mutillidae). By investigating these insect communities, I will contribute to the goals and objectives of the U. S. Fish and Wildlife Service to obtain basic inventories and understand the terrestrial habitat use of invertebrates at AMNWR (U.S. Fish and Wildlife Service 2009). As the impact and interactions of two of the insect groups, antlions and velvet ants, are largely unknown within any ecosystem, this thesis will also include a faunal study of velvet ants at AMNWR and their spatial and temporal variation at the refuge.

Background

Ash Meadows National Wildlife Refuge (AMNWR) is a moderately sized refuge of 93 km² located in the Mojave Desert. The refuge was established in 1984 for the purpose of protecting the endemic, endangered and rare organisms that occur there (U.S. Fish and Wildlife Service 2009). At least 25 endemic plants and animals are found at AMNWR and, for its area, it is considered to have the second greatest concentration of endemic species in the United States. AMNWR is most widely known for housing multiple species of rare, endangered pupfish in the genus *Cyprinodon* (Cyprinodontiformes: Cyprinodontidae) (Dudley and Larson 1976). Besides these fish, relatively few other organisms and habitats on the reserve have been studied (Polhemus & Polhemus 1994; Shepard *et al.* 2000; Stevens & Bailowitz 2008; Crews & Stevens 2009; Raabe 2011).

Ash Meadows National Wildlife Refuge is composed of many different habitats including xeric upland scrub, alkali lowland scrub, alkali marsh, desert wash, riparian shrubland and woodland, several spring fed lacustrine pools and sand dunes. The sand dunes at AMNWR were created in the late Holocene between 1600 and 800 years ago, with additional deposition around 200 years ago, from sands dispersed from the Fortymile wash and Amargosa River deposits (Pavlik 1989; Lutgens & Tarbuck 2003). At AMNWR, sand dunes cover approximately 9.75 km², almost 10%, of the refuge (Lancaster & Mahan 2012). These dunes have variable plant cover and include large expanses of mesquite anchored coppice dunes, smaller salt brush anchored coppice dunes and scattered mesquite or salt brush anchored coppice dunes.

Sand dunes

Sand dunes are mounds of sand particles that have accumulated through wind or water deposition. At AMNWR the sand dunes were created through eolian, or wind, deposition (Lancaster & Mahan 2012). Sand grains blown by the wind only move or jump short distances in a process called saltation. Because of this restricted movement, the sand grains will collect around the base of trees and shrubs, eventually creating large mounds of sand.

Organisms dwelling within sand dune habitats are frequently exposed to drastic changes, often on a daily basis, as shifting soil can move or destroy food sources, cover and fill nests and burrows, and cause physical damage to an organism. While sand dunes can be very destructive habitats, they also offer beneficial qualities for most arid adapted species. One favorable quality of sand dunes is that, under low rainfall conditions, sandy soils can process and store water more efficiently than fine-grained soils (Noy-Meir 1973; Pavlik 1980; Seely 1991). Sand dunes also allow for easy access to underground refuge, which is used by most small desert species to retreat from daily desert extremes (Seely 1991).

Sand dunes are known to support diverse sand-obligate plants and animals, including various insects (Brown 1973; Bechtel *et al.* 1981; 1983; Rust 1985; 1986; Pavlik 1985; 1989; Britten & Rust 1996). In the Mojave Desert, sand dunes are known to support unique suites of insects and high species richness for some insect groups (Bechtel *et al.* 1981; 1983; Griswold *et al.* 1997; 2004-2005). Sand dunes in the northeastern region of the Mojave Desert, for example, are known to support over 300 species of bees,

nearly equal to bee species richness throughout all of New England (Griswold *et al.* 1997: 2004-2005).

Insects

Insects occupy many important roles within an ecosystem as predators, pollinators, detritivores, herbivores and parasitoids. Most insects are also important resources for other organisms, including other insects. Because insects are so important to ecological processes and functions, are behaviorally and taxonomically diverse, and are sensitive to environmental change, they are good indicators of ecosystem health (Greenslade & Greenslade 1984; Brown 1997; McGeoch 1998; 2007). Understanding the spatial variation of some of the most diverse groups of insects in deserts can expose areas or habitats that are healthy in that they support important species and maintain diverse biota, or those that may be lacking important species or be devoid of diverse biota.

Each of the four groups of insects considered in this thesis has a unique trophic position, is typically diverse in arid regions, and has not been studied at AMNWR (White 1983; Michener 2000; Grimaldi and Engel 2005; Marshall 2006; Pitts 2007). These groups include antlions (Neuroptera: Myrmeleontidae), bees (Hymenoptera: Apoidea), darkling beetles (Coleoptera: Tenebrionidae) and velvet ants (Hymenoptera: Mutillidae). Each of these insect groups serves a unique ecosystem function as predators, pollinators, detritivores and parasitoids, respectively.

Antlions are ferocious predators, at least in the larval stage, and consume mainly small pedestrian arthropods. Thirteen antlion genera are known to occur in North America, only one of these genera, *Myrmeleon*, constructs the characteristic pitfall trap

(Triplehorn & Johnson 2005). The other 12 genera are cryptic predators lying in wait to ambush prey at or just below the surface of the sand or loose soil (Stange 1994; Arnett 2000; Grimaldi & Engel 2005; Triplehorn & Johnson 2005). Some antlion species live in leaf litter, and others occupy rock cavities and caves (Stange 1994). Adult antlions are nocturnal and are a known food source for the pallid bat, *Antozous pallidus*, a species of concern for Nevada (Johnson & Fenton 2001; Triplehorn & Johnson 2005; Nevada Natural Heritage Program 2010). Antlions can also be indicators for pollution as they accumulate multiple heavy metals, including iron, manganese, cadmium and lead (Nummelin *et al.* 2007).

Bees provide essential pollination services to many desert plants, both common and rare. Deserts are extremely rich in bee-pollinated plants (Michener 2000). A common and essential resource at AMNWR that supports generalist as well as specialist insects is Mesquite (*Prosopis spp.*) (Simpson *et al.* 1977). Mesquite habitats in Clark County, Nevada, have been identified as areas that are typically very rich in native pollinators (Griswold *et al.* 2004-2005). AMNWR has many endemic plant species, including seven federally listed species that likely require pollination. However, the pollination requirements for many of the endemic and endangered plants are not known (U.S. Fish and Wildlife Service 2009). In addition to their importance as pollinators, bees are also an essential food resource for many predators, parasites and parasitoids.

Darkling beetles are generally known as detritivores and are found throughout the world in nearly every type of environment. Many species of desert-dwelling darkling beetles have specialized morphological and behavioral adaptations for living in arid

environments. For example, the Namib Desert beetle, *Onymacris unguicularis* (Haag), exhibits a fog-basking behavior to collect water on the dorsal surface of its body. The beetles' exoskeleton is water resistant and equipped with shallow ridges that direct the water collected to the beetles' head (Hamilton & Seely 1976). Darkling beetles found in the deserts of western North America, including *Eleodes armata* LeConte, *Asbolus verrucosa* LeConte, *Eusattus muricatus* LeConte and *Edrotes ventricosus* LeConte, also have morphological and behavioral adaptations for living in harsh arid environments, including burrowing or remaining inactive during the warmest time of the day, having modified appendages for burrowing in sand and fused elytra to create a subelytral cavity that reduces water loss by transpiration (Kramm & Kramm 1972; Cloudsley-Thompson 1975). In most arid areas, darkling beetles are the most abundant ground-dwelling beetle (MacMahon 1985).

Lastly, nocturnal velvet ants are parasitoids of bees and related wasps (Krombein 1979; Brothers 1989; Pitts *et al.* 2004), and can be highly abundant with some estimates at 40,000 individuals per hectare during their peak season (J. P. Pitts, pers. comm). The impact of such a large velvet ant population on pollinators, and the plants those pollinators visit, could be significant. Known hosts of velvet ants of the *Sphaerophthalma uro* (Blake) species-group, including *Sphaerophthalma amphion* (Fox) and *S. uro* (Blake), are quite variable and include several bee species of the family Megachilidae, such as *Ashmeadiella bigeloviae* (Cockerell), *A. gillettei* Titus, *A. meliloti* (Cockerell), *Hoplitis fulgida* (Cresson), *H. grinnelli* Cockerell, *H. sambuci* Titus, *Osmia marginata* Michener,

Stelis spp., and others (Pitts *et al.* 2004). Little is known about velvet ant distributions and host preferences at AMNWR.

Objectives

The primary objective of this thesis is to determine if sand dune habitats with varying plant diversity and soil stability differ from each other and from non-sand dune habitats in the richness, diversity and abundance of their insect communities. The insects examined in this thesis were selected because they are typically diverse in arid regions and they each fulfill unique and important functions for ecosystem processes, including possible impacts on the known endemic and endangered species at AMNWR. The insects include antlions, bees, darkling beetles and velvet ants. As the natural history of velvet ants are largely unknown within any ecosystem, this thesis will also include a faunal study of velvet ants at AMNWR and their spatial and temporal variation. With these objectives, I will also contribute to the goals and objectives of the U.S. Fish and Wildlife Service (2009) in their efforts to obtain basic inventories and understand the terrestrial habitat use by invertebrates at the refuge.

Thesis Outline

Chapter 2 is an investigation of the spatial variation of species richness, diversity, abundance and species composition for four insect groups across three habitats: stabilized sand dune, unstabilized sand dune and non-sand dune. This comparison provides an example of how insect communities differ between desert habitats and also identifies the importance of each habitat for each insect group.

Chapter 3 examines one of the insect groups from chapter 2, velvet ants. The velvet ant species of AMNWR are inventoried and their activity patterns and habitat preferences are revealed. Little is known about the natural history of most velvet ant species, and this chapter will provide the first analysis of habitat preferences and activity patterns for velvet ants of western North America. Habitat preferences were observed for multiple species and suggest that spatial niche partitioning may be an important delineator of velvet ant communities. Chapter 3 has been published as Boehme *et al.* 2012.

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CHAPTER 2

SPATIAL VARIATION IN THE RICHNESS, DIVERSITY, AND ABUNDANCE OF
INSECT COMMUNITIES ACROSS SAND DUNE AND NON-SAND DUNE
HABITATS AT ASH MEADOWS NATIONAL WILDLIFE REFUGE**Abstract**

Ash Meadows National Wildlife Refuge (AMNWR) was created to protect multiple endemic and endangered species. Insects fulfill important roles within all ecosystems, including deserts, and undoubtedly interact directly and indirectly with the endemic, endangered and rare species at the refuge. Understanding the spatial variation of some of the most diverse groups of insects in deserts can expose areas, or habitats, that are important for conservation and management. Here I investigate the variability of species richness, diversity, abundance and community composition of four insect groups across three habitat types at AMNWR. I studied three desert habitats: sand dune habitats with high plant diversity and stabilized soils (stabilized sand dune), sand dune habitats with low plant diversity and less stabilized soils (unstabilized sand dune), and non-sand dune shrub steppe habitats (non-sand dune). The four focal insect groups are all most diverse in desert habitats, and fulfill unique niches as predators, pollinators, detritivores, or parasitoids. The groups include antlions (Neuroptera: Myrmeleontidae), bees (Hymenoptera: Apoidea), darkling beetles (Coleoptera: Tenebrionidae), and velvet ants (Hymenoptera: Mutillidae). Generalized linear mixed models were used to identify significant differences in richness, diversity and abundance for each insect group between the three habitat types over the whole season and between months. Differences in species

richness were found for antlions, beetles and velvet ants between habitats over the study period. Diversity differed between habitats for antlions and beetles, and differences in abundance occurred between habitats for all groups over the study period. While some of the habitats did not support the greatest diversity, richness, or abundance, those habitats still supported some unique species. Each insect group exhibited various preferences to habitat and all habitats were important for at least one of the insect groups. These results reveal that management and protection for insects at AMNWR need to be assessed for each insect group individually. All habitat types were important to at least one group and all habitats contributed to the biodiversity of the refuge.

Introduction

Ash Meadows National Wildlife Refuge (AMNWR) is a moderately sized refuge of 93 km² located in the Mojave Desert. The refuge was established in 1984 for the purpose of protecting the endemic and endangered organisms that occur there (U.S. Fish and Wildlife Service 2009). Recent increases in pumping of water from underground aquifers under and surrounding Las Vegas is a concern for the survival of many of the endemic and endangered species that occur at AMNWR, which is located 90 Miles west of Las Vegas (Deacon *et al.* 2007). As the largest remaining oasis in the Mojave Desert, water is critical to, and responsible for the large amount of endemism at AMNWR. At least 25 endemic plants and animals are found at AMNWR and, for its area, the refuge is considered to have the second greatest concentration of endemic species in the United States (U.S. Fish and Wildlife Service 2009). AMNWR is most widely known for housing multiple species of endangered pupfish, *Cyprinodon spp.* (Cyprinodontiformes:

Cyprinodontidae) (Dudley & Larson 1976). While many studies have taken special interest in these pupfish, few other organisms or habitats on the reserve have been studied (e.g., Polhemus & Polhemus 1994; Shepard *et al.* 2000; Stevens & Bailowitz 2008; Crews & Stevens 2009; Raabe 2011).

AMNWR is composed of many different habitat types including xeric upland scrub, sand dunes, alkali lowland scrub, alkali marsh, desert wash, riparian shrubland and woodland, and several spring fed pools. Habitats known to support unique diversity are sand dunes. Sand dunes promote diversity primarily through the instability of the soil. Organisms dwelling within sand dune habitats are frequently exposed to drastic changes, often on a daily basis, as shifting soil can move or destroy food sources, cover and fill nests and burrows, and cause physical damage to an organism. While sand dunes can be very destructive habitats, they also offer beneficial qualities for most arid adapted species. One favorable quality of sand dunes is that their sandy soils can hold more water than other desert substrates (Noy-Meir 1973; Pavlik 1980; Seely 1991). Sand dunes are also generally more useful than finer-grained soils for most small species that seek underground refuge from extreme desert conditions (Seely 1991). Where disturbance is minimal, the soil is most stable. Soil stability in sand dune habitats increases the nutrients in the soil and subsequently is more accessible for plant colonization (Klinkhamer & de Jong 1985; Kuteil & Danin 1987; Titus *et al.* 2002). The sand dunes at AMNWR cover approximately 9.75 km² of the refuge and are all variously vegetated (Lancaster & Mahan 2012). At several locations on the refuge sand dunes act as natural dams for discharge from the springs and other surface runoff (Mehring & Warren 1976; Lancaster &

Mahan 2012). This creates a unique wetland habitat that is dependent upon sand dunes. The most prominent sand dunes include large, north-to south-trending, mesquite-anchored coppice dunes (up to 6 m in height) and lower coppice dunes anchored by saltbrush. Other sand dunes found at AMNWR consist of east-to-west trending reticulate dunes and scattered mesquite or saltbrush anchored coppice dunes that range from 1 to 2 m in height. The three desert habitats used in this study included two sand dune habitats, found within the north-to-south trending mesquite and saltbrush anchored coppice dunes, and non-sand dune shrub steppe habitats (non-sand dune). The non-sand dune habitats had compacted alkaline soils with diverse vegetation distributed in sparse clumps throughout the habitat. Non-sand dune habitats were separated from sand dune habitats by at least 2 km. The sand dune habitats were separated into habitats with high plant diversity and stabilized soils (stabilized sand dune) and habitats with low plant diversity and less stabilized soils (unstabilized sand dune).

Terrestrial insects are abundant and diverse in desert ecosystems, and many insects are specialized for living in specific desert habitats such as sand dunes. Insects are important in fulfilling many ecosystem functions, such as pollination and decomposition. Little is known about the terrestrial insects at AMNWR, including their distributions and their interactions with the terrestrial endemic and endangered species. To provide a baseline for terrestrial insect distributions and diversity, the aim of this study is to investigate and describe variation in richness, diversity, and abundance for various insect groups between distinct desert habitats, specifically stabilized sand dune habitats, unstabilized sand dune habitats and non-sand dune habitats. With this comparison, I can

contribute to the goals and objectives of the U.S. Fish and Wildlife Service (2009) in their efforts to obtain basic inventories and understand the terrestrial habitat use by invertebrates at the refuge.

Four groups of insects are investigated in this study and were chosen because they are typically diverse in arid regions and may impact the known endemic and endangered species at AMNWR. These groups include antlions (Neuroptera: Myrmeleontidae), bees (Hymenoptera: Apoidea), darkling beetles (Coleoptera: Tenebrionidae) and velvet ants (Hymenoptera: Mutillidae). Each insect group represents a different guild and impacts the ecosystem in a unique way as predators, pollinators, detritivores or parasitoids (White 1983; Michener 2000; Grimaldi & Engel 2005; Marshall 2006; Pitts 2007).

Antlions are ferocious predators as larvae and consume mainly small pedestrian arthropods. Only one genus, *Myrmeleon*, of the 13 genera that occur in North America constructs the characteristic pitfall trap (Triplehorn & Johnson 2005). The other 12 genera are cryptic predators lying in wait to ambush prey at or just below the surface of the soil (Stange 1994; Arnett 2000; Grimaldi & Engel 2005; Triplehorn & Johnson 2005). Some antlion species live in leaf litter, and others occupy rock cavities and caves (Stange 1994). Antlions can be indicators for pollution as they accumulate multiple heavy metals, including iron, manganese, cadmium and lead (Nummelin *et al.* 2007). Adult antlions are nocturnal and are a known food source for the pallid bat, *Antrozous pallidus*, a species of concern in Nevada (Johnson & Fenton 2001; Triplehorn & Johnson 2005; Nevada Natural Heritage Program 2010). Antlions can be found worldwide in arid, sandy regions (Grimaldi & Engel 2005). As the larval form of most antlion species requires loose sandy

soils for survival, I expect that most antlion species should be found in sand dune habitats. Within the sand dune habitats at AMNWR, I expect that variation in antlion species richness and diversity will be greater in the stabilized sand dune habitat. Previous studies on aggregations of antlion larvae indicate that low soil disturbance, low soil surface moisture and lower surface temperatures are correlated with the presence of the larvae (Gotelli 1993; Scharf *et al.* 2008). Studies on antlion habitat preferences have only been conducted for pit-building antlions, however, and may not represent non-pit building antlion species. The desirable conditions of low soil disturbance, low soil surface moisture and lower temperatures are more likely to be met within the stabilized sand dune habitat.

The majority of flowering plants require insects for pollination, and the most prolific pollen-gathering insects are bees (Axelrod 1969, Richards 1986, Free 1993, Michener 2000). Deserts are extremely rich in bee-pollinated plants (Michener 2000). AMNWR has many endemic plant species, including seven federally listed that likely require pollination. However, the pollination requirements of many of the plants are not known (U.S. Fish and Wildlife Service 2009). In addition to their importance as pollinators, bees are also an essential food resource for many predators, parasites and parasitoids. Most species of bees, especially desert bees, nest in the ground (Cane 1991, Michener 2000). Of the ground-nesting bees, all families nest in soils containing 30% to nearly 100% sand (Cane 1991). Sand dunes are, thus, considered to be important habitats for bee nesting. Several bee species in North America are known to occur only in sand dune habitats (Hurd & Powell 1958; Bohart *et al.* 1972; Rust *et al.* 1983; Rust 1987;

Griswold *et al.* 1997), and many surveys have associated sandy soils with high bee richness (Rust *et al.* 1983; Griswold *et al.* 1997; Griswold *et al.* 2004-2005). A previous study on bee species richness between sand dune and non-sand dune habitats, however, found that bee species richness did not differ between sand dune and non-sand dune habitats (Toler 2001). This does not mean that all bee species are homogenous between habitats, because even when species richness between the sites is the same, species composition and diversity can differ. In a comparison of multiple dune habitats, Wilson *et al.* (2009) found that bee community composition and diversity differed between all plots within a single habitat type, but bee diversity was similar between locations with similar floral diversity. I, thus, predict that bees at AMNWR should at least differ in composition between habitats, but could also differ in diversity, abundance and richness because plant diversity differs between habitats. The differences are expected to be greater in the stabilized sand dune habitats than in unstabilized sand dune habitats, because the floral diversity in stabilized sand dune habitats is greater than in unstabilized sand dune habitats.

Darkling beetles are generally known as detritivores and are found throughout the world in nearly every type of environment. Many species of desert-dwelling darkling beetles have specialized morphological and behavioral adaptations for living in arid environments. For example, the Namib Desert beetle, *Onymacris unguicularis* (Haag), exhibits a fog-basking behavior to collect water on the dorsal surface of its body. The beetle's exoskeleton is water resistant and equipped with shallow ridges that direct the water collected to its head (Hamilton & Seely 1976). Darkling beetles found in the

deserts of western North America, including *Eleodes armata* LeConte, *Asbolus verrucosa* LeConte, *Eusattus muricatus* LeConte and *Edrotes ventricosus* LeConte, also have morphological and behavioral adaptations for living in harsh arid environments, including burrowing and remaining inactive during the warmest time of the day, having modified appendages for burrowing in sand and fused elytra to create a subelytral cavity that reduces water loss by transpiration (Kramm & Kramm 1972; Cloudsley-Thompson 1975). In most arid areas, darkling beetles are the most abundant ground-dwelling beetle (MacMahon 1985). Many of the studies on community-level distributions of darkling beetles have found little correlation between beetle distributions and many abiotic or environmental constraints (Ahearn 1971; Wallwork 1976; Franco et al. 1979; Thomas 1979; 1983; Barrows 2000). Environmental variables that have been associated with differences in species composition and abundance, however, include differences in soil type and soil moisture (Thomas 1979; 1983; Rust 1986; Ayal & Merkl 1994; Krasnov & Shenbrot 1996; Barrows 2000). Species composition has been found to differ between sandy and compact soils (Thomas 1983; Ayal & Merkl 1994; Krasnov & Shenbrot 1996), and I expect to observe variation in darkling beetle species diversity and composition between sand dune and non-sand dune habitats. Differences in beetle abundance have been strongly correlated with soil moisture (Thomas 1979; Rust 1986; Ayal & Merkl 1994; Barrows 2000). As sandy soils are known to hold more water (Noy-Meir 1973; Seely 1991), I anticipate beetle species occupying sand dune habitats will be very abundant. As detritivores of mostly plant material, I would expect stabilized sand dunes to support a higher abundance and diversity of species, but previous studies show no

evidence of an association between darkling beetle distribution and plant diversity (Ahearn 1971; Wallwork 1976; Franco *et al.* 1979; Thomas 1979; 1983; Barrows 2000).

Lastly, nocturnal velvet ants are parasitoids of bees and related wasps (Krombein 1979; Brothers 1989; Pitts *et al.* 2004) and can be highly abundant, with some estimates at 40,000 individuals per hectare during their peak season (J. P. Pitts, personal communication). The impact of such a large velvet ant population on pollinators, and the plants those pollinators visit, could be significant. Known hosts of velvet ants of the *Sphaerophthalma uro* (Blake) species-group, including *Sphaerophthalma amphion* (Fox) and *S. uro* (Blake), are quite variable and include several bee species of the family Megachilidae, such as *Ashmeadiella bigeloviae* (Cockerell), *A. gillettei* Titus, *A. meliloti* (Cockerell), *Hoplitis fulgida* (Cresson), *H. grinnelli* Cockerell, *H. sambuci* Titus, *Osmia marginata* Michener, *Stelis* spp., and others (Pitts *et al.* 2004). Boehme *et al.* (see Chapter 3) examined velvet ant habitat preferences at AMNWR. Prior to the Boehme *et al.* (Chapter 3) study, habitat preferences for many velvet ant species have been based on the nesting habits of their prey. In consideration of potential bee prey, this would include twig and soil nesting habits. Velvet ants are typically considered generalist in prey choice and may not be limited by habitat (Brothers 1989; Pitts *et al.* 2004). Boehme *et al.* (see Chapter 3) indicated that seven of 25 velvet ant species at AMNWR were more abundant in either the sand dune habitats or the non-sand dune habitats. All other species were found uniformly over both habitats. Due to the small amount of variability in species abundance and generalist behavior, I do not expect to find differences in species richness,

diversity or abundance for velvet ants at the community level between the three habitat types examined in this study.

Biotic communities occupying sand dunes are typically considered unique to surrounding desert habitats because sand dune habitats can host a myriad of sand obligate biota including plants (Pavlik 1985; 1989), mammals (Brown 1973), and insects (Hardy & Andrews 1976; 1979; Andrews *et al.* 1979; Bechtel *et al.* 1981; 1983; Rust 1985; 1986; Britten & Rust 1996; Rahn & Rust 2000; Evans & O'Neill 2007). For some insect groups, sand dune habitats may also appear to support greater species richness, diversity or abundance. In most deserts the difference in these measures of biodiversity for most insect groups between unique desert habitat types is unknown. Knowing the differences between such measures of target insect groups between habitats is important for conservation and management of the insects and those potentially threatened and endangered species in their communities.

Materials and Methods

Field work took place from January through December of 2009. Collections were made at seven sites across the refuge. These sites differed in various aspects including soil type, dominant plant cover, plant diversity and percent plant cover. The seven sites were grouped into three habitat types: 1) non-sand dune habitats, 2) stabilized sand dune habitats, and 3) unstabilized sand dune habitats. Originally, three sites were selected for each habitat type. However, one site of each dune type was excluded from this study, because the sand dunes were much smaller (between approximately 2,400 to 12,000 m²) than the other sand dune sites. All other sand dune sites were approximately 91,000 to

260,000 m², and the non-sand dune sites ranged between nearly 19,000 to just over 96,000 m². Non-sand dune sites were selected based upon their similarity and proximity to areas occupied by rare plants of interest at the refuge including alkali mariposa lily (*Calochortus striatus*), Ash Meadows blazingstar (*Mentzelia leucophylla*), Ash Meadows ivesia (*Ivesia kingii eremica*), Ash Meadows milkvetch (*Astragalus phoenix*), Ash Meadows sunray (*Enceliopsis nudicaulis corrugata*), mountain blue-eyed grass (*Sisyrinchium funereum*), spring-loving centaury (*Centaureum namophilum*) and Tecopa bird's beak (*Cordylanthus tecopensis*). Non-sand dune habitats had packed alkaline clay soils with diverse vegetation (Table A.1).

AMNWR dune systems have varying levels of soil stability, which is reflected by the plant communities that occupy them. These unique plant communities were separated into sand dune communities with high plant richness or low plant richness. The stabilized sand dune habitats had high plant richness with 10 commonly occurring species, whereas the unstabilized sand dune habitats had only four plant species (Table A.1) (Bio-West 2011). As vegetation is an important component of soil stabilization, the drastic difference in the plant communities between the sand dune habitats is indicative of the distinct difference in stability between the soils in each habitat type.

At each site insect specimens were collected by hand or net, with light traps, pan traps, malaise traps and pitfall traps depending on the taxon. Pitfall traps targeted darkling beetles and female velvet ants, light traps targeted antlions and male nocturnal velvet ants, and pan trapping and net collecting targeted bees. Net collections were taken during 15 minute random walks within a site and were performed bi-monthly. One set of

pan traps was run for approximately four hours between dawn and mid-day at each of the seven specified sites once every other week from mid-March through October 2009. A set of pan traps consisted of 25 bowls: nine white, eight blue, and eight yellow. The pan colors white, yellow and blue have been found to be most attractive to bees (Leong & Thorp 1999; Wilson *et al.* 2008). These bowls were set singly in an alternating color pattern two feet apart along two intersecting transects. The bowl at the intersection of the transects was always white, and the transects alternated their color pattern with one transect ending with a blue bowl closest to the center bowl and another having yellow bowls on either side of the central white bowl. The outermost bowls were always white. All bowls were filled with soapy water.

One light trap was run at each of the seven specified sites once every other week from April 2009, when nighttime temperatures sometimes rose above 0°C, to the beginning of November when temperatures again declined and insect activity ceased. Light traps were composed of a camping lantern equipped with an LED light surrounded by six alternating yellow and white bowls filled with soapy water. Each night that trapping occurred, a light trap was randomly placed within a site usually between 50 to 150 m from the access road.

One malaise trap was run per site for three days every other week. Within each site, a Townes style malaise trap was erected in a location where insect activity was observed or expected to occur, such as near a blooming plant. Twenty-eight pitfall traps were placed across the seven sites in late December 2008 with four pitfall traps per site. A single pitfall trap was constructed of two 32 ounce cups, nested one within the other,

and buried to the rim of the inner cup. Two twigs were placed across the top of the inner cup to coax insects to climb out over the trap opening. The twig also created separation between the ground and the trap cover that consisted of a small plate secured into the ground with two five-inch nails. The cover functioned to protect the trap and its contents, and to entice insects into the trap by providing refuge from environmental extremes, such as heat and wind. The traps were covered by a chicken-wire dome secured to a wooden frame that was staked into the ground with 12 inch wooden stakes to prevent coyotes and other large mammals from removing the traps. Within a site, each of the four traps was placed randomly at least 50 m apart from the other three pitfall traps near a perennial shrub, where possible. Traps were left open continually, and their contents were collected every four weeks. All pitfall traps were removed in December 2009.

Collected insects were identified to species or morphospecies using published keys where available. Antions and velvet ants were deposited at the Utah State University Insect Collection, Logan, UT, USA (EMUS). Bees were deposited at the U.S. National Pollinating Insect Collection, USDA-ARS Bee Biology and Systematics Laboratory, Utah State University, Logan, UT, USA (BBSL), and the darkling beetles were deposited at the University of Georgia Entomology Collection, Athens, GA, USA (UGCA).

Each insect group was analyzed independently. Species accumulation curves were created in the program Species Diversity and Richness IV with 1000 random selections of sample order (Seaby & Henderson 2006). Species richness values were obtained by pooling the number of species collected within each insect group by month per site. Similarly, abundance values were obtained by pooling the number of individuals within

an insect group by month per site. Diversity was calculated using the Shannon-Weiner diversity index for each insect group by month per site using the program Species Diversity and Richness IV (Seaby & Henderson 2006). The combined effects of habitat type and month were compared for all insect groups. For abundance and species richness, data sets were evaluated using a generalized linear mixed model with a negative binomial distribution and an identity link (Gbur *et al.* 2012) [using PROC GLIMMIX (SAS Institute Inc., Cary, NC, USA)]. Habitat type and month and their interaction were included in the model as fixed effects. The replicates within habitat type and their interactions with habitat type and month were treated as random effects. A Tukey-Kramer HSD was applied to further discern significant results. Diversity for all insect groups was evaluated similarly; however, a gamma distribution was used instead of a negative binomial distribution. Variation in species composition was investigated by comparing the relative proportions of the six most abundant species and the number of unique and shared species per group, and for all groups combined, per habitat type.

Because too few species or specimens (<2) from at least one of the three habitats were found in certain months, data for these months were excluded in the comparison of species richness, diversity and abundance for all insect groups by month and for all months combined. Antlion species richness, diversity and abundance considered the months of May through September, all variables for bee analyses considered the months of March through October, beetle species richness and abundance analyses considered the months of April through November, the beetle diversity analysis included April through October, velvet ant species richness and abundance analyses considered the months of

May through October, and the velvet ant diversity analysis included May through September.

Results

A total of 189 species were identified from 8382 specimens consisting of 25 antlion species from 1092 specimens, 96 bee species from 870 specimens, 34 beetle species from 2155 specimens, and 34 velvet ant species from 4265 specimens (Tables 2.1, 2.2 & 2.3; Fig. 2.1). None of the species were endemic to AMNWR.

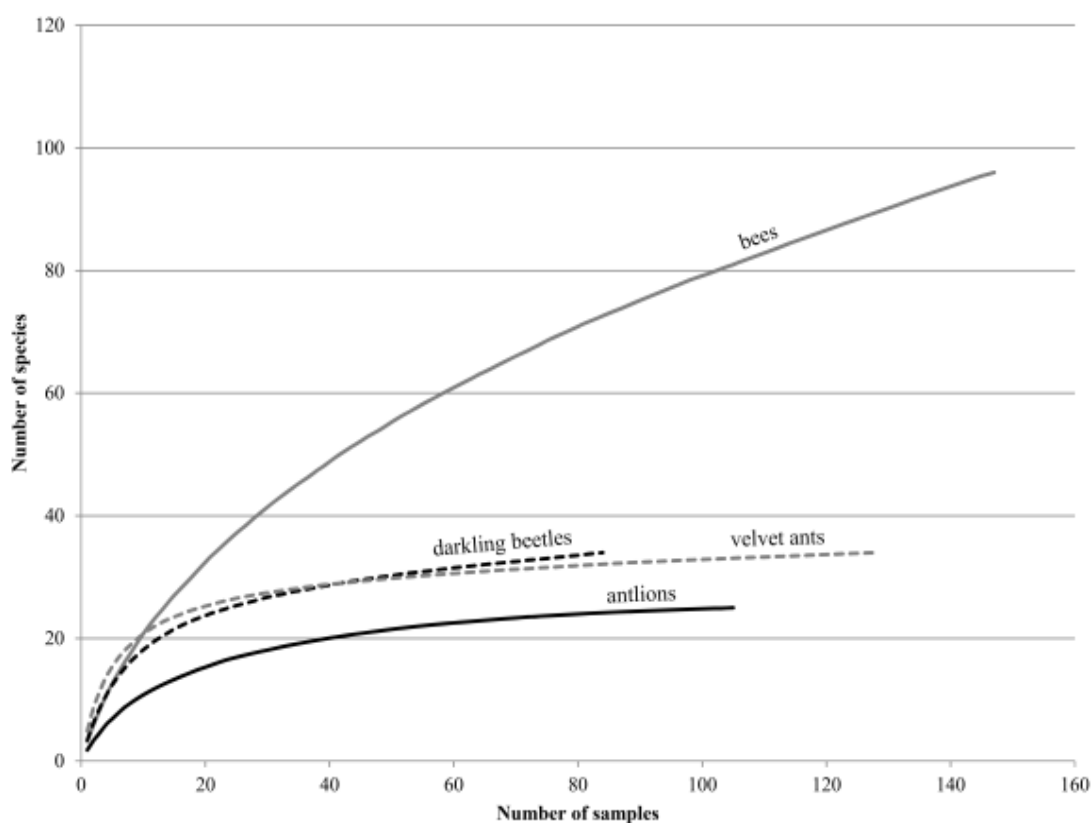


Figure 2.1. Species accumulation curves for each insect group at Ash Meadows National Wildlife Refuge December 2008 – December 2009.

Table 2.1. Number of species for each insect group and for all groups combined in each of three habitat types at Ash Meadows National Wildlife Refuge.

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune | All habitats |
|------------|----------------------|-----------------------------|-------------------------------|---------------------|
| Antlion | 19 | 17 | 14 | 25 |
| Bee | 62 | 52 | 44 | 96 |
| Beetle | 22 | 22 | 25 | 34 |
| Velvet ant | 33 | 25 | 23 | 34 |
| All groups | 136 | 116 | 106 | 189 |

Significant differences in species richness between habitats were found in all insect groups except for bees (Table 2.4 a; Fig. 2.2 a). Diversity significantly differed between habitats for antlions and beetles, and significant differences in abundance occurred between habitats for all insect groups (Table 2.4 a; Fig. 2.2 b&c). The interaction of habitat type by month for species richness was not significant for any insect group (Table 4b). For diversity, the only significant interaction of habitat by month occurred for beetles and for abundance, the interaction of habitat by month significantly differed for antlions, beetles and velvet ants (Table 2.4 b; Fig. 2.3 a-c).

Table 2.2. Number of specimens for each insect group and for all groups combined in each of three habitat types at Ash Meadows National Wildlife Refuge.

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune | Total number of specimens |
|------------|----------------------|-----------------------------|-------------------------------|----------------------------------|
| Antlion | 123 | 357 | 612 | 1092 |
| Bee | 402 | 293 | 175 | 870 |
| Beetle | 272 | 943 | 940 | 2155 |
| Velvet ant | 1467 | 1892 | 906 | 4265 |
| All groups | 2264 | 3485 | 2633 | 8382 |

Table 2.3. All species and their abundances at each of the three habitat types for each of four insect groups surveyed at Ash Meadows National Wildlife Refuge.

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|--|--------------------------|---------------------------------|-----------------------------------|
| Antlions | | | |
| <i>Brachynemurus hubbardi</i> | 1 | 0 | 4 |
| <i>Brachynemurus pulchellus</i> | 0 | 47 | 13 |
| <i>Brachynemurus sackeri</i> | 50 | 7 | 2 |
| <i>Chaetoleon pusillus</i> | 1 | 2 | 1 |
| <i>Clathroneuria arapahoe</i> | 3 | 1 | 0 |
| <i>Clathroneuria coquilletti</i> | 5 | 13 | 2 |
| <i>Clathroneuria navajo</i> | 1 | 3 | 2 |
| <i>Clathroneuria schwarzi</i> | 18 | 0 | 0 |
| <i>Eremoleon insipidus</i> | 1 | 0 | 0 |
| <i>Gnopleon delicatulus</i> | 1 | 0 | 0 |
| <i>Myrmeleon rusticus</i> | 0 | 5 | 0 |
| <i>Paranthaclisis congener</i> | 4 | 1 | 13 |
| <i>Paranthaclisis hageni</i> | 2 | 0 | 3 |
| <i>Purenleon inscriptus</i> | 2 | 4 | 5 |
| <i>Scotoleon carrizonus</i> | 1 | 8 | 0 |
| <i>Scotoleon deflexus</i> | 0 | 5 | 0 |
| <i>Scotoleon eiseni</i> | 1 | 0 | 0 |
| <i>Scotoleon expansus</i> | 5 | 0 | 0 |
| <i>Scotoleon intermedius</i> | 0 | 18 | 86 |
| <i>Scotoleon longipalpis</i> | 22 | 22 | 17 |
| <i>Scotoleon minisculus</i> | 2 | 171 | 392 |
| <i>Scotoleon minutus</i> | 0 | 6 | 0 |
| <i>Scotoleon quadripunctata</i> | 1 | 29 | 57 |
| <i>Scotoleon singularis</i> | 0 | 15 | 15 |
| <i>Tytholeon puerilis</i> | 2 | 0 | 0 |
| Total | 123 | 357 | 612 |
| Bees | | | |
| <i>Agapostemon angelicus/texanus</i> | 36 | 6 | 5 |
| <i>Agapostemon melliventris</i> | 19 | 5 | 14 |
| <i>Andrena</i> sp. 1 | 8 | 1 | 3 |
| <i>Andrena</i> sp. 2 | 1 | 0 | 0 |
| <i>Andrena</i> sp. 4 | 0 | 0 | 1 |
| <i>Anthidiellum notatum</i> | 2 | 0 | 0 |
| <i>Anthidiellum</i> sp. 1 | 1 | 0 | 2 |

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|--------------------------------|------------------|-------------------------|---------------------------|
| <i>Anthophora</i> sp. 1 | 0 | 23 | 14 |
| <i>Anthophora</i> sp. 2 | 2 | 2 | 1 |
| <i>Anthophora</i> sp. 3 | 6 | 0 | 1 |
| <i>Anthophora</i> sp. 4 | 4 | 1 | 4 |
| <i>Anthophora</i> sp. 5 | 4 | 0 | 0 |
| <i>Anthophora</i> sp. 6 | 1 | 0 | 0 |
| <i>Anthophora</i> sp. 8 | 2 | 0 | 0 |
| <i>Anthophora</i> sp. 9 | 0 | 1 | 4 |
| <i>Anthophora</i> sp. 10 | 4 | 22 | 14 |
| <i>Anthophora</i> sp. 11 | 6 | 0 | 1 |
| <i>Anthophora</i> sp. 12 | 0 | 1 | 4 |
| <i>Anthophora</i> sp. 13 | 1 | 0 | 0 |
| <i>Anthophora vaginera</i> | 4 | 0 | 1 |
| <i>Apis mellifera</i> | 31 | 6 | 8 |
| <i>Ashmeadiella aridula</i> | 2 | 11 | 1 |
| <i>Ashmeadiella bigeloviae</i> | 7 | 19 | 3 |
| <i>Ashmeadiella breviceps</i> | 0 | 1 | 1 |
| <i>Ashmeadiella buconis</i> | 0 | 1 | 0 |
| <i>Ashmeadiella difugita</i> | 1 | 0 | 0 |
| <i>Ashmeadiella leucozona</i> | 0 | 2 | 0 |
| <i>Ashmeadiella opuntiae</i> | 1 | 1 | 0 |
| <i>Ashmeadiella prosopidis</i> | 2 | 17 | 1 |
| <i>Ashmeadiella rufipes</i> | 7 | 11 | 5 |
| <i>Ashmeadiella rufitarsis</i> | 1 | 3 | 0 |
| <i>Ashmeadiella nr. sonora</i> | 2 | 0 | 0 |
| <i>Ashmeadiella xenomaslax</i> | 1 | 3 | 1 |
| <i>Calliopsis puellae</i> | 9 | 5 | 7 |
| <i>Calliopsis</i> sp. 1 | 1 | 0 | 0 |
| <i>Centris</i> sp. 2 | 0 | 0 | 6 |
| <i>Centris</i> sp. 5 | 1 | 0 | 0 |
| <i>Centris</i> sp. 6 | 1 | 0 | 0 |
| <i>Colletes</i> sp. 1 | 0 | 0 | 7 |
| <i>Colletes</i> sp. 2 | 2 | 2 | 2 |
| <i>Colletes</i> sp. 3 | 0 | 0 | 1 |
| <i>Diadasia australis</i> | 2 | 0 | 0 |
| <i>Diadasia diminuta</i> | 1 | 0 | 0 |
| <i>Diadasia megamorpha</i> | 0 | 0 | 10 |
| <i>Diadasia vallicola</i> | 3 | 1 | 0 |
| <i>Dialictus</i> sp. 1 | 47 | 24 | 4 |

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|-------------------------------|------------------|-------------------------|---------------------------|
| <i>Dialictus</i> sp. 2 | 2 | 0 | 0 |
| <i>Dialictus</i> sp. 4 | 0 | 3 | 0 |
| <i>Dialictus</i> sp. 5 | 1 | 0 | 0 |
| <i>Dialictus</i> sp. 6 | 103 | 39 | 16 |
| <i>Dialictus</i> sp. 7 | 16 | 28 | 2 |
| <i>Dialictus</i> sp. 9 | 0 | 3 | 0 |
| <i>Dialictus</i> sp. 10 | 1 | 0 | 0 |
| <i>Dianthidium implicatum</i> | 1 | 0 | 0 |
| <i>Dianthidium</i> sp. 2 | 1 | 0 | 0 |
| <i>Dieunomia xerophila</i> | 9 | 0 | 0 |
| <i>Dufourea</i> sp. 1 | 0 | 2 | 0 |
| <i>Halictus ligatus</i> | 8 | 0 | 4 |
| <i>Hesperapis</i> sp. 2 | 0 | 1 | 1 |
| <i>Hylaeus</i> sp. 1 | 0 | 1 | 0 |
| <i>Hylaeus</i> sp. 2 | 0 | 1 | 0 |
| <i>Hylaeus</i> sp. 3 | 0 | 2 | 0 |
| <i>Lasioglossum</i> sp. 1 | 2 | 7 | 4 |
| <i>Lasioglossum</i> sp. 2 | 0 | 1 | 0 |
| <i>Lasioglossum</i> sp. 3 | 1 | 1 | 1 |
| <i>Megachile augustina</i> | 0 | 1 | 0 |
| <i>Megachile chilopsidis</i> | 1 | 0 | 0 |
| <i>Megachile lippiae</i> | 1 | 0 | 0 |
| <i>Megachile nevadensis</i> | 1 | 8 | 6 |
| <i>Megachile odontostoma</i> | 0 | 2 | 0 |
| <i>Megachile xerophila</i> | 3 | 0 | 0 |
| <i>Megachile</i> sp. 1 | 0 | 0 | 1 |
| <i>Melissodes</i> sp. 1 | 2 | 1 | 0 |
| <i>Melissodes</i> sp. 2 | 1 | 1 | 4 |
| <i>Melissodes</i> sp. 3 | 1 | 0 | 0 |
| <i>Melissodes</i> sp. 4 | 2 | 2 | 1 |
| <i>Melissodes</i> sp. 5 | 0 | 0 | 1 |
| <i>Melissodes</i> sp. 7 | 3 | 0 | 1 |
| <i>Melissodes</i> sp. 8 | 1 | 1 | 4 |
| <i>Melissodes</i> sp. 9 | 1 | 0 | 0 |
| <i>Neolarra</i> sp. 1 | 0 | 1 | 0 |
| <i>Neolarra</i> sp. 2 | 0 | 0 | 1 |
| <i>Osmia titusi</i> | 0 | 1 | 0 |
| <i>Perdita</i> sp. 1 | 6 | 0 | 0 |
| <i>Perdita</i> sp. 6 | 0 | 1 | 0 |

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|-------------------------------------|---------------|----------------------|------------------------|
| <i>Perdita</i> sp. 8 | 1 | 0 | 0 |
| <i>Perdita</i> sp. 11 | 3 | 0 | 0 |
| <i>Perdita</i> sp. 13 | 0 | 0 | 1 |
| <i>Perdita</i> sp. 15 | 0 | 1 | 0 |
| <i>Perdita</i> sp. 17 | 0 | 0 | 1 |
| <i>Perdita</i> sp. 19 | 0 | 2 | 0 |
| <i>Perdita</i> sp. 20 | 1 | 4 | 0 |
| <i>Perdita</i> sp. 23 | 0 | 2 | 0 |
| <i>Perdita</i> sp. 24 | 0 | 3 | 0 |
| <i>Perdita</i> sp. 25 | 6 | 0 | 0 |
| <i>Stelis</i> sp. 1 | 0 | 4 | 0 |
| Total | 402 | 293 | 175 |
| Beetles | | | |
| <i>Alaephus macilentus</i> | 25 | 0 | 0 |
| <i>Alaephus nevadensis</i> | 1 | 42 | 3 |
| <i>Anepsius delicatulus</i> | 19 | 0 | 1 |
| <i>Asbolus verrucosa</i> | 23 | 47 | 106 |
| <i>Batuliodes spatulatus</i> | 0 | 0 | 1 |
| <i>Blapstinus</i> sp. 1 | 34 | 0 | 0 |
| <i>Blapstinus</i> sp. 2 | 16 | 1 | 2 |
| <i>Blapstinus</i> sp. 3 | 0 | 0 | 1 |
| <i>Chilometopon abnorme</i> | 8 | 168 | 271 |
| <i>Chilometopon helopioides</i> | 8 | 14 | 2 |
| <i>Chilometopon pallidum</i> | 0 | 20 | 220 |
| <i>Coniontis</i> sp. 1 | 0 | 0 | 1 |
| <i>Coniontis</i> sp. 2 | 4 | 0 | 0 |
| <i>Cryptoglossa muricata</i> | 1 | 0 | 0 |
| <i>Cynaenus angustus</i> | 0 | 1 | 0 |
| <i>Edrotes ventricosus</i> | 0 | 24 | 42 |
| <i>Eleodes armata</i> | 9 | 10 | 7 |
| <i>Eupsophulus castaneus</i> | 11 | 81 | 18 |
| <i>Eusattus muricatus muricatus</i> | 0 | 0 | 1 |
| <i>Eusattus phreatophilus</i> | 14 | 1 | 9 |
| <i>Hylocrinus</i> sp. 1 | 0 | 10 | 0 |
| <i>Hymenorus irritus</i> | 8 | 132 | 33 |
| <i>Hymenorus capensis</i> | 13 | 1 | 0 |
| <i>Hymenorus testaceus</i> | 24 | 250 | 34 |

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|------------------------------------|------------------|-------------------------|---------------------------|
| <i>Hymenorus thoracicus</i> | 36 | 53 | 63 |
| <i>Mechysmus angustus</i> | 1 | 0 | 3 |
| <i>Metapoloba pruinosa</i> | 0 | 3 | 1 |
| <i>Metaponium</i> sp. 1 | 6 | 19 | 2 |
| <i>Palorus subdepressus</i> | 0 | 0 | 2 |
| <i>Telabis</i> sp. 1 | 7 | 50 | 60 |
| <i>Telabis</i> sp. 2 | 1 | 1 | 1 |
| <i>Triorophus laevis politus</i> | 3 | 0 | 0 |
| <i>Trogloderus constatus</i> | 0 | 14 | 56 |
| <i>Zophobas subnitens</i> | 0 | 1 | 0 |
| Total | 272 | 943 | 940 |
| Velvet ants | | | |
| <i>Acanthophtopsis falciformis</i> | 1 | 0 | 0 |
| <i>Dasymutilla arenivaga</i> | 3 | 7 | 15 |
| <i>Dilophotopsis concolor</i> | 54 | 27 | 16 |
| <i>Dilophotopsis paron</i> | 15 | 0 | 2 |
| <i>Odontophotopsis acmaea</i> | 11 | 27 | 15 |
| <i>Odontophotopsis armata</i> | 1 | 0 | 0 |
| <i>Odontophotopsis aufidia</i> | 1 | 0 | 0 |
| <i>Odontophotopsis bellona</i> | 13 | 1 | 2 |
| <i>Odontophotopsis biramosa</i> | 1 | 0 | 0 |
| <i>Odontophotopsis clypeata</i> | 350 | 673 | 179 |
| <i>Odontophotopsis inconspicua</i> | 260 | 96 | 74 |
| <i>Odontophotopsis mamata</i> | 168 | 1 | 1 |
| <i>Odontophotopsis melicausa</i> | 60 | 204 | 87 |
| <i>Odontophotopsis microdonta</i> | 42 | 2 | 0 |
| <i>Odontophotopsis piute</i> | 2 | 32 | 0 |
| <i>Odontophotopsis serca</i> | 30 | 1 | 0 |
| <i>Odontophotopsis setifera</i> | 1 | 0 | 2 |
| <i>Odontophotopsis sonora</i> | 0 | 65 | 3 |
| <i>Sphaerophthalma amphion</i> | 1 | 0 | 0 |
| <i>Sphaerophthalma arota</i> | 26 | 46 | 2 |
| <i>Sphaerophthalma becki</i> | 61 | 14 | 45 |
| <i>Sphaerophthalma blakeii</i> | 41 | 12 | 6 |
| <i>Sphaerophthalma difficilis</i> | 77 | 68 | 151 |
| <i>Sphaerophthalma macswaini</i> | 1 | 0 | 0 |
| <i>Sphaerophthalma marpesia</i> | 17 | 33 | 20 |

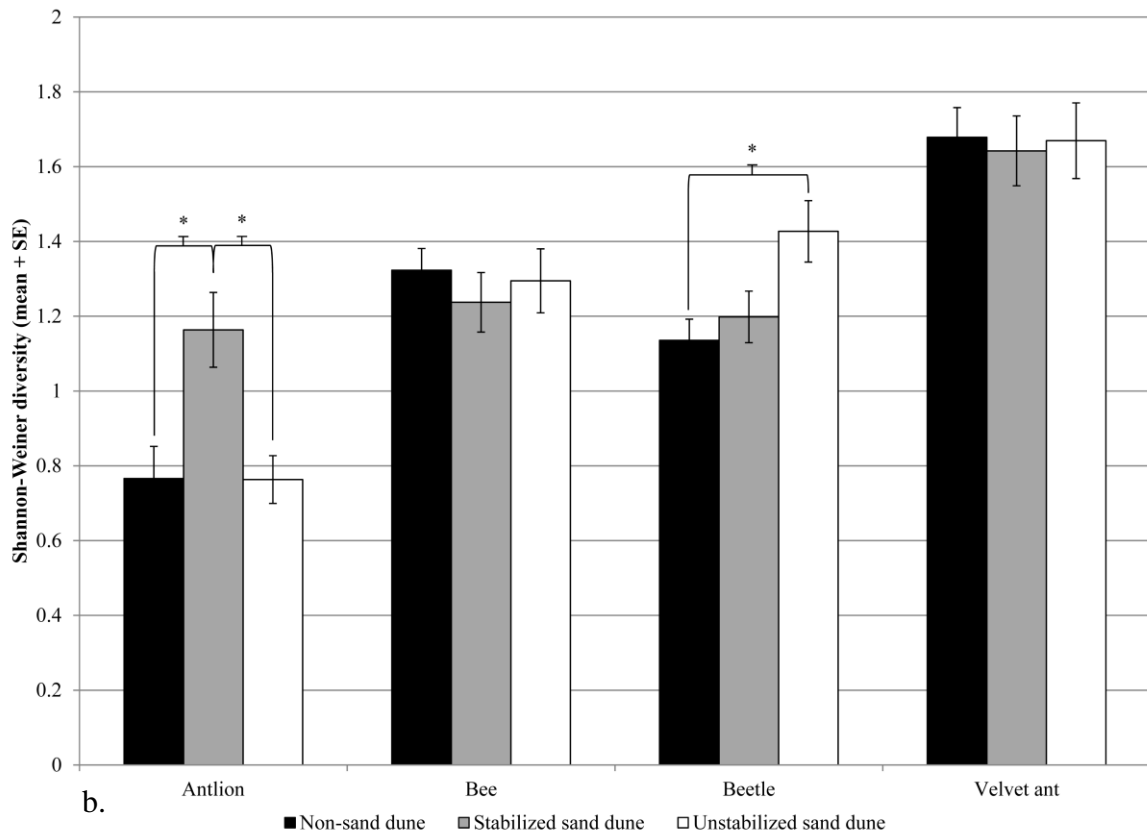
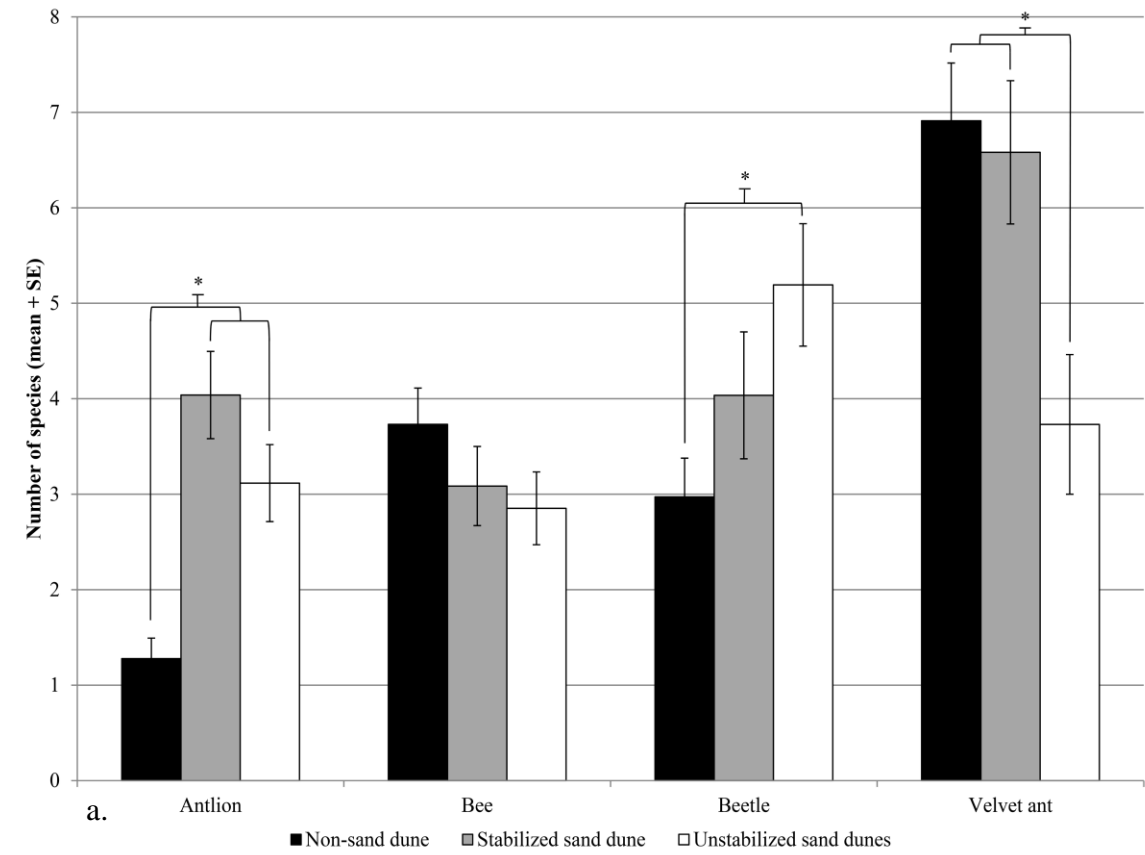
| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|-------------------------------------|----------------------|-----------------------------|-------------------------------|
| <i>Sphaerophthalma megagnathos</i> | 4 | 1 | 0 |
| <i>Sphaerophthalma mendica</i> | 65 | 1 | 1 |
| <i>Sphaerophthalma nana</i> | 3 | 2 | 0 |
| <i>Sphaerophthalma orestes</i> | 4 | 295 | 168 |
| <i>Sphaerophthalma pallida</i> | 21 | 2 | 4 |
| <i>Sphaerophthalma parkeri</i> | 2 | 0 | 2 |
| <i>Sphaerophthalma triangularis</i> | 54 | 107 | 55 |
| <i>Sphaerophthalma uro</i> | 61 | 155 | 54 |
| <i>Sphaerophthalma yumaella</i> | 16 | 20 | 2 |
| Total | 1467 | 1892 | 906 |

Antlions

The results from the analysis of habitat type for antlions at AMNWR identified greater species richness and abundance in both of the sand dune habitats over the non-sand dune habitat (Table 2.5 a,c; Fig. 2.2 a,c). Antlion species diversity was significantly greater in the stabilized sand dune habitat than in either the non-sand dune habitat or the unstabilized sand dune habitat (Table 2.5 b; Fig. 2.2 b).

No effect of the interaction of habitat type and month was found for antlion richness and diversity (Table 2.4 b). The effect of the interaction of habitat type and month for antlion abundance, however, was significant (Table 2.4 b). In July, the abundance of antlions was significantly greater in both the stabilized and unstabilized sand dune habitats compared to the non-sand dune habitats (Table 2.6 a, Fig. 2.3 a). Antlion abundance was also significantly greater in the unstabilized sand dune habitat than in the non-sand dune habitat in August (Table 2.6 a, Fig. 2.3).

Figure 2.2 a-b. Mean \pm standard error for all sample dates in (a) species richness and (b) diversity between habitats for each insect group. Significant differences are shown with an asterisk (*). Species richness (a) is represented by the mean number of species collected for each sampling event within a habitat type. Diversity (b) is displayed as the mean Shannon-Weiner diversity index value estimated from the combination of diversity index values for each sampling event within a habitat type.



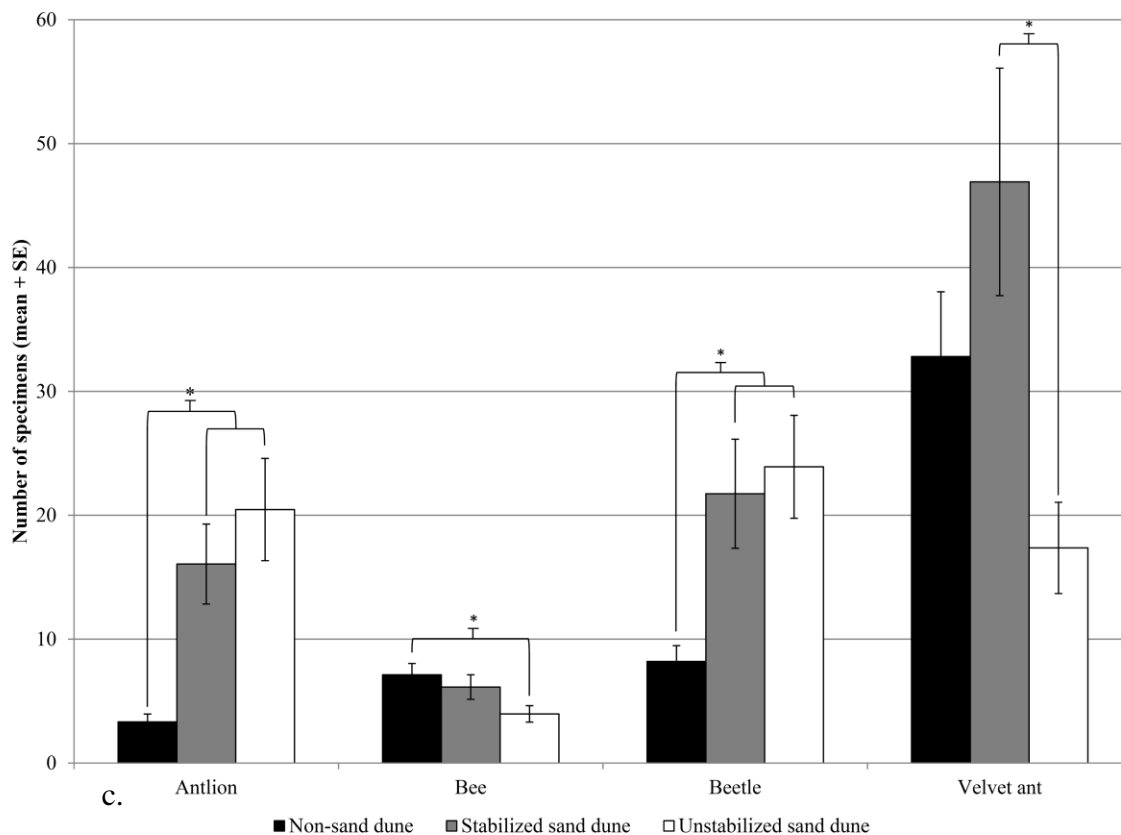


Figure 2.2 c. Mean \pm standard error for all sample dates in abundance (c) between habitats for each insect group. Significant differences are shown with an asterisk (*). Abundance (c) of specimens encountered was presented as the mean number of specimens encountered in each sampling event at each site within a habitat type.

In the comparison of antlion species composition, the six most abundant species found within a habitat type made up greater than 80% of the specimens collected in that habitat (Fig. 2.4 a). The most abundant antlion species were identical between both sand dune habitats with only slight differences in the proportion of each species. Only one of these species, *Scotoleon longipalpis* (Hagen), was also found in non-sand dune habitats. This supports the significant difference in species richness found between both sand dune habitats and the non-sand dune habitat. Both stabilized sand dune and non-sand dune

habitats supported unique species, but the unstabilized sand dune habitat had no unique species (Table 2.7).

Table 2.4 a&b. Results from the generalized linear mixed models of habitat type (a) and the interaction of habitat type and month (b) for each insect group at Ash Meadows National Wildlife Refuge.

| a. Habitat Type | Antlion | | Bee | | Beetle | | Velvet ant | |
|------------------------|----------------|----------|------------|----------|---------------|----------|-------------------|----------|
| Statistical Measures | F | P | F | P | F | P | F | P |
| Richness | 16.3 | p<0.0001 | 1.45 | p=0.2493 | 4.6 | p=0.0176 | 4.2 | p=0.0273 |
| Diversity | 7.43 | p=0.0063 | 0.37 | p=0.6938 | 4.71 | p=0.0199 | 0.04 | p=0.9564 |
| Abundance | 25.83 | p<0.0001 | 3.95 | p=0.0292 | 12.81 | p<0.0001 | 6.04 | p=0.0075 |

| b. Habitat Type & Month | Antlion | | Bee | | Beetle | | Velvet ant | |
|------------------------------------|----------------|----------|------------|----------|---------------|----------|-------------------|----------|
| Statistical Measures | F | P | F | P | F | P | F | P |
| Richness | 1.75 | p=0.1486 | 0.77 | p=0.6919 | 0.51 | p=0.9079 | 1.52 | p=0.1912 |
| Diversity | 1.28 | p=0.3277 | 2.03 | p=0.0636 | 3.51 | p=0.0052 | 0.46 | p=0.8682 |
| Abundance | 2.76 | p=0.0314 | 1 | p=0.4779 | 2.21 | p=0.0311 | 2.33 | p=0.0439 |

Bees

Bee species richness and diversity was similar across all habitat types (Table 2.4 a; Fig. 2.2 a&b). Bees were significantly more abundant in non-sand dune habitats than in unstabilized sand dune habitats (Table 2.4 a; Fig. 2.2 c). The abundance of stabilized sand dune habitats did not significantly differ from the non-sand dune or the unstabilized sand dune habitats (Table 2.4 a; Fig. 2.2 c). The effect of the interaction of habitat type and month was not significant for bee richness, diversity or abundance (Table 2.4 b).

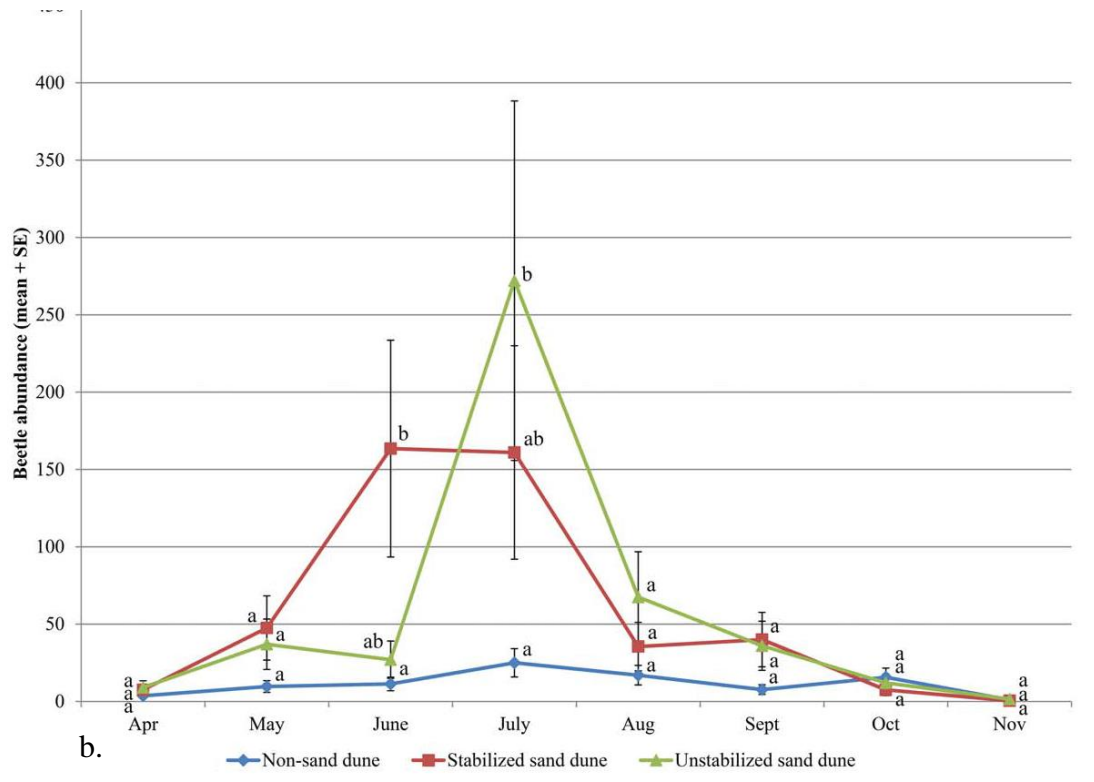
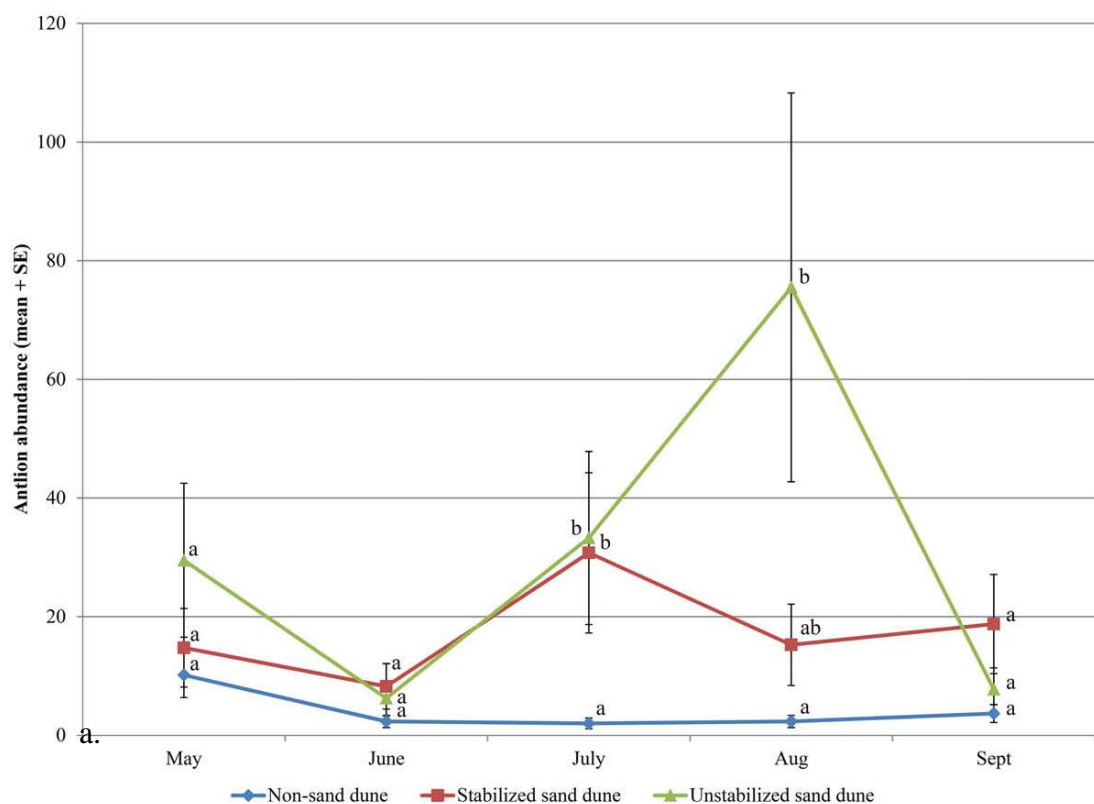
Table 2.5 a-c. Results of the Tukey's test comparing (a) species richness, (b) diversity, and (c) abundance between each of three habitats at Ash Meadows National Wildlife Refuge for each insect group that significantly differed from the generalized linear mixed models for habitat type.

| a. Richness | Antlion | | Beetle | | Velvet ant | |
|---------------------------------------|----------------|----------|---------------|----------|-------------------|----------|
| Habitats | T | Adj. P | t | Adj. P | t | Adj. P |
| Non-dune vs. Stabilized dune | -5.68 | p<0.0001 | -1.43 | p=0.3377 | 0.34 | p=0.938 |
| Non-dune vs. Unstabilized dune | -4.2 | p=0.0012 | -3.03 | p=0.0129 | 2.87 | p=0.022 |
| Stabilized dune vs. Unstabilized dune | -1.51 | p=0.3081 | 1.22 | p=0.4478 | -2.5 | p=0.0494 |

| b. Diversity | Antlion | | Beetle | |
|---------------------------------------|----------------|----------|---------------|----------|
| Habitats | t | Adj. P | t | Adj. P |
| Non-dune vs. Stabilized dune | -2.96 | p=0.0263 | -0.71 | p=0.7628 |
| Non-dune vs. Unstabilized dune | 0.02 | p=0.9997 | -3 | p=0.0174 |
| Stabilized dune vs. Unstabilized dune | -3.51 | p=0.009 | 2.15 | p=0.1035 |

| c. Abundance | Antlion | | Bee | | Beetle | | Velvet ant | |
|---------------------------------------|----------------|----------|------------|----------|---------------|----------|-------------------|----------|
| Habitats | t | Adj. P | t | Adj. P | t | Adj. P | t | Adj. P |
| Non-dune vs. Stabilized dune | -5.69 | p<0.0001 | 0.73 | p=0.7474 | 3.82 | p=0.0016 | -1.42 | p=0.3487 |
| Non-dune vs. Unstabilized dune | 6.56 | p<0.0001 | 2.79 | p=0.0233 | 4.59 | p=0.0002 | 2.4 | p=0.0615 |
| Stabilized dune vs. Unstabilized dune | 0.85 | p=0.6772 | -1.88 | p=0.1614 | 0.36 | p=0.9323 | -3.44 | p=0.0058 |

Figure 2.3 a-b. The interaction of habitat type and month for abundance values in (a) antlions and (b) darkling beetles. Habitat types are indicated by points of various shapes and different colored lines (blue line with solid circles = non-sand dune habitat, red line with solid squares = stabilized sand dune habitat, and green line with solid triangles = unstabilized sand dune habitat). This is consistent between all charts. Error bars provide standard error values in all charts, and all charts identify significant differences with an asterisk (*) and adjoining guide bars.



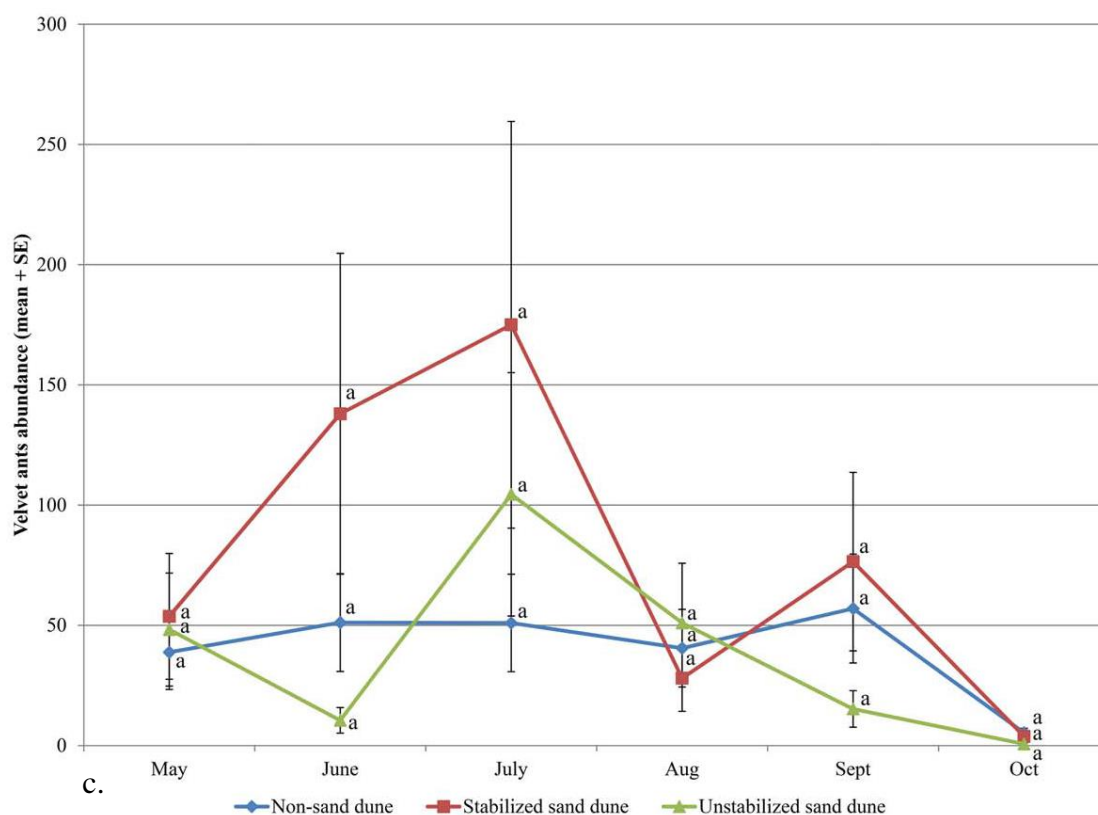


Figure 2.3 c. The interaction of habitat type and month for abundance values in (c) velvet ants (c). Habitat types are indicated by points of various shapes and different colored lines (blue line with solid circles = non-sand dune habitat, red line with solid squares = stabilized sand dune habitat, and green line with solid triangles = unstabilized sand dune habitat). This is consistent between all charts. Error bars provide standard error values in all charts, and all charts identify significant differences with an asterisk (*) and adjoining guide bars.

Nearly all of the six dominant bee species found within a habitat type made up greater than 50% of the specimens collected in that habitat (Fig. 2.4b). The unstabilized sand dune habitats had less than 50% of specimens being one of the six dominant bee species. Only 35% of the specimens collected in unstabilized sand dune habitats were one of the six dominant species within the habitat. The composition of the bee species was different across all habitats, but many of the six dominant species were shared between

two habitats. One bee species, *Dialictus* sp. 6, was the most abundant across all habitat types. Four other species were shared between one of the sand dune habitats and the non-sand dune habitat. *Dialictus* sp.1 and *Dialictus* sp. 7 were two of the five most abundant species in non-sand dune and stabilized sand dune habitats. *Agapostemon melliventris* Cresson and *Apis mellifera* Linnaeus were two of the five other most abundant species in non-sand dune and unstabilized sand dune habitats. Other than *Dialictus* sp. 6, the sand dune habitats also had two other species in common, *Anthophora* sp. 1 and *Anthophora* sp. 10. Nearly 60% of all bee species found at AMNWR were unique to one type of habitat (Table 2.7).

Table 2.6 a-c. Results of Tukey's test of significant effects of the interaction between habitat type and month for (a) antlion abundance, (b) darkling beetle diversity, and (c) darkling beetle abundance between each of three habitats at Ash Meadows National Wildlife Refuge.

| a. Antlion Abundance | July | | Aug | |
|---------------------------------------|-------------|----------|------------|----------|
| | t | Adj. P | t | Adj. P |
| Non-dune vs. Stabilized dune | 4.32 | P=0.0185 | - | - |
| Non-dune vs. Unstabilized dune | 4.45 | P=0.0141 | -5.62 | P=0.0012 |
| Stabilized dune vs. Unstabilized dune | - | - | - | - |

| b. Beetle Diversity | May | |
|---------------------------------------|------------|----------|
| | t | Adj. P |
| Non-dune vs. Stabilized dune | - | - |
| Non-dune vs. Unstabilized dune | - | - |
| Stabilized dune vs. Unstabilized dune | 5.12 | P=0.0047 |

| c. Beetle Abundance | June | | July | |
|---------------------------------------|-------------|----------|-------------|----------|
| | t | Adj. P | t | Adj. P |
| Non-dune vs. Stabilized dune | 4.62 | P=0.0097 | - | - |
| Non-dune vs. Unstabilized dune | - | - | -4.24 | P=0.0254 |
| Stabilized dune vs. Unstabilized dune | - | - | - | - |

Figure 4 a-d. A comparison of the proportion of overall fauna from each insect group represented by the top six most abundant species between habitat types. Proportions are represented as the percentage of total abundance. Charts presented for (a) antlions, (b) bees, (c) beetles and (d) velvet ants.

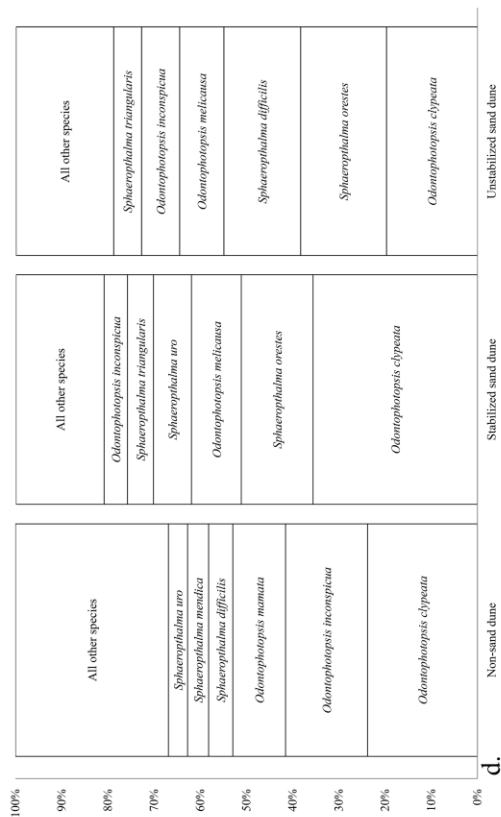
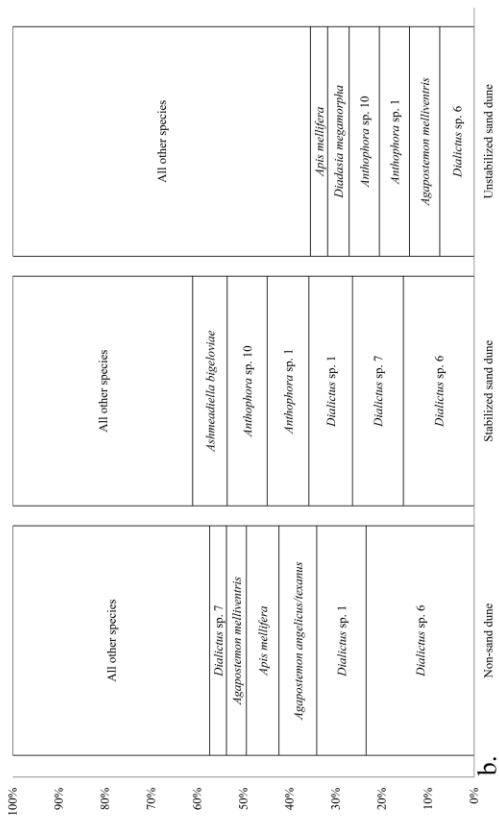
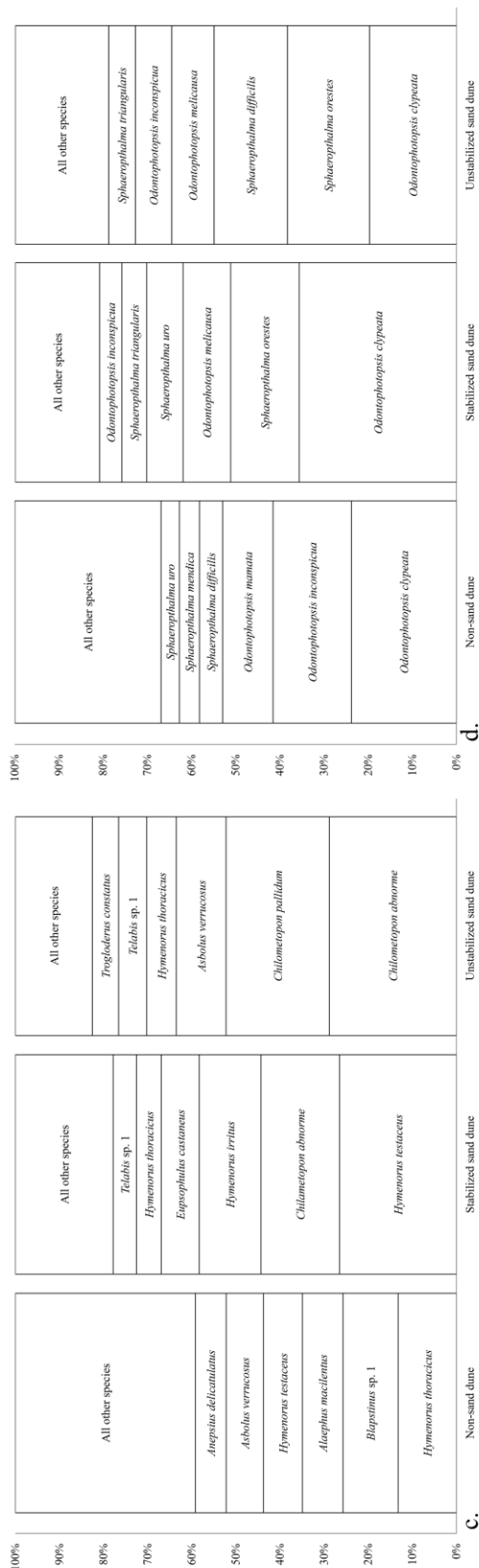
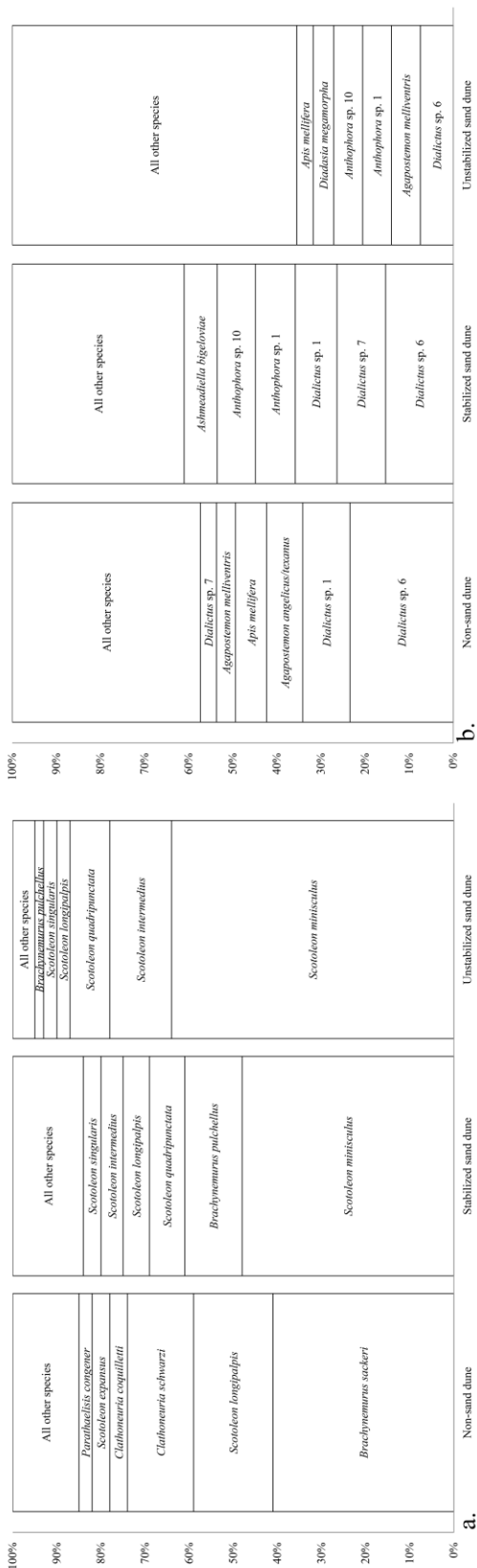


Table 2.7. Number of species unique to a particular habitat type for each insect group and for all groups combined in each of three habitat types at Ash Meadows National Wildlife Refuge.

| | Non-sand dune | Stabilized sand dune | Unstabilized sand dune | Total number of unique species |
|------------|----------------------|-----------------------------|-------------------------------|---------------------------------------|
| Antlion | 6 | 3 | 0 | 9 |
| Bee | 28 | 19 | 10 | 57 |
| Beetle | 5 | 3 | 5 | 13 |
| Velvet ant | 6 | 0 | 0 | 6 |
| All groups | 45 | 25 | 15 | 85 |

Darkling Beetles

The analysis of habitat type for beetles revealed significantly greater species richness and were significantly more diverse in the unstabilized sand dune habitat than in the non-sand dune habitat (Table 2.5 a,b; Figure 2.2 a,b). Beetle abundance was significantly greater in both sand dune habitats over the non-sand dune habitats (Table 2.5 c; Fig. 2.2 c).

The effect of the interaction between habitat type and month was significant for species diversity and abundance (Table 2.4 b). Beetle diversity was significantly greater in May in the unstabilized sand dune habitat compared to the stabilized sand dune habitat (Table 2.6 b; Fig. 2.5). Beetle abundance was significantly different between habitats in June and July (Table 2.6 c; Fig. 2.3 b). In June, stabilized sand dune habitats had significantly greater abundance than the non-sand dune habitats, and in July, the unstabilized sand dune habitats had greater abundance than the non-sand dune habitats.

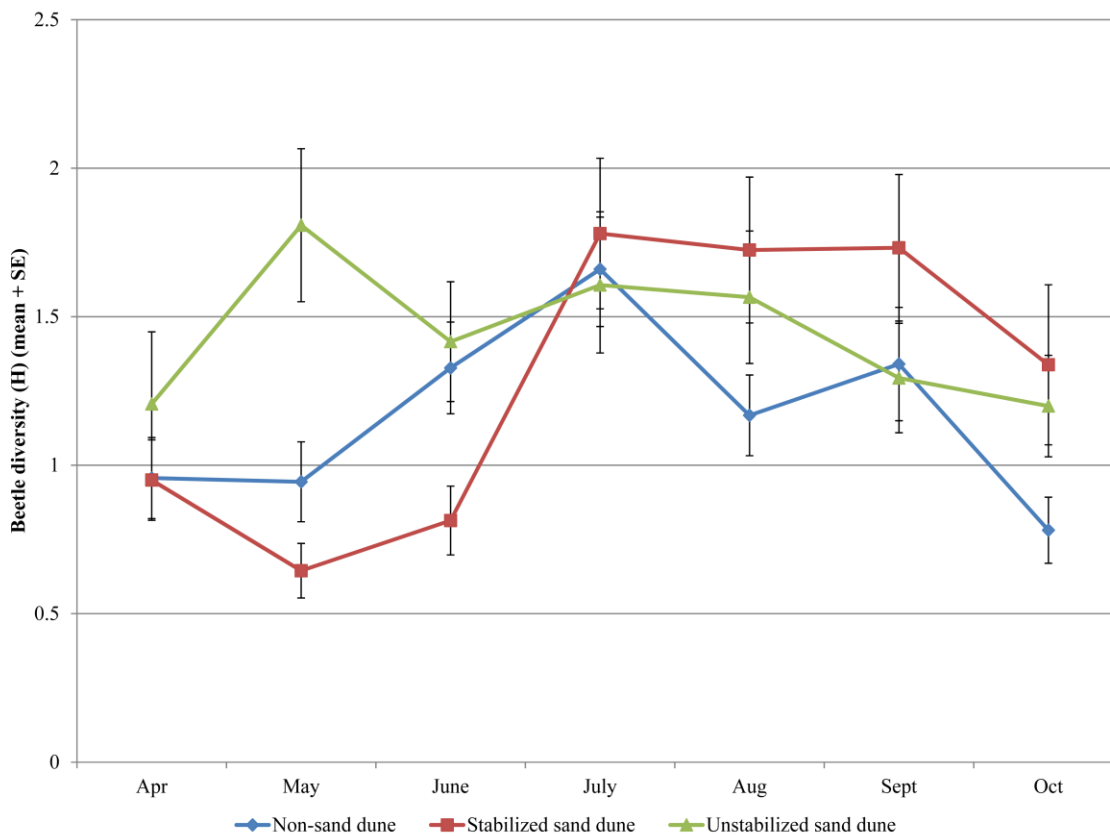


Figure 2.5. The interaction of habitat type and month for diversity values in beetles. Habitat types are indicated by points of various shapes and different colored lines (blue line with solid circles = non-sand dune habitat, red line with solid squares = stabilized sand dune habitat, and green line with solid triangles = unstabilized sand dune habitat). This is consistent between all charts. Error bars provide standard error values in all charts, and all charts identify significant differences with an asterisk (*) and adjoining guide bars.

Of the six most abundant beetle species, *Hymenorus thorsicus* Fall, was found across all sites, although it was not the most abundant species in either sand dune habitat (Fig. 2.4 c). Two other species, *Chilometopon abnorme* (Horn) and *Telabis* sp. 1, were among the six most abundant species in both sand dune habitats. Nearly 40% of beetle species found at AMNWR were unique to one type of habitat (Table 2.7). The number of

unique species found in any habitat was equal between non-sand dune and unstabilized sand dune habitats.

Velvet Ants

Velvet ants had significantly greater species richness in both the non-sand dune and stabilized sand dune habitats than in the unstabilized sand dune habitat, and abundance was greater only in stabilized sand dune habitats than in unstabilized sand dune habitats (Table 2.5 a,c; Fig. 2.2 a,c). Velvet ants were evenly diverse between all habitat types (Table 2.5 b; Fig. 2.2 b). The effect of the interaction of habitat type and month was significant for velvet ant abundance (Table 2.5 c; Fig. 2.3 c). All of these differences occurred between months, however, and no significant differences occurred between habitats within the same month (Fig. 2.3 c).

Composition of the dominant velvet ant species within the velvet ant community was similar across all habitats (Fig. 2.4 d). One velvet ant species, *Odontophotopsis clypeata* Schuster, was the most abundant species across all three habitats. Both sand dune habitats only differed by one of the five other most abundant velvet ant species, and the species that differed, *Sphaerophthalma uro* and *Sphaerophthalma difficilis* (Baker), were both one of the six most abundant species found in non-sand dune habitats. No species were unique to either of the sand dune habitats and only one species, *Odontophotopsis sonora* Schuster, was not found in the non-sand dune habitats (Table 2.3).

Discussion

Our survey of antlions, bees, darkling beetles and velvet ants across the three habitat types at AMNWR revealed some dramatic differences in measures of species richness, diversity and especially abundance. None of the identified species from any insect group were undetermined or are endemic species to AMNWR. Some specimens were not identified to species as their identifications are difficult to confirm and those specimens were separated into morphospecies.

Antlions

At AMNWR, both stabilized and unstabilized sand dune habitats exhibited greater antlion species richness and abundance than the non-sand dune habitat. The non-sand dune habitat, however, hosted the greatest number of unique species for all three of the habitat types. This reveals that sand dunes are important habitats for most antlion species, but non-sand dune habitats are also important as they contribute to antlion biodiversity at the refuge by supporting several species that do not occur in sand dune habitats. The larvae of most antlion species hunt and live in loose, deep sand (Arnett 2000; Stange 1994). Like the predacious antlion larvae, most sand dune obligate species are carnivores (Holm & Scholtz 1980; Rust 1986). Thus, the sand dune habitats at AMNWR may offer a more optimal substrate for those dune species than the substrate used by other species in the more compacted non-sand dune habitats.

No estimates of antlion species richness are presently known for the deserts of western North America. In other desert regions of the world, such as the desert regions of the Abu Dhabi Emirate and two desert national parks in Tunisia, the number of antlion

species collected at a single locality ranged between 21 and 27 species (Güsten 2002; Saji & Whittington 2008). Twenty-five species of antlions were found at AMNWR, and, thus, AMNWR antlion species richness is similar to other desert regions in the world. The greatest difference in antlion abundance between habitats occurred in the mid-to late summer months of July and August at AMNWR, with sand dune habitats supporting greater abundance than the non-sand dune habitats. Peak abundance and species richness also has been observed for Palaearctic antlions in August (Krivokhatsky 1998; Güsten 2002). Seasonal segregation between species has been observed in antlions (Güsten 2002), and suggests that these peaks may represent only a few very abundant species.

Antlion diversity at AMNWR in stabilized sand dune habitats was greater than both unstabilized sand dune and non-sand dune habitats. In the sand dunes of the northern Namib Desert, carnivorous species, like antlions, were greater in number of species and individuals in more mesic dune habitats (Crawford & Seely 1987). As it is for other sand-obligate carnivores this suggests that moisture availability may be a limiting factor for antlions. Multiple abiotic factors have been documented as having an impact on pit building antlion species including soil moisture, litterfall abundance, temperature, rainfall, soil compactness and soil density (Simberloff *et al.* 1978; Boake *et al.* 1984; Marsh 1987; Lucas 1989; Gotelli 1993; Van Zyl *et al.* 1996; Gatti & Farji-Berner 2002). However, only one pit building species, *Myrmeleon rusticus* Hagen, was found at one of our study sites and it occurred in low abundance. Few studies are available on the habitat preferences and environmental variables that influence the distribution of non-pit building antlion species, especially in North America. The difference in antlion diversity

at AMNWR between the sand dune habitats suggests that habitat preferences occur for more than just the pit-building species, and what factors may drive these preferences is unknown.

As expected, our results suggest that sand dune habitats stabilized by a diverse flora will support a greater diversity of antlions. This may be due to greater moisture availability or because diverse resources that create a large breadth of niches to serve as antlion dwellings, hunting grounds, and harbor for prey species. Variation in abundance and richness of antlion species was greater in both sand dune habitats than the non-dune habitats. Although the non-sand dune habitats did not support the greatest number of species, the antlion community in non-sand dune habitats support a unique suite of species that were absent from the sand dune habitats. Again, little is known about the life histories and the biotic or abiotic interactions that impact most North American antlion species. Most studies investigate the habitat preferences, behavior and life history of pit-building species, which represent the minority of species found at AMNWR. Understanding all species within the antlion community is important for identifying the contribution those antlions make to the health of the rest of the biotic community at AMNWR as predators and prey.

Bees

Ninety-six bee species were collected across three habitat types at AMNWR. This is a relatively small number of species compared to the 163 species from 9579 specimens in a Great Basin sand dune complex (Wilson *et al.* 2009), and to a study on the pollinators in adjacent Clark County, Nevada, where nearly 600 bee species were

encountered from over 48,271 specimens (Griswold *et al.* 1999). The number of sand dunes and sampling years in the Great Basin sand dune complex and the number of sampled habitats in Clark County, however, were greater than those sampled at AMNWR. The steepness of the bee species accumulation curve for AMNWR (Fig. 2.1) indicates that increased sampling for bees across all habitats and in more years at AMNWR would reveal the presence of more bee species than were found in this study.

Bee species richness and diversity did not differ between habitats. These results resemble those from the previous study by Toler (2001) in the Great Basin Desert in which the sand dune habitats hosted similar species richness to the non-sand dune habitats. High bee diversity also has been previously associated with sand dunes and mesquite thickets (Simpson *et al.* 1977; Griswold *et al.* 1997), but this was not the case at AMNWR. Golubov *et al.* (1999) identified that in some populations of honey mesquite brush (*Prosopis glandulosa* var. *torreyana*), nearly 50% of individuals do not produce a nectar reward, and the nectarless honey mesquite individuals do not attract as many pollinators as nectar producing individuals. Honey mesquite brush populations at AMNWR were not tested for this lack of nectar production, but many insects, including bees, were observed visiting the mesquite flowers of multiple honey mesquite brush stands by the author.

Although bee species richness and diversity was similar between habitats at AMNWR, the species composition was not the same. Nearly 60% of all bee species collected at AMNWR were unique to a particular habitat, and, thus, the bee communities largely differed between habitats. Similar variability in bee communities has been

observed between different sites of the same habitat type (Wilson *et al.* 2009).

Similarities in bee community composition and beta diversity between sites and habitats have been correlated with floral assemblage similarities between those sites or habitats (Brosi *et al.* 2008; Wilson *et al.* 2009). Each habitat at AMNWR had a relatively unique floral assemblage, which likely explains the differences in bee community composition.

Bee abundance was greater in non-sand dune habitats than in unstabilized sand dune habitats. Higher plant diversity in non-sand dune habitats likely contributed to this difference as few forage options were available in the unstabilized sand dune habitats. Also, some of the most abundant bees in non-sand dune habitats were social or communal in nesting behavior, including honey bees, *Apis mellifera*, and sweat bees, *Agapostemon angelicus* and *Ag. texanus*. Some species of *Dialictus* are also known to exhibit social nesting behaviors; however, this could not be confirmed for the species at AMNWR. The preference for eusocial and communal bees to nest in one habitat over another will greatly increase the number of individuals collected there, which may be the sole reason bee abundance is greater in the non-sand dune habitat than in the unstabilized sand dune habitat. Bee abundance in stabilized sand dune habitats did not significantly differ from either of the other habitats. This is interesting because stabilized sand dune habitats had greater plant diversity than the unstabilized sand dunes and would have been expected to support more individuals.

As several of the endemic and endangered organisms at AMNWR are flowering plants, understanding the pollinator community is important. All three of the habitats at AMNWR supported similar bee richness and diversity, but the species composition

revealed that the variety of bee species occupying each habitat was not similar. Each of the three habitats are important because they contribute to the overall diversity of bees at AMNWR by supporting unique suites of bees. This supports the idea that bee communities are variable due to the differences in floral assemblages between habitats, and likely even between sites (Toler 2001; Brosi *et al.* 2008; Wilson *et al.* 2009). As the bee communities are equally rich and distinct in each habitat, efforts to preserve bee diversity should not prioritize one habitat over another. For the purpose of preserving the pollination systems for the endemic and endangered plants at AMNWR, preservation of the bee communities occurring in the non-sand dune habitats with the endemic and endangered plants are likely most important for the propagation and survival of those plants.

Darkling Beetles

Thirty-four darkling beetle species were found from 2155 specimens collected at AMNWR. This is less than the 46 species found from 14,650 specimens collected at the Nevada Test Site (NTS), which is part of the Great Basin Desert and is about 42 km northeast of AMNWR (Tanner & Packham 1965). However, the NTS study included four years of sampling in seven plant communities with nearly 170 more pitfall traps than were used in this study at AMNWR. The diversity of darkling beetles at the NTS may also be greater due to the presence of species that are endemic to the Great Basin Desert, such as was seen in a comparison of velvet ants between AMNWR and the NTS (see Chapter 3). Thomas (1983) determined that on a global scale, the diversity of darkling beetle species in the Mojave Desert is low. Darkling beetle species richness obtained in

the Thomas (1983) study from the eastern Mojave Desert was similar to beetle species richness at AMNWR, with 32 darkling beetle species found across four habitats with varying plant communities and substrate composition.

Unstabilized sand dune habitats at AMNWR supported greater darkling beetle species richness and diversity than non-sand dune habitats. In the Namib Desert sand dunes, detritivorous species were also most abundant in the least stable sands (Seely & Louw 1980). There are few associations between beetle species distributions and most abiotic or environmental variables (Ahearn 1971; Wallwork 1976; Franco *et al.* 1979; Thomas 1979; 1983; Crawford 1986; Barrows 2000), but darkling beetle species composition has been found to differ between soil types (Thomas 1983; Sheldon & Rogers 1984; Crawford 1986; Ayal & Merkl 1994; Krasnov & Shenbrot 1996) and likely contributes to the difference in species richness and diversity seen for the darkling beetles at AMNWR. Other studies assessing the diversity of surface active arthropods, mostly darkling beetles in habitats with sandy soils, including sand dunes with other non-dune habitats, have also concluded that habitats with sandy soils support greater species richness (Crawford & Seely 1987; Crawford 1988).

Stabilized sand dune habitats did not differ in beetle richness and diversity from either the unstabilized sand dune habitat or the non-sand dune habitat. The reason for this difference at AMNWR is unknown, but Ayal & Merkl (1994) found that habitats with stabilized sandy soils had low species richness and were occupied by several darkling beetle species typically found in habitats with compact soils. The potential for competition to occur between sand obligate species and those non-sand obligate species

may be greater in stabilized sand dune habitats, which could reduce the number of species able to co-exist in the stabilized sand dune habitat. The idea that competition may be reducing the richness and diversity of darkling beetles in stabilized sand dune habitats at AMNWR is supported by the greater abundance of sand dune obligate beetle species, including *Edrotes ventricosus*, *Eussatus muricatus*, *Trogloderus constatus*, *Chilometopon pallidum*, in unstabilized sand dune habitats (Table 2.3). Two of the sand dune obligate species, *Trogloderus constatus* and *Chilometopon pallidum*, were in the top six most abundant species for the unstabilized sand dune habitat (Fig. 2.4).

Total darkling beetle abundance was greater in both sand dune habitats than in non-sand dune habitats. These differences in beetle abundance can also be linked to soil type and have repeatedly been associated with variation in soil moisture (Thomas 1979; Rust 1986; Ayal & Merkl 1994; Barrows 2000). Habitats with deep sandy-soils typically hold more water than other substrates, and subsequently habitats with sandy soils experience higher primary productivity and plant cover (Noy-Meir 1973; Goudie & Wilkinson 1977; Seely 1991). This provides a larger food source as well as shelter for darkling beetles, which are typically very abundant in sand dune habitats (Seely 1991; Fet *et al.* 1998).

The composition of the six dominant darkling beetle species at AMNWR had few similarities between any of the three habitats, and each habitat supported unique species. Beetle diversity significantly differed between sand dune habitats in May, with unstabilized sand dune habitats supporting greater diversity than stabilized sand dune habitats. Beetle abundance was significantly greater in stabilized sand dune habitats in

June and unstabilized sand dune habitats in July than in the non-sand dune habitats.

Darkling beetle activity in the Mojave Desert has been linked to the ephemeral summer rains (Thomas 1979), which may be partly responsible for the increased abundance.

Differences in resource availability may also explain the differences in the timing of peak beetle abundance between the stabilized and unstabilized sand dune habitats.

Most species of darkling beetles at AMNWR appear to have a significant preference for unstabilized sand dune habitats over non-sand dune habitats; thus, management considerations for most darkling beetle species could be focused in the unstabilized sand dune habitat. Each of the three habitats did, however, support a unique suite of species and community structure, and management of darkling beetle diversity should consider all habitats.

Velvet Ants

In the southwestern United States, 29 velvet ant species are known from the Algodones sand dunes and 34 species from the Boyd Deep Canyon Desert Research Center (Pitts *et al.* 2009; 2010). Both of these locations have similar, if not identical, number of species to the 34 velvet ant species found at AMNWR. AMNWR actually supports a total of 42 known species examined in Boehme *et al.* (see Chapter 3), but more locations and sampling events were included in that study than in this one.

At AMNWR, velvet ants had significantly higher species richness in non-sand dune and stabilized sand dune habitats than unstabilized sand dune habitats. Differences in habitat preferences were identified based on soil type for seven velvet ant species at AMNWR (see Chapter 3), but at the community level, species richness differs between

habitats with the same soil type. Velvet ant abundance was also significantly greater in stabilized sand dune habitats than unstabilized sand dune habitats, which provides additional support against soil type as a primary indicator of velvet ant distribution. Both non-sand dune and stabilized sand dune habitats support a greater diversity of plants than the unstabilized sand dune habitat, which may impact velvet ants' host distribution. Bees are potential hosts for velvet ants, and at AMNWR they were also more abundant in non-sand dune habitats than unstabilized sand dune habitats (Fig. 2.2 c). Greater plant cover and diversity in non-sand dune and stabilized sand dune habitats may provide more nesting sites for velvet ant hosts in the form of stable soils for soil nesting species and more plant twigs and stems for cavity nesters.

Velvet ant diversity was similar between all habitats. This was reflected in velvet ant community composition with all habitats having multiple dominant species in common; only the non-sand dune habitat supported unique species. This supports the current opinion that velvet ants are largely generalists in their host choice (Brothers 1989; Pitts *et al.* 2004).

Velvet ants at AMNWR are least speciose and abundant in unstabilized sand dune habitats. While some velvet ant species prefer different soil types to others (see Chapter 3), most species are indifferent to soil type and may be influenced by other variables such as plant cover or diversity and host diversity. Velvet ant life history is still poorly understood, and more research is needed to explain their distributions in any habitat.

Conclusion

This basic inventory of antlions, bees, darkling beetles, and velvet ants that occur at AMNWR revealed that the number of antlion, darkling beetle, and velvet ant species were similar to the number of species found in other studies (Thomas 1983; Güsten 2002; Saji & Whittington 2008; Pitts *et al.* 2009; 2010). The number of bee species found at AMNWR, however, was much lower than other studies in similar, but larger, desert sites. As bees are very diverse within and between habitats, the restriction of sampling to select sand dune and non-sand dune habitats at AMNWR excluded many other habitats that are likely occupied by unique bee communities. The bee species accumulation curve also indicates more species are expected to occur at the refuge. With additional sampling in other habitats, more bee species are expected to be found.

The results of the habitat comparison revealed that the variation in richness, diversity, and abundance between habitats was unique for each insect group. The only similarities were for bee and velvet ant diversity and antlion and beetle abundance. Both bees and velvet ants exhibited equal diversity across all habitat types, and abundance for both antlions and darkling beetles was greater in both sand dune habitats over non-sand dune habitats. Species composition and the number of unique species in each habitat for bees and velvet ants revealed that, although the diversity appeared the same between habitats, the variety of bee species greatly differed between habitats for bees and nearly 60% of species were unique to one habitat. The opposite was true for velvet ants that had no unique species in either sand dune habitats and whose species composition was similar between all habitats.

Previous investigations of sand dune invertebrate fauna have found that most invertebrates occupying sand dune habitats are carnivores and detritivores (Rust 1986; Holm & Scholtz 1980; Crawford & Seely 1987; Seely & Louw 1980; Seely 1991). The similarity in the abundance between habitats at AMNWR for predatory antlions and detritivorous darkling beetles follows the same trend. The diversity of antlions and darkling beetles at AMNWR were greatest in different sand dune habitats, with darkling beetles having the greatest diversity in the unstabilized sand dune habitat. Proportions of detritivorous and carnivorous species in the northern Namib Desert similarly differed between habitats, with detritivorous species occurring in the least stable sand habitats (Crawford & Seely 1987; Seely & Louw 1980).

Overall, each insect group was distributed differently between the three habitat types, making each habitat important for at least one of the insect groups. For each of these insect groups, both sand dune habitats hosted levels of diversity equal to, or greater than, the diversity in non-sand dune habitats at the refuge. Sand dune habitats are important for supporting insect biodiversity at AMNWR, but the species found in those habitats do not always include other species found only in non-sand dune habitats.

The conservation and protection of endemic, endangered and rare organisms is the purpose for the founding of AMNWR (U.S. Fish and Wildlife Service 2009). Insects are an important resource for ecosystem health and the health of those endemic and endangered organisms, and this study shows that sand dunes play an important role in shaping insect communities. However, as each insect group was distributed uniquely in the different habitat types non-sand dune habitats are also important. The looming threat

of loss of the aquatic habitats at AMNWR will undoubtedly impact the terrestrial systems on the refuge both directly and indirectly. Insects are good bioindicators and as changes are inevitable for AMNWR understanding the distribution of the terrestrial insect communities, such as antlions, bees, darkling beetles, and velvet ants at AMNWR will aid in future management decisions aimed at preserving insect biodiversity and evaluating the impacts and interactions of these species with those endemic and endangered organisms at AMNWR.

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CHAPTER 3

FAUNAL STUDY OF VELVET ANTS (HYMENOPTERA: MUTILLIDAE) AND
THEIR ACTIVITY PATTERNS AND HABITAT PREFERENCE AT ASH
MEADOWS NATIONAL WILDLIFE REFUGE, NYE COUNTY, NEVADA, USA¹**Abstract**

The diversity of velvet ants at Ash Meadows National Wildlife Refuge (AMNWR) is investigated along with seasonal flight time and habitat preference for each species. Of the 45 ($SD \pm 2$) species expected to occur at AMNWR via first order jackknife estimator, 42 species were found to occur based on 8843 specimens. Variation in flight times between species were minor and revealed a unique pattern of niche partitioning in only one species, *Dasymutilla arenivaga* Mickel. Habitat preferences were observed for seven species at AMNWR. *Dasymutilla arenivaga*, *Odontophotopsis melicausa* (Blake), and *Sphaerophthalma orestes* (Fox) were found to be more abundant in sand dune habitats than in non-sand dune habitats. While four other species, *Odontophotopsis mamata* Schuster, *O. microdonta* Ferguson, *O. serca* Viereck, and *Sphaerophthalma mendica* (Blake), were found to be more abundant in non-sand dune habitats. The diversity of velvet ants found at AMNWR was compared to the diversity of velvet ants found at the Nevada Test Site (NTS) located approximately 25 miles northeast of Ash Meadows. This comparison identified six velvet ant species that occurred at the

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NTS, but were not found at AMNWR. Diagnoses and a key are provided for the velvet ants of AMNWR. The hitherto unknown female of *Sphaerophthalma megagnathos* Schuster is described, and an updated key to the females is provided for *S. imperialis* species-group. Lectotypes are designated for twelve species.

Introduction

Ash Meadows National Wildlife Refuge (AMNWR) is located approximately 90 miles northwest of Las Vegas in the Amargosa Valley of southern Nye County, Nevada, and encompasses 93 square km of land in the Mojave Desert at the southern edge of the Great Basin Desert with over 30 seeps and springs (U.S Fish and Wildlife Service 2011). This creates a unique combination of spring fed wetland habitats surrounded by alkaline desert upland. Because of these varied habitats, AMNWR supports at least 25 endemic plants and animals and for its area is considered to have the second greatest concentration of endemic species in the United States, based on plants and fish.

One group of insects containing species endemic to the deserts of North America are velvet ants or mutillid wasps (Hymenoptera). Females parasitize the mature larval or pupal stages of holometabolous insects with most known hosts being aculeate Hymenoptera (Brothers *et al.* 2000). A female velvet ant spends much of her time presumably underground in pursuit of her hosts, and in many areas females are less frequently encountered than males. Male velvet ants are more often encountered, especially in flight as they search for emerging females. Less is known about the nocturnal species due primarily to their being active at night.

Only sparse natural history information is known for most species of velvet ants. Many of the known hosts of velvet ants in the deserts of the USA are habitat specialists. For example, *Microbembex nigrifrons* (Provancher), a host of *Dasymutilla gloriosa* (de Saussure), typically nests in sandy soils, such as those found on sand dunes (Krombein 1979; Evans & O'Neill 2007). Current opinion of host selection in velvet ants also suggests that a single species of velvet ant can prey upon a variety of host species and likely selects a host based on life stage and size at the time of the encounter (Brothers 1989). Host range for a single species can be broad. For example, females of the nocturnal velvet ant, *Sphaerophthalma amphion* (Fox), were reared from 27 different host species in two orders, Diptera and Hymenoptera (Pitts *et al.* 2004). With the limited dispersal abilities of female velvet ants, it would be advantageous to be generalized in host selection, but within a community of multiple velvet ant species the competitive exclusion principle indicates that some form of niche differentiation must restrict each species in order for all species to coexist. Thus, host use could be differentiated by factors other than host species. To date the limited knowledge of host use and most other natural history traits in velvet ants have never identified what forms of niche differentiation are contributing to a velvet ant community.

The objectives of this study are to determine what species of velvet ants exist at AMNWR, to provide a means for identifying those species using diagnoses and keys, and to identify preferences of velvet ant species for sand dune versus non-sand dune habitats. I associate the sexes of *Sphaerophthalma megagnathos* Schuster and describe the female. This is the only species in the *S. imperialis* species-group that was known only for one

sex (Pitts 2006). I provide an updated key for the females of the *S. imperialis* species-group. I also discuss the potential for additional species to be found on the refuge and speculate on which additional species may occur there by the comparison of the AMNWR species and those species found at the NTS (Ferguson 1967, Allred 1973). This comparison is also made to better understand what species are restricted to a given desert.

The NTS, located approximately 25 miles northeast of AMNWR, lies on the border between the Great Basin Desert and the Mojave Desert (Ferguson 1967, Allred 1973). The Mojave Desert is a warm desert, while the Great Basin Desert is a cold desert (MacMahon 2000, West & Young 2000). Due to the high variability in temperatures, elevation, geology and precipitation between the Great Basin Desert and Mojave Desert, many distributions of flora and fauna are restricted to one desert or the other. For example, creosote bush (*Larrea tridentata*) is common in the Mojave Desert, but is not found in the Great Basin Desert. The predominate vegetation in the Great Basin Desert is big sagebrush (*Artemisia tridentata*), which is mostly absent in the Mojave Desert (Billings 1951, Beatley 1975). Other organisms including multiple species of birds, reptiles and mammals are also restricted by this boundary (Hall 1946, Behle 1978, Stebbins 1985). The transition zone between these two desert types can be observed at the NTS as the southern portion of the NTS is dominated by creosote brush while the northern portion of the NTS lacks creosote (Allred 1973). Through a comparison of the diversity of velvet ants from the NTS with those found at AMNWR, I would expect to observe differences in velvet ant diversity between sites due to those climatic conditions

that are known to restrict some species. The NTS is expected to have the greatest diversity because both Mojave and Great Basin adapted species would be present.

Materials and Methods

Field work occurred at AMNWR from April 2008 to December 2009. Collections were made at 16 sites across the refuge. Specimens were collected by hand or net, and with light traps (LT), malaise traps (MT) and pitfall traps (PT). Attempts to catch females by hand were made monthly throughout the collecting period, while attempts to collect males with light traps were made bi-monthly when the nighttime temperatures were above 0°C. Hand collections, using forceps, a sieve or an empty vial, were made upon encounter with a specimen. Thirty-six pitfall traps were placed across 12 sites in late June 2008 with three pitfall traps per site. Due to excessive disturbance by wildlife and a modification in experimental design, pitfall traps were relocated across 10 sites and the trap structure modified in late October 2008. Four more pitfall traps were implemented bringing the total number of pitfall traps to 40 with four traps per site. Traps were left open continually and their contents collected every four weeks. All pitfall traps were removed in December 2009. Light traps were run 18 times throughout 2008. In 2009, light traps were run overnight one trap at each of the 10 specified sites once every other week from April 2009, when nighttime temperatures sometimes rose above 0°C to the beginning of November when temperatures again declined and male activity ceased. All specimens collected at AMNWR are deposited in the Department of Biology Insect Collection, Utah State University, Logan, UT (EMUS). Acronyms for collectors of velvet

ants in AMNWR are: NFB—N.F. Boehme, SDB—S.D. Boehme, DAT—D.A. Tanner, and JPP—J.P. Pitts.

Acronyms for collections from which specimens were borrowed are:

ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

BMNH —The Natural History Museum, London, United Kingdom.

CASC—Department of Entomology, California Academy of Sciences, San Francisco, California, USA.

CNCI—Canadian National Collection of Insects, Ottawa, Canada.

CUIC—Cornell University, Ithaca, New York, USA.

EMUS—Department of Biology Insect Collection, Utah State University, Logan, Utah, USA.

MNHN—Muséum National d'Histoire Naturelle, Paris, France.

NMNH—National Museum of Natural History, Washington D.C., USA.

SEMC—Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

UMIC—University of Mississippi, University, Mississippi, USA.

UMSP—University of Minnesota Insect Collection, St. Paul, Minnesota, USA.

Of the 16 localities sampled throughout the refuge, only 10 localities were used in determining habitat preference. This is because collecting methods were consistent across these locations. The 10 localities that were used in determining habitat preference include **Non-dune site 1**: Non-dune tree and grass site northwest of Point of Rocks road 0.8 km from the junction with Ash Meadows road and Spring Meadows drive (11s 0563176

4029978), **Non-dune site 2:** Non-dune salt soil site southeast of Point of Rocks road 0.7 km from junction with Ash Meadows road and Spring Meadows drive (11s 0563204 4029801), **Non-dune site 3:** Non-dune salt soil site 0.21 to 0.39 km south of an unnamed road connecting Peterson reservoir road to Longstreet springs road (11s 0559092 4034754), **Non-dune site 4:** Isolated salt brush dominated area 0.59 to 0.64 km south of an unnamed road connecting Peterson reservoir road to Longstreet springs road (11s 0559024 4034705), **Non-dune site 5:** School Springs area 0.1 to 0.31 km from an unnamed road to School Springs and 0.75 km from the junction of the same unnamed road with Spring Meadows drive (11s 0561614 4030973), **Sand dune site 1:** Creosote brush dominated sand dune 0.28 km from Peterson reservoir road and 1.41 km from the junction with Spring Meadows drive (11s 0558238 4032743), **Sand dune site 2:** Horseshoe marsh/ Crystal reservoir salt brush dominated sand dunes 1.28 km down the road south of the gate at the southwest corner of Horseshoe marsh loop the dunes are at the end of the road (11s 0559112 4028705), **Sand dune site 3:** Horseshoe marsh/ Crystal reservoir mesquite brush dominated sand dunes 1.28 km down the road south of the gate at the southwest corner of Horseshoe marsh loop and the dunes are 0.2 km west to 0.45 km northwest from the end of the road (11s 0558927 4028767), **Sand dune site 4:** Mesquite brush dominated sand dune on the south side of Spring meadows drive 0.1 km from junction with Peterson reservoir road (11s 0558407 4031016), and **Sand dune site 5:** Peterson reservoir sand dune 0.31 west to 0.75 km southwest of the parking lot at the reservoir (11s 0557875 4033237). The remaining six sites sampled were **Copeland site:** Mesquite brush dominated area located on either side of Bill Copeland memorial road

and 3.02 km from the junction with Ash Meadows road on the refuge (11s 0565573 4027785), **Spring meadows site**: Salt brush dominated sand dune on the north side of Spring meadows drive and 0.1 km from the junction with Peterson reservoir road (11s 0558282 4032462), **Mesquite site 1**: Mesquite brush dominated area on either side of Ash Meadows road and 5.25 km from the junction with Bell Vista road (11s 0562550 4027620), **Mesquite site 2**: Mesquite brush dominated sand dune 1 km west of Ash Meadows road and 4.8 km from the junction with Bell Vista road (11s 0561625 4026977), **Mesquite site 3**: Mesquite brush dominated sand dune 1.81 km from Ash Meadows road and 4.8 km from junction with Bell Vista road (11s 0560821 4026823), and the **Wash site**: a drainage wash located north of the refuge office.

For identifications, all specimens were examined with a Wild M-5 stereomicroscope, and all measurements were made with an ocular micrometer. Mandibular ratios were calculated by dividing the width at the ventral tooth, the excision after the ventral tooth, and the greatest apical width by the width at the base of the mandibles. Male genitalia were dissected from the specimens by using minuten pins and placed in genitalia capsules with glycerin. Genitalia were observed with a light microscope and illustrated using a camera lucida.

I use the term "simple setae" for setae that are smooth and do not have barbed surfaces. "Brachyplumose setae" refers to setae with barbs that are less than or equal to the diameter of the shaft at the attachment of the barb. "Plumose setae" have longer barbs. I use the abbreviations T2, T3, etc., to denote the second, third, etc., metasomal terga while S2, S3, etc., denote the second, third, etc., metasomal sterna. The digitus or cuspis

length relative to the free paramere length is used in here to quantify differences in genitalic structure. For ease of comparison and to facilitate identification without dissecting the genitalic capsule, the cuspis, digitus, and paramere measurements are taken from the apical margin of the basal paramere lobe in dorsal view to the apex of each respective structure. This method facilitates making all measurements from the dorsal view.

A species accumulation curve was created using the program Species Diversity and Richness IV with 100 random selections of sample order (Seaby & Henderson 2006). The data were organized by the abundance of each species collected per sampling event. A single sampling event consisted of one collection event with one type of trap. An example of a single sampling event could include a light trap that was used over one night. An estimate of species richness for AMNWR based on the number of species collected per sampling event was calculated using the non-parametric first order jackknife estimator with 100 random selections of sample order (Seaby & Henderson 2006). The estimate was then plotted against the species accumulation curve.

Only male seasonal activity is reported, because males were collected more consistently than females, and females are long lived and may not have a specific season of activity, but are most active during warmer parts of the year. Dates of female collection at AMNWR are included for species whose females are known and were found at AMNWR. Male seasonal activity was analyzed for bi-monthly samples by identifying presence or absence of a species. Seasons were designated as spring from mid-March to

mid-June, summer from mid-June to mid-September, autumn from mid-September to mid-December, and winter from mid-December to mid-March.

To identify habitat preference, a comparison of each species' abundance, pooled over all sampling dates for each site, for sand dune and non-sand dune habitats in 2009 via light trapping was performed using the two-tailed Mann-Whitney test under the null hypothesis that there was no difference in the abundance of a species collected in sand dune and non-sand dune habitats. Samples were pooled for all sampling dates for each site, and sites were divided into sand dune and non-sand dune habitats. If this null hypothesis was rejected ($P \leq 0.05$), the habitat with the greatest number of individuals was identified as the preferred habitat for a species.

I have studied the original NTS velvet ant specimens from Ferguson's (1967) study. Some were left unidentified or thought to be new species by Ferguson. I identified those specimens left unidentified by Ferguson. Those specimens he thought were new species were described by Mickel (Mickel & Clausen 1983). I have studied them as well. All these specimens are accounted for here except for those of *Dasymutilla gloriosa*.

Results

There were 42 species of velvet ants collected at AMNWR in 2008 and 2009 totaling 8843 specimens (Table 3.1). According to the first order jackknife estimator, 45 ($SD \pm 2$) species are expected to occur at AMNWR (Fig. 3.1). *Odontophotopsis clypeata* Schuster (n=2532) and *Sphaerophthalma orestes* (Fox) (n=1163) are the most abundant of all the species found at the refuge (Table 3.1). The rarest species, those with less than 10 individuals found throughout the course of the study, include *Acanthophotopsis*

falciformis Schuster (9), *Dasymutilla pseudopappus* (Cockerell) (8), *O. setifera* Schuster (7), *S. nana* (Fox) (7), *S. angulifera* Schuster (5), *D. satanas* Mickel (4), *O. aufidia* Mickel (4), *O. quadrispinosa* Schuster (4), *O. biramosa* Schuster (3), *D. chisos* Mickel (1), *O. armata* Schuster (1), *S. amphion* (1), *S. edwardsii* (Cresson) (1), *S. macswaini* Ferguson (1). Three of these species, *A. falciformis*, *S. macswaini*, and *O. setifera*, were also considered rare according to surveys of the NTS (Ferguson 1967).

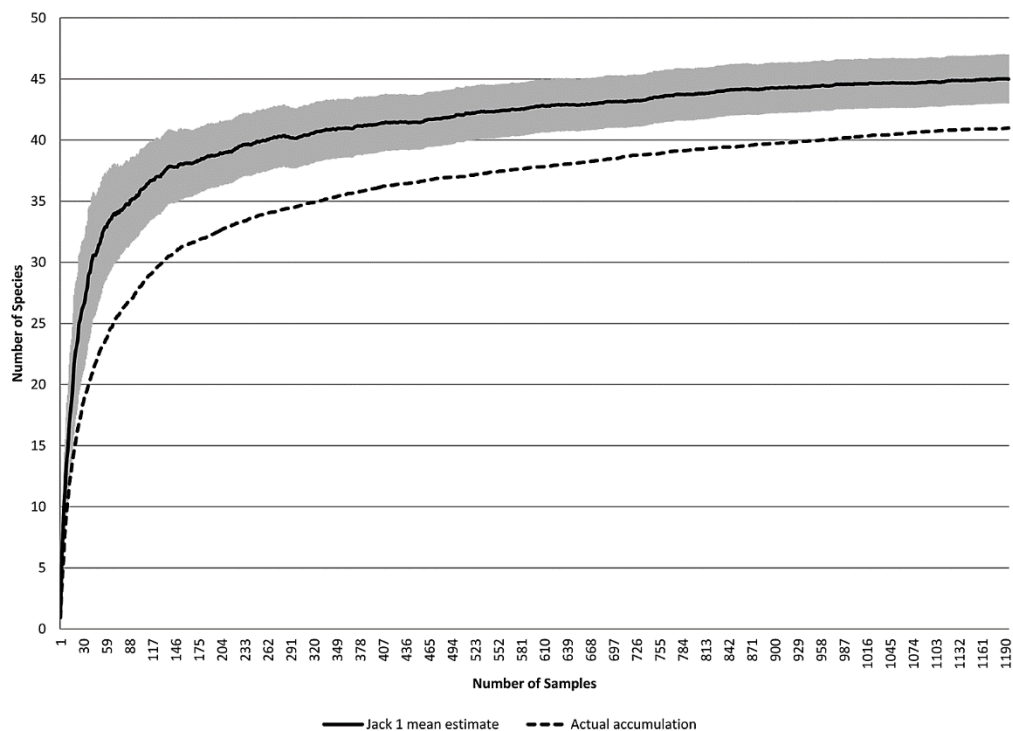


Figure 3.1. Species accumulation curve (dotted-line) and the estimated species accumulation via the first order jackknife estimator (solid-line), with standard deviation (gray area), for velvet ants of Ash Meadows National Wildlife Refuge.

Seasonal activity of all male velvet ants occurred from mid-spring through mid-autumn (late April through October in 2008 and 2009) (Fig. 3.22). Nearly every species began flying in May and persisted throughout the season for variable amounts of time, with the exception of *D. arenivaga*, which was first collected in July. With the

incorporation of abundance to each species activity times, variation in peak abundance is apparent. Species specific variation based on seasonal abundance will not be analyzed here as only one year of data is available. Those species found throughout the whole season typically had the greatest abundance.

Table 3.1. Velvet ant total abundance by species at Ash Meadows National Wildlife Refuge.

| Species | Abundance AMWR | | | | Abundance NTS |
|-------------------------------------|----------------|------|--------|--------------|---------------|
| | Total | Male | Female | Relative (%) | Relative (%) |
| <i>Odontophotopsis clypeata</i> | 2532 | 2375 | 157 | 28.63 | 1.29 |
| <i>Sphaerophthalma orestes</i> | 1163 | 965 | 198 | 13.15 | 0.00 |
| <i>Odontophotopsis melicausa</i> | 724 | 558 | 166 | 8.19 | 2.95 |
| <i>Odontophotopsis inconspicua</i> | 567 | 567 | 0 | 6.41 | 2.49 |
| <i>Sphaerophthalma difficilis</i> | 534 | 522 | 12 | 6.04 | 2.49 |
| <i>Sphaerophthalma becki</i> | 488 | 488 | 0 | 5.52 | 1.66 |
| <i>Sphaerophthalma triangularis</i> | 432 | 395 | 37 | 4.89 | 0.00 |
| <i>Sphaerophthalma uro</i> | 397 | 393 | 4 | 4.49 | 0.00 |
| <i>Odontophotopsis mamata</i> | 303 | 303 | 0 | 3.43 | 13.92 |
| <i>Sphaerophthalma arota</i> | 212 | 212 | 0 | 2.40 | 0.09 |
| <i>Sphaerophthalma blakeii</i> | 194 | 189 | 5 | 2.19 | 0.46 |
| <i>Dilophotopsis concolor</i> | 156 | 156 | 0 | 1.76 | 0.09 |
| <i>Odontophotopsis acmaea</i> | 130 | 130 | 0 | 1.47 | 0.00 |
| <i>Sphaerophthalma mendica</i> | 125 | 122 | 3 | 1.41 | 19.82 |
| <i>Odontophotopsis microdonta</i> | 119 | 119 | 0 | 1.35 | 10.32 |
| <i>Odontophotopsis sonora</i> | 106 | 106 | 0 | 1.20 | 15.02 |
| <i>Sphaerophthalma megagnathos</i> | 96 | 68 | 28 | 1.09 | 0.00 |
| <i>Sphaerophthalma marpesia</i> | 95 | 92 | 3 | 1.07 | 0.00 |
| <i>Sphaerophthalma yumaella</i> | 92 | 92 | 0 | 1.04 | 0.92 |
| <i>Dasymutilla arenivaga</i> | 70 | 62 | 8 | 0.79 | 0.00 |
| <i>Odontophotopsis piute</i> | 52 | 52 | 0 | 0.59 | 0.37 |
| <i>Dilophotopsis paron</i> | 47 | 47 | 0 | 0.53 | 0.28 |
| <i>Sphaerophthalma pallida</i> | 42 | 42 | 0 | 0.47 | 0.65 |
| <i>Odontophotopsis serca</i> | 37 | 37 | 0 | 0.42 | 1.47 |
| <i>Odontophotopsis bellona</i> | 33 | 33 | 0 | 0.37 | 0.00 |
| <i>Dasymutilla gloriosa</i> | 19 | 0 | 19 | 0.21 | 0.65 |
| <i>Odontophotopsis parva</i> | 11 | 0 | 11 | 0.12 | 0.00 |

| Species | Abundance AMWR | | | | Abundance NTS |
|--------------------------------------|----------------|------|--------|--------------|---------------|
| | Total | Male | Female | Relative (%) | Relative (%) |
| <i>Sphaerophthalma parkeri</i> | 11 | 11 | 0 | 0.12 | 0.00 |
| <i>Acanthophtopsis falciformis</i> | 9 | 9 | 0 | 0.10 | 0.74 |
| <i>Dasymutilla pseudopappus</i> | 8 | 0 | 8 | 0.09 | 0.00 |
| <i>Odontophotopsis setifera</i> | 7 | 7 | 0 | 0.08 | 0.18 |
| <i>Sphaerophthalma nana</i> | 7 | 7 | 0 | 0.08 | 1.84 |
| <i>Sphaerophthalma angulifera</i> | 5 | 0 | 5 | 0.06 | 1.94 |
| <i>Dasymutilla satanas</i> | 4 | 0 | 4 | 0.05 | 4.24 |
| <i>Odontophotopsis aufidia</i> | 4 | 4 | 0 | 0.05 | 0.00 |
| <i>Odontophotopsis quadrispinosa</i> | 4 | 4 | 0 | 0.05 | 3.23 |
| <i>Odontophotopsis biramosa</i> | 3 | 3 | 0 | 0.03 | 0.00 |
| <i>Dasymutilla chisos</i> | 1 | 1 | 0 | 0.01 | 0.00 |
| <i>Odontophotopsis armata</i> | 1 | 1 | 0 | 0.01 | 4.79 |
| <i>Sphaerophthalma amphion</i> | 1 | 1 | 0 | 0.01 | 0.92 |
| <i>Sphaerophthalma edwardsii</i> | 1 | 0 | 1 | 0.01 | 0.00 |
| <i>Sphaerophthalma macswaini</i> | 1 | 1 | 0 | 0.01 | 0.18 |

Habitat preferences were assigned if a species was collected significantly more often in sand dune, collected significantly more often in non-sand dune, collected uniformly over sand dune and non-sand dune habitats, or too rarely encountered to determine preference (Table 3.2). *Dasymutilla arenivaga* Mickel, *O. melicausa* (Blake), and *S. orestes* were found to be significantly more abundant in sand dune habitats ($U \geq 23$, $P < 0.05$). *Odontophotopsis mamata* Schuster, *O. microdonta* Ferguson, *O. serca* Viereck, and *S. mendica* (Blake) were found to be significantly more abundant in non-sand dune habitats ($U \geq 23$, $P < 0.05$). *Dilophotopsis concolor* (Cresson), *D. paron* (Cameron), *O. acmaea* Schuster, *O. bellona* Mickel, *O. clypeata*, *O. inconspicua* (Blake), *O. piute* Mickel, *O. sonora* Schuster, *S. arota* (Cresson), *S. becki* Ferguson, *S. blakeii* (Fox), *S. difficilis* (Baker), *S. marpesia* (Blake), *S. megagnathos*, *S. pallida* (Blake), *S. triangularis*

(Blake), *S. uro* (Blake), and *S. yumaella* Schuster were all uniformly abundant over sand dune and non-sand dune habitats ($U < 23$, $P > 0.05$). The 17 remaining species collected at AMNWR were too rarely encountered to determine a habitat preference.

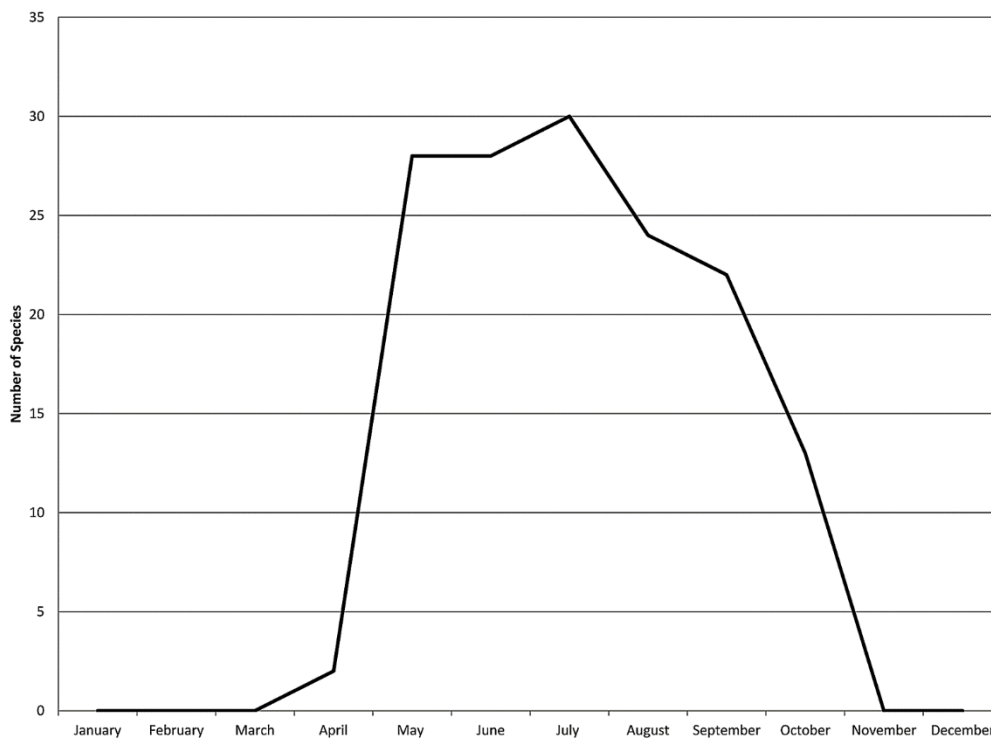


Figure 3.22. Number of velvet ant species found per month for the 2008 and 2009 field seasons.

Thirty-four velvet ant species were found at the NTS throughout the course of a four year survey from 1960 to 1964 (Ferguson 1967, Allred 1973). Six species were found at the NTS that were not found at AMNWR. I suggest that some of the six species could make up the difference between the observed and expected number of species for AMNWR. The six species include *Acrophotopsis dirce* (Fox, 1899) (referred to as *A. eurygnathus* Schuster, 1958), *Dasymutilla monticola* (Cresson, 1865) (referred to as *D. paenulata* Mickel, 1928), *S. ferruginea* (Blake, 1879), *S. parapenalis* Ferguson, 1967, *O.*

cassia Mickel in Mickel & Clausen, 1983 (misidentified by Ferguson (1967) as *O. cookii* Baker, 1905), and *O. obliqua* Viereck, 1924. Of these species *D. monticola* and *S. parapenalis* are known to occur throughout the southwestern United States, *A. dirce* have been found in the Sonoran and Mojave deserts, *S. ferruginea* is also known from the Mojave Desert, and *O. obliqua* is known from the Sonora, Mojave and Great Basin deserts and north into Canada. With the distributions of these five species including the Mojave Desert I would expect to find these species with additional sampling on AMNWR. I do not expect to find *O. cassia* at AMNWR as it seems to be endemic to the Great Basin Desert. Fifteen species were found at AMNWR that were not found at the NTS including *Dasymutilla arenivaga*, *D. chisos*, *D. pseudopappus*, *O. acmaea*, *O. aufidia*, *O. bellona*, *O. biramosa*, *O. parva* Schuster, *S. edwardsii*, *S. marpesia*, *S. megagnathos*, *S. orestes*, *S. parkeri* Schuster, *S. triangularis*, and *S. uro*. Only five of these species were considered rare in our study (Table 3.2).

***Acanthophtopsis falciformis* Schuster, 1958**

Acanthophtopsis falciformis falciformis Schuster, 1958: 108, ♂. Holotype:

California, Palm Springs (UMIC).

Acanthophtopsis falciformis furcisterna Schuster, 1958: 111, ♂. Holotype: Arizona,

Tucson (UMIC).

Diagnosis. MALE. This species is easily distinguished from other nocturnal velvet ants by the presence of a fourth mandibular tooth, which is found along the internal margin and projects posteriorly over the apex of the clypeus (see Tanner *et al.* 2009: Fig. 6). This species also has 1) the dorsal carina of the mandible extending from the base of the

mandible to the innermost tooth; 2) the base of the clypeus slightly raised, although it is neither carinate nor tuberculate and is not horizontally produced; 3) the frons coarsely punctate while the vertex moderately punctate; 4) the length of flagellomere 1 is $2 \times$ its width; 5) the head behind the eyes strongly convergent; 6) the length of the stigma slightly shorter ($\sim 0.8 \times$) than the length of the marginal cell along the costa; and 7) the paramere in lateral view equally broad throughout its length except for the apex, which narrows to an acute angle, and the paramere is as broad as the cuspis medially (see Pitts *et al.* 2009: Fig. 1). FEMALE. Unknown.

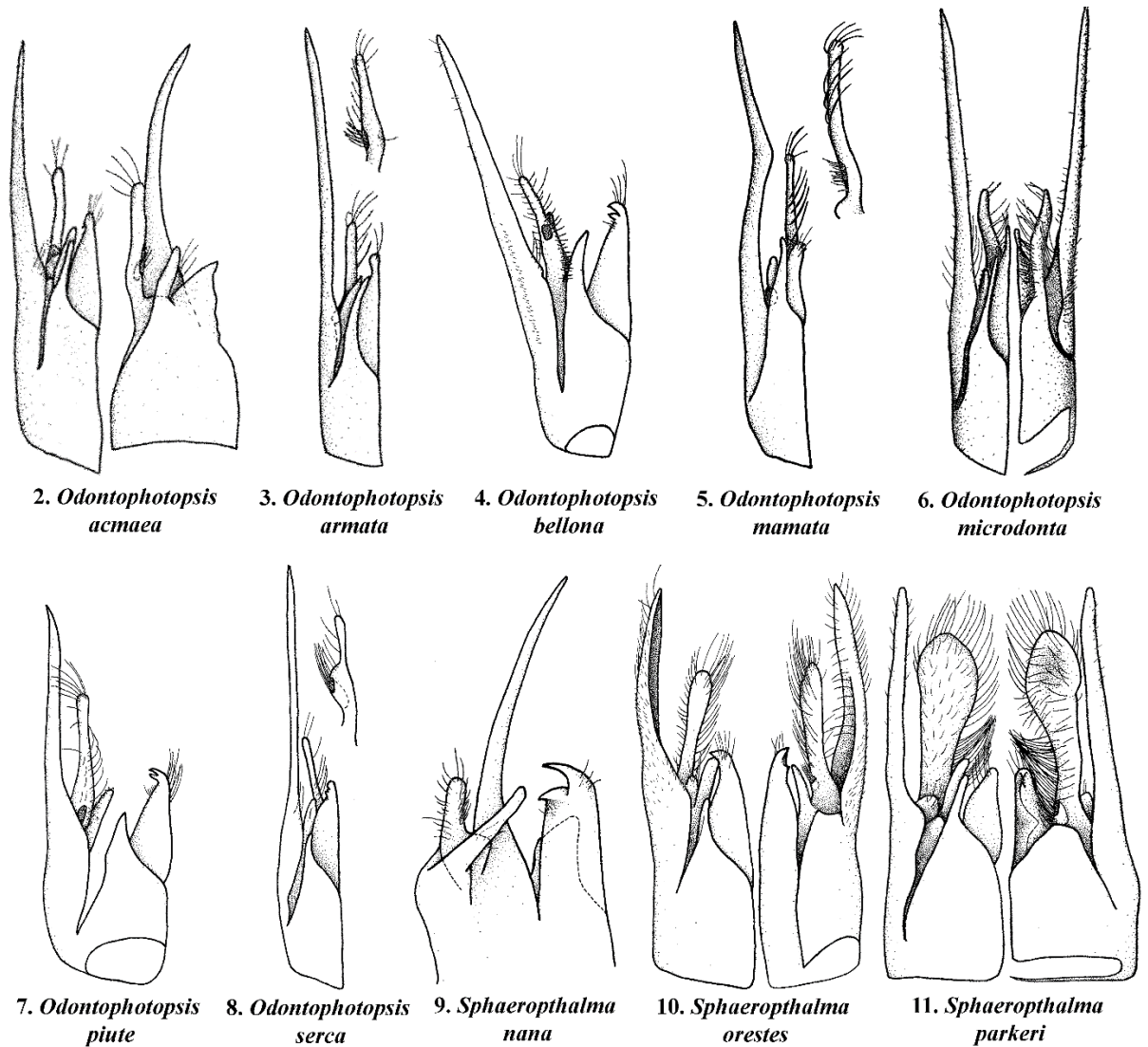
Table 3.2. Velvet ant habitat preference by species for Ash Meadows National Wildlife Refuge.

| Species | Abundance | | Mann-Whitney test (U) | p-value | Habitat preference ¹ |
|------------------------------------|-----------|-----------|-----------------------|---------|---------------------------------|
| | Non-dune | Sand dune | | | |
| <i>Acanthophtopsis falciformis</i> | 9 | 0 | 17.5 | p>0.2 | Rare |
| <i>Dasymutilla arenivaga</i> | 6 | 48 | 24.5 | p=0.015 | Sand dune |
| <i>Dasymutilla chisos</i> | - | - | - | - | Rare |
| <i>Dasymutilla gloriosa</i> | - | - | - | - | Rare |
| <i>Dasymutilla pseudopappus</i> | - | - | - | - | Rare |
| <i>Dasymutilla satanas</i> | - | - | - | - | Rare |
| <i>Dilophotopsis concolor</i> | 90 | 53 | 16 | p>0.2 | Uniform |
| <i>Dilophotopsis paron</i> | 25 | 8 | 21.5 | p>0.05 | Uniform |
| <i>Odontophotopsis acmaea</i> | 28 | 95 | 20 | p=0.2 | Uniform |
| <i>Odontophotopsis armata</i> | 1 | 0 | 15 | p>0.2 | Rare |
| <i>Odontophotopsis aufidia</i> | 4 | 0 | 17.5 | p>0.2 | Rare |
| <i>Odontophotopsis bellona</i> | 18 | 6 | 19 | p>0.2 | Uniform |
| <i>Odontophotopsis biramosa</i> | 3 | 0 | 17.5 | p>0.2 | Rare |
| <i>Odontophotopsis clypeata</i> | 841 | 1284 | 15 | p>0.2 | Uniform |
| <i>Odontophotopsis inconspicua</i> | 339 | 222 | 13 | p>0.2 | Uniform |
| <i>Odontophotopsis mamata</i> | 269 | 8 | 25 | p=0.01 | Non-dune |
| <i>Odontophotopsis melicausa</i> | 138 | 348 | 23 | p=0.05 | Sand dune |
| <i>Odontophotopsis microdonta</i> | 111 | 3 | 24 | p=0.02 | Non-dune |
| <i>Odontophotopsis parva</i> | - | - | - | - | Rare |
| <i>Odontophotopsis piute</i> | 6 | 32 | 18 | p>0.2 | Uniform |

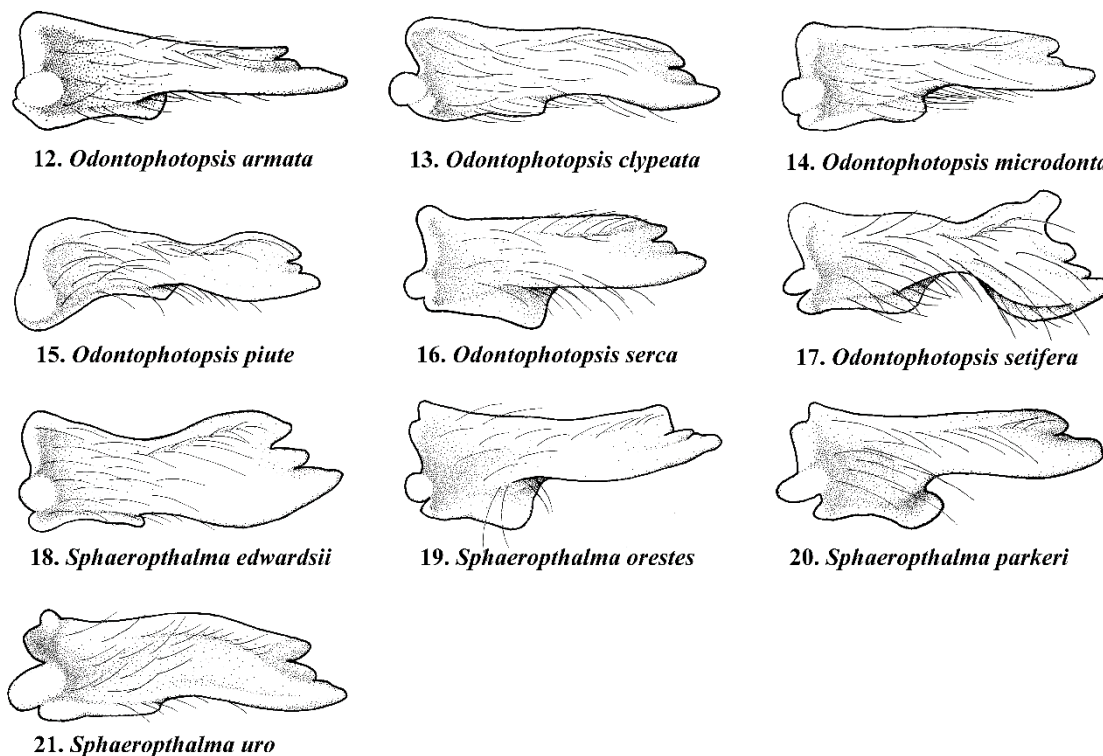
| Species | Abundance | | Mann-Whitney test (U) | p-value | Habitat preference ¹ |
|--------------------------------------|-----------|-----------|-----------------------|---------|---------------------------------|
| | Non-dune | Sand dune | | | |
| <i>Odontophotopsis quadrispinosa</i> | 2 | 0 | 15 | p>0.2 | Rare |
| <i>Odontophotopsis serca</i> | 32 | 1 | 24 | p=0.02 | Non-dune |
| <i>Odontophotopsis setifera</i> | 3 | 2 | 13.5 | p>0.2 | Rare |
| <i>Odontophotopsis sonora</i> | 12 | 85 | 18 | p>0.2 | Uniform |
| <i>Sphaerophthalma amphion</i> | 1 | 0 | 15 | p>0.2 | Rare |
| <i>Sphaerophthalma angulifera</i> | - | - | - | - | Rare |
| <i>Sphaerophthalma arota</i> | 94 | 73 | 16 | p>0.2 | Uniform |
| <i>Sphaerophthalma becki</i> | 134 | 311 | 13.5 | p>0.2 | Uniform |
| <i>Sphaerophthalma blakeii</i> | 76 | 51 | 19 | p>0.2 | Uniform |
| <i>Sphaerophthalma difficilis</i> | 202 | 273 | 18 | p>0.2 | Uniform |
| <i>Sphaerophthalma edwardsii</i> | - | - | - | - | Rare |
| <i>Sphaerophthalma macswaini</i> | 1 | 0 | 15 | p>0.2 | Rare |
| <i>Sphaerophthalma marpesia</i> | 23 | 59 | 20 | p=0.2 | Uniform |
| <i>Sphaerophthalma megagnathos</i> | 15 | 2 | 20.5 | p>0.1 | Uniform |
| <i>Sphaerophthalma mendica</i> | 115 | 7 | 24 | p=0.02 | Non-dune |
| <i>Sphaerophthalma nana</i> | 5 | 2 | 17 | p>0.2 | Rare |
| <i>Sphaerophthalma orestes</i> | 79 | 699 | 25 | p=0.01 | Sand dune |
| <i>Sphaerophthalma pallida</i> | 30 | 11 | 15.5 | p>0.2 | Uniform |
| <i>Sphaerophthalma parkeri</i> | 3 | 3 | 12.5 | p>0.2 | Rare |
| <i>Sphaerophthalma triangularis</i> | 133 | 210 | 18 | p>0.2 | Uniform |
| <i>Sphaerophthalma uro</i> | 106 | 270 | 21 | p=0.1 | Uniform |
| <i>Sphaerophthalma yumaella</i> | 29 | 55 | 13 | p>0.2 | Uniform |

Note: Those fields denoted with a dash (-) indicate that this species was not collected via light trap in 2009 and/or the species is only known from females.

¹ Habitat preferences are indicated by the words: "Uniform" for those species that were found uniformly distributed over non-sand dune and sand dune habitats, "Non-dune" for those species that were found in greater abundance in non-sand dune habitats, "Sand dune" for those species found in greater abundance in sand dune habitats, and "Rare" for those species with fewer than 10 individuals collected in 2009.



Figures 3.2–3.11. Male genitalia. 2. *Odontophotopsis acmaea*: dorsal view (left) and internal view (right); 3. *O. armata*: dorsal view and lateral view of cuspis (inset); 4. *O. bellona*: dorsal view; 5. *O. mamata*: dorsal view and lateral view of cuspis (inset); 6. *O. microdonta*: dorsal view (right) and ventral view (left); 7. *O. piute*: dorsal view; 8. *O. serca*: dorsal view and lateral view of cuspis (inset); 9. *Sphaerophthalma nana*: internal view; 10. *S. orestes*: dorsal view (left) and ventral view (right); and 11. *S. parkeri*: dorsal view (left) and ventral view (right).



Figures 3.12–3.21. Male mandibles: 12. *Odontophotopsis armata*; 13. *O. clypeata*; 14. *O. microdonta*; 15. *O. piute*; 16. *O. serca*; 17. *O. setifera*; 18. *Sphaerophthalma edwardsii*; 19. *S. orestes*; 20. *S. parkeri*; and 21. *S. uro*.

Material examined. Type material. *Holotypes*: *Acanthophotopsis falciformis*

falciformis: California, Palm Springs, fall 1932, T. Zschokke (UMIC); *A. falciformis*

furcisterna: Arizona, Tucson, 5 October 1935, O. Bryant (UMIC). Other material.

Nevada, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 12-14.V.2009, NFB; Non-dune site 5: 8 ♂, LT, 12-14.V.2009, NFB.

Distribution. USA (Arizona, California, and Nevada), northern Mexico.

Activity. Males were active in mid-spring (May 09).

Remarks. *Acanthophotopsis falciformis* were too rarely encountered to determine their habitat preference. Nine *A. falciformis* males were collected on the same night in

May at light traps. Eight specimens of *A. falciformis* were found at the NTS from June through August via hand collecting at incandescent and UV lights, as well as two specimens in pitfall traps (Ferguson 1967; Allred 1973). This species seems to be rare throughout its range.

***Dasymutilla arenivaga* Mickel, 1928**

Dasymutilla arenivaga Mickel, 1928: 278, ♀. Holotype: California, Coyote Wells (CUIC).

Dasymutilla megalophtalma Mickel, 1928: 282, ♂. Holotype: Yuma County, Arizona, September 1903 (NMNH).

Diagnosis. MALE. The male of this species is recognized by having the following combination of characters: the setae of the dorsum are yellow to orange, the eyes and ocelli are large with the diameter of ocellus being longer than distance between lateral and anteromedian ocelli, the axillae are truncate posterolaterally, the wings are fuscous, orange setae are present on T2, but are restricted to the apical fringe, S2 lacks a median pit filled with setae, and an apical fringe of setae is present on the pygidium. FEMALE. The female of this species is recognized by having the following combination of characters: the eyes are enlarged, the dorsum of the head, mesosoma and T2 are clothed with yellow to orange setae while the setae of T3-6 are black, and the dorsum of the mesosoma is longer than broad.

Material examined. Type material. *Holotype* of *D. arenivaga*: California, Colorado Desert, Coyote Wells, 11 August 1914, J.C. Bradley (CUIC). Other material. **Nevada,** Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.IX.2009,

NFB; Non-dune site 4: 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 1: 7 ♂, LT, 6-8.VII.2009, 1 ♀, 17 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♀, PT, 3.X.2009, NFB; Sand dune site 2: 1 ♀, PT, 2-3.IX.2008, 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Sand dune site 3: 1 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, 1 ♀, hand collected, 19.VIII.2009, 1 ♀, hand collected, 4.IX.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 4: 3 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 5: 8 ♂, LT, 24.VI.2008, DAT & NFB, 7 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 4-6.VIII.2009, 1 ♀, PT, 1 ♂, LT, 4-6.IX.2009, NFB, 1 ♀, PT, 30.X.2009, NFB & SDB; Non-dune site 5: 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Mesquite site 2: 2 ♀, PT, 4-5.VIII.2008, NFB; Mesquite site 3: 1 ♀, PT, 17-18.X.2008, NFB & SDB.

Distribution. USA (Arizona, California and Nevada), Mexico (Baja California, Hidalgo and Sonora).

Activity. Males were active throughout the summer (late June through early September). Females were collected late in the summer (August through October 08, Late July through October 09).

Remarks. *Dasyutilla arenivaga* is closely related to *D. nocturna*, and, similarly, is active both diurnally and nocturnally (Pitts *et al.* 2009). Individuals of *D. arenivaga* were collected significantly more often in sand dune habitats than in non-sand dune habitats ($U=24.5$, $p=0.015$). Seventy *D. arenivaga* specimens, 62 males and 8 females, were collected. Males were collected from June through September at light traps and females were collected from July through October via hand collecting, light trapping and pitfall trapping. This species was not found at the NTS.

***Dasymutilla chisos* Mickel, 1928**

Dasymutilla chisos Mickel, 1928: 284, ♂. Holotype: Texas, Brewster County, Chisos Mountains, 10-12 June 1908, Mitchell and Cushman, Cat. No. 40751 (NMNH).

Diagnosis. MALE. The males of *D. chisos* have the head and mesosoma clothed entirely with black setae and the fringe of T2 and T3-6 with orange setae, the posterior margin of the head is extended medially, the anterior pronotal margin is emarginate medially, there is a medially situated, longitudinally ovate, seta-filled pit on S2, and the pygidium lacks an apical fringe of setae. FEMALE. Unknown.

Material examined. Type material. **Holotype** of *D. chisos*: Texas, Brewster County, Chisos Mountains, 10-12 June 1908, Mitchell and Cushman, Cat. No. 40751 (NMNH).

Other material. **Nevada**, Nye Co., AMNWR: Sand dune site 5: 1 ♂, net collected, 4.VIII.2009, NFB.

Distribution. USA (California, Nevada, and Texas).

Activity. One male specimen found in August 09.

Remarks. *Dasymutilla chisos* were too rarely encountered to determine their habitat preference. A single *D. chisos* male was collected during the daytime in August. This species was not found at the NTS. This species is suspected to be a color morph of *D. gloriosa* based on morphology.

***Dasymutilla gloriosa* (de Saussure, 1868)**

Mutilla gloriosa de Saussure, 1868: 359, ♀. Lectotype (designated by Mickel 1936): Baja California, Saunders (MHNG).

Mutilla tecta Cresson, 1875: 119, ♀. Holotype: California, H. Edwards (ANSP).

Dasymutilla reperticia Mickel, 1928: 287, ♂. Holotype: Arizona, Empire Mountains, 3 Jul 1924, A.A. Nichol (UMSP).

Diagnosis. MALE. The male of this species possesses black integument and the setae of the dorsum concolorous yellow to red, the posterior margin of head is extended medially, the anterior margin of pronotum is emarginate medially, and S2 has an oval pit filled with setae. FEMALE. The females of *D. gloriosa* are clothed entirely with white setae, have a thickened transverse carina anterior to the scutellar scale, have the mesosoma longer than broad, and have the pygidium rugose or rugo-striate, lacking raised and separated striae in the basal half.

Material examined. Type material. *Lectotype* of *M. gloriosa*: Baja California, Saunders (MNHN). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 4: 1 ♀, LT, 24.VI.09, 1 ♀, hand collected, 4-6.IX.2009, NFB; Sand dune site 1: 1 ♀, PT, 30.X.2009, NFB & SDB, 1 ♀, PT, 20.XI.2009, NFB; Sand dune site 2: 1 ♀, PT, 2-3.IX.2008, NFB; Sand dune site 5: 1 ♀, 24.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 17-18.X.2008, NFB & SDB; Non-dune site 5: 1 ♀, PT, 17-18.X.2008, NFB & SDB, 1 ♀, net collected, 4.VIII.2009, 1 ♀, PT, 4-6.IX.2009, NFB; Copeland site: 1 ♀, PT, 17-18.X.2008, NFB & SDB; Spring meadows site: 1 ♀, PT, 2-3.IX.2008, NFB; Mesquite site 1: 2 ♀, PT, 2-3.IX.2008, NFB, 3 ♀, PT, 17-18.X.2008, NFB & SDB; Mesquite site 3: 1 ♀, PT, 2-3.IX.2008, NFB, 1 ♀, PT, 17-18.X.2008, NFB & SDB.

Distribution. USA (Arizona, California, Idaho, Nevada, Texas, and Utah), Mexico (Baja California Norte, Baja California Sur, Nayarit, Sinaloa and Sonora).

Activity. No males were collected. Females were collected primarily in late summer and into late autumn (September through October 2008, August through November 2009). In both 2008 and 2009 a single female was collected in late June.

Remarks. *Dasymutilla gloriosa* were too rarely encountered to determine their habitat preference. Nineteen *D. gloriosa* females were collected from June through November via hand collecting, net collecting and pitfall traps. Seven female *D. gloriosa* females were found at the NTS from June through September via hand collecting and pitfall trapping (Ferguson 1967; Allred 1973). Pitts *et al.* (2009) discussed the difficulty in distinguishing this species from other closely related *Dasymutilla* species.

Mickel (1928) stated that a syntype (referenced as the Holotype) of *D. gloriosa* supposedly was in the Paris Museum, but that he was unable to find it. He subsequently (1936) found the only other syntype and designated it as a lectotype (so labeled) in the Museum d'Histoire Naturelle, Geneva. Manley & Pitts (2007) located and examined both of these specimens and found them to be identical. Manley & Pitts (2007) referenced the specimen in the Paris Museum as the 'holotype', when, in fact, the specimen in the Museum d'Histoire Naturelle should be considered as the true type (lectotype) of this species and that in the Paris Museum is a paralectotype.

***Dasymutilla pseudopappus* (Cockerell, 1895)**

Sphaerophthalma [sic!] *gloriosa* var. *pseudopappus* Cockerell, 1895: 6, ♀. Lectotype

(designated here): New Mexico, Las Cruces (NMNH).

Diagnosis. FEMALE. The females are clothed entirely with white setae, have the mesosoma longer than broad, lack or have a weak transverse carina anterior to the

scutellar scale, and have raised, separated, longitudinally parallel striae on the basal half of the pygidium. MALE. Unknown.

Material examined. Type material. *Lectotype* of *S. gloriosa* var. *pseudopappus*: New Mexico, Las Cruces (NMNH). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 3: 1 ♀, hand collected, 3.X.2009, NFB; Sand dune site 1: 3 ♀, PT, 10.VI.2009, NFB & DAT; Sand dune site 2: 1 ♀, hand collected, 24.VI.2009, NFB; Sand dune site 4: 1 ♀, PT, 10.VI.2009, NFB & DAT; Sand dune site 5: 1 ♀, MT, 26.VI.2008, NFB, DAT & JPP, 1 ♀, net collected, 28.V.2009, NFB.

Distribution. USA (Arizona, California, Colorado, Nevada, New Mexico, and Texas), Mexico (Nayarit). Not found in Baja California, Mexico.

Activity. Females were found in late spring into early summer (June 08, late May through early June 2009).

Remarks. *Dasymutilla pseudopappus* were too rarely encountered to determine their habitat preference. Eight *D. pseudopappus* females were collected from May to October via net collecting, malaise traps and pitfall traps. *Dasymutilla pseudopappus* was not found at the NTS, but this is likely due to the difficulty in separating *D. pseudopappus* from *D. gloriosa*. I were unable to study these specimens.

For this study I have designated a lectotype from the available syntypes. I selected the lectotype from the only specimen available. The label data are as follows [Las Cruces, June 18, Cockerell] [Collection of CF Baker].

***Dasymutilla satanas* Mickel, 1928**

Dasymutilla satanas Mickel, 1928: 239, ♀. Holotype: Arizona, Bill Williams Fork (SEMC).

Dasymutilla mimula Mickel, 1928: 255, ♂. Holotype: California (NMNH).

Diagnosis. MALE. The females of *D. satanas* are clothed dorsally with pale yellow to orange setae, the ventral mesosomal setae are black and the setae of S2-5 are concolorous with the dorsal setae, the antennal scrobe is carinate dorsally, the gena is ecarinate and weakly punctate, the mesosoma is longer than broad, the scutellar scale is well defined, and the pygidium is irregularly rugose. FEMALE. The females of *D. satanas* are clothed dorsally with pale yellow to orange setae, the ventral mesosomal setae are black and the setae of S2-5 are concolorous with the dorsal setae, the antennal scrobe is carinate dorsally, the gena is ecarinate and weakly punctate, the mesosoma is longer than broad, the scutellar scale is well defined, and the pygidium is irregularly rugose.

Material examined. Type material. *Holotype* of *D. satanas*: Arizona, Bill Williams Fork, August, F.H. Snow (SEMC). Other material. Nevada, Nye Co., AMNWR: Non-dune site 4: 1 ♀, hand collected, 7.VII.2009, NFB; Non-dune site 5: 2 ♀, PT, 2-3.IX.2008, NFB, 1 ♀, PT, 17-18.X.2008, NFB & SDB.

Distribution. USA (Arizona, California, and Nevada), Mexico (Baja California).

Activity. No males were collected. Females were found in mid to late summer (September-October 2008, and early July 2009).

Remarks. *Dasymutilla satanas* were too rarely encountered to determine their habitat preference. Four *Dasymutilla satanas* females were collected from July through October

in pitfall traps and one specimen via hand collection. Forty-six *D. satanas* specimens were found at the NTS from June through September via hand collecting, ultraviolet light trapping, and pitfall trapping (Ferguson 1967; Allred 1973). Only two of the 46 specimens were male.

***Dilophotopsis concolor* (Cresson, 1865)**

Mutilla concolor Cresson, 1865: 390, ♂. Holotype: "Colorado" (ANSP).

Mutilla nanula Dalla Torre, 1897: 65. New name for *Mutilla pygmea* Blake, 1879, ♀.

Lectotype (designated here): "Boulder, Colorado" (ANSP), nom. praeocc., nec Gerstaecker, 1874.

Odontophotopsis alamonis Viereck, 1904: 87, ♂. Holotype: New Mexico, Alamogordo (ANSP).

Odontophotopsis crassus Viereck, 1924: 112, ♂. Holotype: British Columbia, Oliver (CNCI).

Dilophotopsis concolor laredo Schuster, 1958: 86, ♂. Holotype: Texas, Winterhaven (UMSP).

Dilophotopsis concolor utahensis Schuster, 1958: 87, ♂. Holotype: Utah, Delle (CUIC).

Diagnosis. MALE. The male of this species can be easily identified by male genitalic characters. The external margin of the cuspis is angulate, with a dorsal carina present at the elbowed region, although the shape of the cuspis and the size of this carina vary to some degree (see Wilson & Pitts 2008: Figs 3-11). Also, the mesosternal tubercles are peg-like, a sternal felt line is lacking, and the hypopygidium is flattened and

anterolaterally possesses a short longitudinal carina. The coloration of *D. concolor* is variable; the body coloration ranges from stramineous to castaneous, and many specimens have piceous areas under the tergal felt lines and near the apices of the femora. The mandibles are similar to *Acrophotopsis campylognatha* illustrated by Pitts *et al.* (2010a: Fig. 2). FEMALE. The female of this species can be diagnosed by the following unique combination of characters: a distinct basal tooth on ventral margin of mandible and a tooth-like projection at the anterior termination of the dorsal mandibular carina, the first metasomal segment is petiolate with the second, the second metasomal tergite lacks rasp-like tubercles between the integumental punctures anteriorly, and the pygidium is laterally defined by carinae with granulate sculpturing. The coloration and setal pattern is diagnostic.

Material examined. Type material. *Holotypes*: *M. concolor*: "Colorado" (ANSP); *O. alamonis*: New Mexico, Alamogordo, 15 May 1902 (ANSP); *O. crassus*: British Columbia, Oliver, 24 July 1923, E. R. Buckell, type no. 754 (CNCI); *D. concolor laredo*: Texas, Winterhaven, 9 April 1935, S. E. Jones (UMSP); *D. concolor utahensis*: Utah, Delle, 16 July 1927, J. C. Bradley (CUIC). *Lectotype* of *M. pygmaea* Blake: "Boulder, Colorado" (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 2: 3 ♂, LT, 12-14.V.2009, 12 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 6-8.VII.2009, 7 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Non-dune site 3: 3 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, 7 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-

23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 11 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 8 ♂, LT, 23-25.VI.2009, 8 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 1: 2 ♂, LT, 26.VI.2008, NFB, DAT & JPP, 2 ♂, LT, 12-14.V.2009, 2 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 2: 4 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 6-8.VII.2009, 4 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 3: 1 ♂, LT, 12-14.V.2009, 2 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 4: 3 ♂, LT, 9.VI.2008, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 9 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 5: 2 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Non-dune site 5: 1 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, NFB; Copeland site: 1 ♂, LT, 5.V.2008, DAT, 4 ♂, LT, 14.V.2008, 1 ♂, LT, 13.VI.2008, NFB & DAT.

Distribution. USA (California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, Oklahoma, Texas, Washington, Wyoming and Utah), Mexico (Chihuahua, Coahuila, Durango, Jalisco, Tamaulipas, and Zacatecas), Canada (British Columbia).

Activity. Males were active from mid-spring through late summer (May through September). No females were collected.

Remarks. *Dilophotopsis concolor* were uniformly distributed across sand dune and non-sand dune habitats ($U=16$, $p>0.2$). One hundred fifty-six *D. concolor* males were collected from May through September at light traps. Only one *D. concolor* specimen was found at the NTS (Ferguson 1967).

This genus was reviewed by Wilson and Pitts (2008), where they discovered that this species is morphologically and molecularly distinct from the other three subspecies, and raised it to the species level from the subspecies level. The female of this species was described by Pitts *et al.* (2007).

For this study I have designated a lectotype from the available syntypes. The lectotype was selected based on having extruded genitalia and the quality of the specimen. The label data are as follows [Boulder] [Col.] [Type no. 4616] [pygmea. Bl.].

***Dilophotopsis paron* (Cameron, 1896)**

Sphaerophthalma [sic!] *paron* Cameron, 1896: 381, ♂. Lectotype (designated here):

Mexico, Northern Sonora (BMNH).

Dilophotopsis concolor sonorensis Schuster, 1958: 88, ♂. Holotype: Arizona, Gila

Bend (UMSP).

Diagnosis. MALE. The male of this species is quite similar to the previous species from which it can be differentiated only by genitalic characters. The cuspis is dorsoventrally flattened and the cuspis elbowed, but lacks a dorsal carina in this region (see Wilson &

Pitts 2008: Figs 12-14). The mandibles are similar to *Acrophotopsis campylognatha* illustrated by Pitts *et al.* (2010a: Fig. 2). FEMALE. Unknown.

Material examined. Type material. *Lectotype* of *S. paron*: Mexico, Northern Sonora (BMNH). *Holotype* of *D. concolor sonorensis*: Arizona, Gila Bend, 24 Apr 1935, F.H. Parker (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Non-dune site 2: 3 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Non-dune site 3: 2 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, 3 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Non-dune site 4: 4 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 3 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 1: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 2: 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 5: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 5: 1 ♂, LT, 12-14.V.2009, NFB; Copeland site: 5 ♂, LT, 5.V.2008, DAT, 7 ♂, LT, 14.V.2008, 2 ♂, LT, 13.VI.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada), Mexico (Baja California, Baja California Sur, and Sonora).

Activity. Males were active from mid-spring through the summer (May through August).

Remarks. *Dilophotopsis paron* were uniformly distributed across sand dune and non-sand dune habitats ($U=21.5$, $p>0.05$). Forty-seven *D. paron* males were collected from May through August at light traps. Only three *D. paron* specimens were found at the NTS (Ferguson 1967).

This genus was reviewed by Wilson and Pitts (2008), where they discovered that this species is morphologically and molecularly distinct from the other three subspecies, and raised it to the species level from the subspecies level.

For this study I have designated a lectotype from the available syntypes. I selected the lectotype from the only specimen available.

***Odontophotopsis acmaea* Viereck, 1904**

(Fig. 2.2)

Odontophotopsis acmaeus Viereck, 1904: 84, ♂. Lectotype (designated here):

Arizona (NMNH).

Odontophotopsis (Odontophotopsis) grata Schuster (nec Melander, nec Schuster

1958 p. 53, 57, 58), 1958.: 55, ♂.

Diagnosis. MALE. This species is recognized by having the following combination of characters: the mandible excised ventrally forming an angle, but does not taper towards the apex, the apex of the mandible is slightly dilated (see Pitts *et al.* 2010a: Fig. 3), the mesosternum has a pair of large distinct spines that have a posterior face that is longitudinally sulcate and have an apex that is bifid, the metasternum is bidentate, and the pygidium is granulate, but not defined laterally by carinae. Genitalia are illustrated in Fig. 2. FEMALE. Unknown.

Material examined. Type material. *Lectotype* of *O. acmaeus*: Arizona, Type no. 6994 (NMNH). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 2: 3 ♂, LT, 26-28.V.2009, NFB; Non-dune site 3: 7 ♂, LT, 26-28.V.2009, NFB; Non-dune site 4: 4 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-

15.VI.2009, NFB & DAT; Sand dune site 1: 1 ♂, LT, 12-14.V.2009, 43 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 2: 1 ♂, LT, 12-14.V.2009, 9 ♂, LT, 26-28.V.2009, 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 3: 7 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT; Sand dune site 4: 4 ♂, LT, 26-28.V.2009, NFB, 9 ♂, LT, 8-15.VI.2009, NFB & DAT, 5 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 3 ♂, LT, 26-28.V.2009, 1 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 5: 1 ♂, LT, 13.VI.2008, NFB & DAT, 10 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 21-23.VII.2009, NFB; Copeland site: 1 ♂, LT, 14.V.2008, 3 ♂, LT, 30.V.2008, 1 ♂, LT, 13.VI.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada), Mexico (Sonora).

Activity. Males were active from mid-spring through early summer (May through July).

Remarks. *Odontophotopsis acmaea* were distributed uniformly over sand dune and non-dune habitats ($U=20$, $p=0.2$). One hundred thirty *O. acmaea* males were collected from May through early September at light traps. *Odontophotopsis acmaea* was not found at the NTS. Pitts *et al.* (2009) discuss the confusion caused by Schuster (1958) concerning this species.

For this study I have designated a lectotype from the available syntypes. I selected the lectotype from the only specimen available. The label data are as follows [Ariz 2304] [♂ Type no. 6994 USNM]. The genitalia are extracted and in a vial beneath the specimen.

***Odontophotopsis armata* Schuster, 1958**

(Figs 3.3, 3.12)

Odontophotopsis (Odontophotopsis) armata Schuster, 1958: 60, ♂. Neotype

(designated by Pitts *et al.* 2010a): California, Riverside County, Deep Canyon (EMUS).

Diagnosis. MALE. This species can be recognized by the presence of mesosternal processes, a deeply emarginate, tridentate, mandible that is slightly oblique apically (Fig. 12 and Pitts *et al.* 2010a: Fig. 4), and a distinct tubercle located medially on the posterior margin of the clypeus, while usually lacking a sternal felt line. In many of the specimens from Deep Canyon and other areas a trace of a sternal felt line is present, but it is defined by little more than a small cluster of micropunctures. Genitalia are illustrated in Fig. 3.3. FEMALE. Unknown.

Material examined. Type material. *Neotype* of *O. armata*: California, Riverside County, Deep Canyon, 15 ♂, 23-24 May 2007, Wilson, Williams and Pitts (EMUS).

Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 21-23.VII.2009, NFB.

Distribution. USA (California and Nevada), Mexico (Baja California).

Activity. Male found in mid-summer (late July 2009).

Remarks. *Odontophotopsis armata* were too rarely encountered to determine their habitat preference. Only one *O. armata* male was collected in July at a light trap. Fifty-two male specimens of *O. armata* were found at the NTS via light trapping (Ferguson 1967). This species can be sometimes confused with *O. serca*, from which it only can be

separated by the presence of the clypeal tubercle. This species is discussed in further detail in Pitts *et al.* (2010a).

***Odontophotopsis aufidia* Mickel in Mickel & Clausen, 1983**

Odontophotopsis (Odontophotopsis) aufidia Mickel in Mickel & Clausen, 1983: 541,

♂. Holotype: California, Taft (UMSP).

Diagnosis. MALE. This species is recognized by having the following combination of characters: the mandible is excised ventrally forming an angle and tapering towards the apex (see Pitts *et al.* 2009: Fig. 43), the mesosternum only has one pair of distinct spines, the metasternum is bidentate, and the pygidium is granulate, but is not defined laterally by carinae. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 9). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. aufidia*: California, Taft, 12 Jun 1942, W.C. Cook (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 4: 3 ♂, LT, 26-28.V.2009, NFB.

Distribution. USA (California and Nevada).

Activity. Males were active in early summer (late May 2010).

Remarks. *Odontophotopsis aufidia* were too rarely encountered to determine their habitat preference. Four *O. aufidia* males were collected in May via light trapping. *Odontophotopsis aufidia* was not found at the NTS. The taxonomy of this species is discussed in further detail in Pitts *et al.* (2009).

***Odontophotopsis bellona* Mickel in Mickel & Clausen, 1983**

(Fig. 3.4)

Odontophotopsis (Odontophotopsis) bellona Mickel in Mickel & Clausen, 1983: 541,

♂. Holotype: Arizona, Pima County, Cortaro (UMSP).

Diagnosis. MALE. This species is differentiated by having the mandible tridentate with a large basal tooth on the ventral margin (Mickel & Clausen 1983: Fig. 17) and by the pygidium being defined laterally by carinae and having distinctly granulate sculpturing. Also this species has a mesosternal process that is bifid apically (Pitts *et al.* 2009: Fig. 106, Mickel & Clausen 1983: Fig. 25). The genitalia are illustrated in Fig. 3.4 and by Mickel and Clausen (1983: Fig. 4). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. bellona*: Arizona, Pima County, Cortaro, 2100 ft, 5 Jun 1969, J. Burger (UMSP). Other material. **Nevada,** Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 2: 6 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 3: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 4: 1 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT; Sand dune site 1: 2 ♂, LT, 26-28.V.2009, 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 2: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 3: 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 5: 1 ♂, LT, 10.VII.2008, NFB & DAT, 3 ♂, LT, 24.VI.2008, NFB, DAT & JPP; Non-dune site 5: 2 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 6-8.VII.2009, NFB; Copeland site: 1 ♂, LT, 11.V.2008, 2 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active from mid-spring through early summer (May through July).

Remarks. *Odontophotopsis bellona* were uniformly distributed across sand dune and non-dune habitats (U=19, p>0.2). Thirty-three *O. bellona* males were collected from May through September at light traps. *Odontophotopsis bellona* was not found at the NTS. This species is discussed in further detail in Pitts *et al.* (2009).

***Odontophotopsis biramosa* Schuster, 1952**

Odontophotopsis (Odontophotopsis) biramosa Schuster, 1952: 43, ♂. Holotype:

California, Imperial County, Holtville (NMNH); 1958: 56, ♂.

Diagnosis. MALE. This species is diagnosed by having a tridentate mandible with an extremely large dorsal tooth that is separated from the lower portion of the mandibular apex by a deep, wide sinus, which makes the mandibular apices appear biramose (see Pitts *et al.* 2009: Fig. 29), and by the clypeus, which has a horseshoe-shaped tubercle posteromedially that overhangs the clypeus as a slight hood-like or nasutiform process. Also, this species has a single mesosternal process on each side of the midline, and has the cuspis being approximately half the free length of the paramere (see Pitts *et al.* 2009: Fig. 10). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. biramosa*: California, Imperial County, Holtville, 2 Jul 1929, P.W. Owens (NMNH). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 1 ♂, LT, 21-23.VII.2009, NFB.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active in late summer and mid-autumn (late July and late September).

Remarks. *Odontophotopsis biramosa* were too rarely encountered to determine their habitat preference. Three *O. biramosa* males were collected in July and September via light trapping. *Odontophotopsis biramosa* was not found at the NTS. A more thorough taxonomic discussion of this species can be found in Pitts (2007). This species is currently placed in the *O. setifera* species-group, but Pitts *et al.* (2010b) found them to not be closely related.

***Odontophotopsis clypeata* Schuster, 1958**

(Fig. 3.13)

Odontophotopsis (Odontophotopsis) clypeata Schuster, 1958: 59, ♂. Holotype:

Arizona, Tucson (UMSP).

Diagnosis. MALE. This species has a head that is rounded posteriorly, deeply excised mandibles that are slightly dilated apically (Fig. 3.13 and Pitts *et al.* 2010a: Fig. 8), has a transverse clypeus that is slightly depressed below mandibular margins, but lacks a tubercle situated posteromedially on the clypeus, has a pair of denticulate mesosternal processes situated anteromedially, has a shiny glabrous pygidium and the metasoma is usually castaneous, at least around the felt lines. Genitalia are illustrated by Pitts *et al.* 2009: Fig. 11. FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. clypeata*: Arizona, Tucson, 26 Aug 1939, O. Bryant (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune

site 1: 4 ♂, LT, 26-28.V.2009, 7 ♂, LT, 23-25.VI.2009, 9 ♂, LT, 21-23.VII.2009, 4 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 22 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 2-4.X.2009, 6 ♂, LT, 16-18.X.2009, NFB; Non-dune site 2: 2 ♂, LT, 12-14.V.2009, 20 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & DAT, 24 ♂, LT, 23-25.VI.2009, 31 ♂, LT, 21-23.VII.2009, 12 ♂, LT, 4-6.VIII.2009, 18 ♂, LT, 17-19.VIII.2009, 6 ♂, LT, 4-6.IX.2009, 37 ♂, LT, 18-23.IX.2009, 4 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 2 ♂, LT, 12-14.V.2009, 23 ♂, LT, 26-28.V.2009, 39 ♂, LT, 23-25.VI.2009, 22 ♂, LT, 21-23.VII.2009, 16 ♂, LT, 4-6.VIII.2009, 9 ♂, LT, 17-19.VIII.2009, 8 ♂, LT, 1 ♂, PT, 4-6.IX.2009, 16 ♂, LT, 18-23.IX.2009, 1 ♂, PT, 3.X.2009, NFB; Non-dune site 4: 44 ♂, LT, 1 ♂, MT, 26-28.V.2009, NFB, 34 ♂, LT, 8-15.VI.2009, NFB & DAT, 53 ♂, LT, 23-25.VI.2009, 21 ♂, LT, 6-8.VII.2009, 76 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 1 ♂, PT, 4-6.VIII.2009, 27 ♂, LT, 17-19.VIII.2009, 13 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, 2 ♂, PT, 3.X.2009, 3 ♂, LT, 16-17.X.2009, NFB; Sand dune site 1: 13 ♂, 26.VI.2008, NFB, DAT & JPP, 7 ♂, PT, 5.VIII.2008, NFB, 1 ♂, PT, 17-18.X.2008, NFB & SDB, 4 ♂, LT, 12-14.V.2009, 93 ♂, LT, 1 ♂, MT, 26-28.V.2009, NFB, 19 ♂, LT, 8-15.VI.2009, NFB & DAT, 58 ♂, LT, 23-25.VI.2009, 12 ♂, LT, 6-8.VII.2009, 122 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 47 ♂, LT, 17-19.VIII.2009, 33 ♂, LT, 2 ♂, PT, 4-6.IX.2009, 30 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2-4.X.2009, 7 ♂, LT, 16-18.X.2009, NFB, 1 ♂, LT, 29-31.X.2009, NFB & SDB; Sand dune site 2: 4 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 44 ♂, LT, 1 ♂, MT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 30 ♂, LT, 17-19.VIII.2009, 3 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 1 ♂, LT, 12-14.V.2009, 12 ♂, LT, 26-

28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 18 ♂, LT, 23-25.VI.2009, 8 ♂, LT, 6-8.VII.2009, 60 ♂, LT, 1 ♂, MT, 21-23.VII.2009, 21 ♂, LT, 4-6.VIII.2009, 7 ♂, LT, 17-19.VIII.2009, 9 ♂, LT, 4-6.IX.2009, 26 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2 ♂, PT, 2-4.X.2009, 3 ♂, LT, 16-17.X.2009, NFB; Sand dune site 4: 18 ♂, LT, 9.VI.2008, NFB & DAT, 4 ♂, PT, 5-6.VIII.2008, 1 ♂, PT, 2-3.IX.2008, 1 ♂, LT, 12-14.V.2009, 15 ♂, LT, 26-28.V.2009, NFB, 58 ♂, LT, 8-15.VI.2009, NFB & DAT, 52 ♂, LT, 23-25.VI.2009, 247 ♂, LT, 21-23.VII.2009, 7 ♂, LT, 4-6.VIII.2009, 17 ♂, LT, 17-19.VIII.2009, 38 ♂, LT, 1 ♂, PT, 4-6.IX.2009, 67 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2 ♂, PT, 2-4.X.2009, 5 ♂, LT, 16-18.X.2009, NFB; Sand dune site 5: 113 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 10 ♂, LT, 10.VII.2008, 5 ♂, LT, 24.VII.2008, NFB & DAT, 1 ♂, PT, 2-3.IX.2008, 4 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 42 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 1 ♂, PT, 4-6.VIII.2009, 33 ♂, LT, 17-19.VIII.2009, 1 ♂, PT, 4.IX.2009, NFB; Non-dune site 5: 4 ♂, LT, 13.VI.2008, NFB & DAT, 11 ♂, LT, 22-24.VII.2008, NFB & DAT, 1 ♂, PT, 17-18.X.2008, NFB & SDB, 3 ♂, LT, 12-14.V.2009, 14 ♂, LT, 26-28.V.2009, NFB, 19 ♂, LT, 8-15.VI.2009, NFB & DAT, 31 ♂, LT, 23-25.VI.2009, 66 ♂, LT, 21-23.VII.2009, 10 ♂, LT, 4-6.VIII.2009, 23 ♂, LT, 4-6.IX.2009, 47 ♂, LT, 18-23.IX.2009, 3 ♂, LT, 16-18.X.2009, NFB, 1 ♂, LT, 29-31.X.2009, NFB & SDB; Copeland site: 10 ♂, LT, 14.V.2008, 5 ♂, LT, 30.V.2008, 21 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, PT, 24-26.VI.2008, NFB, DAT & JPP, 1 ♂, PT, 5.VIII.2008, NFB & SDB; Wash site: 4 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active from mid-spring through mid-autumn (May through October).

Remarks. *Odontophotopsis clypeata* were uniformly distributed across sand dune and non-sand dune habitats (U=15, $p>0.2$). Two thousand three hundred seventy-five *O. clypeata* males were collected from May to October at light traps, pitfall traps and malaise traps. This was the most commonly collected species (Table 1). Fourteen *O. clypeata* specimens were found at the NTS from July to September via light and pitfall traps (Ferguson 1967). This species is widespread and common in many parts of its range, and its taxonomy is discussed in further detail in Pitts *et al.* (2009). This species is easily confused with *O. microdonta*. However, mandibular morphology and placement of the mesosternal tubercles differ (Ferguson 1967).

***Odontophotopsis inconspicua* (Blake, 1886)**

Photopsis inconspicuus Blake, 1886: 272, ♂. Holotype: California (ANSP).

Mutilla infelix Dalla Torre, 1897: 50. Replacement name for *Photopsis inconspicuus* Blake, nec *Mutilla inconspicuus* Smith, 1879.

Diagnosis. MALE. This species is recognized by having the following combination of characters: the mandible is excised ventrally forming a slight tooth that is dilated towards the apex (see Pitts *et al.* 2009: Fig. 32), the mesosternum only has one pair of large distinct spines that are flattened to slightly concave on the posterior side, the metasternum is tridentate, the second sternum of the metasoma lacks a felt line, and the pygidium is granulate and is defined laterally by carinae. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 12). FEMALE. The female of this species can be diagnosed by dense appressed setae

present on the dorsum that obscures the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically. Also the ventral margin of the mandible has a distinct angulation, flagellomere 1 is much longer than flagellomere 2, the mesosoma is hexagonal in dorsal view, the first segment of the metasoma is sessile with the second, and the second metasomal segment is of normal length being $\sim 1 \times$ as long as anterior width or just slightly greater.

Material examined. Type material. *Holotype* of *Ph. inconspicuus*: California (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 3 ♂, LT, 23-25.VI.2009, Collectors, 6 ♂, LT, 21-23.VII.2009, Collectors, 3 ♂, LT, 17-19.VIII.2009, 32 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 16-18.X.2009, NFB; Non-dune site 2: 1 ♂, LT, 26-28.V.2009, 7 ♂, LT, 23-25.VI.2009, 9 ♂, LT, 6-8.VII.2009, 56 ♂, LT, 21-23.VII.2009, 17 ♂, LT, 4-6.VIII.2009, 23 ♂, LT, 17-19.VIII.2009, 14 ♂, LT, 4-6.IX.2009, 39 ♂, LT, 18-23.IX.2009, 3 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 1 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, 7 ♂, LT, 21-23.VII.2009, 8 ♂, LT, 4-6.VIII.2009, 7 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 4-6.IX.2009, 18 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2-4.X.2009, 1 ♂, LT, 16-17.X.2009, NFB; Non-dune site 4: 2 ♂, LT, 23-25.VI.2009, 13 ♂, LT, 21-23.VII.2009, 27 ♂, LT, 17-19.VIII.2009, 7 ♂, LT, 4-6.IX.2009, 22 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-17.X.2009, NFB; Sand dune site 1: 21 ♂, LT, 21-23.VII.2009, 9 ♂, LT, 17-19.VIII.2009, 4 ♂, LT, 4-6.IX.2009, 17 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 2: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 6-8.VII.2009, 21 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 8 ♂, LT, 17-19.VIII.2009, 15 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 14 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-

19.VIII.2009, 5 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 4: 2 ♂, LT, 9.VI.2008, NFB & DAT, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 4 ♂, LT, 23-25.VI.2009, 32 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 4-6.IX.2009, 34 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 21 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 3 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 22-23.IX.2009, NFB; Non-dune site 5: 1 ♂, LT, 13.VI.2008, NFB & DAT, 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Copeland site: 1 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, LT, 17-18.X.2008, NFB and SDB.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active from late-spring through mid-autumn (June through mid-October). No females were collected.

Remarks. *Odontophotopsis inconspicua* were uniformly distributed across sand dune and non-sand dune habitats (U=13, p>0.2). Five hundred sixty-seven *O. inconspicua* males were collected from May through October at light traps. Twenty-seven *O. bellona* males were found at the NTS (Ferguson 1967). Pitts *et al.* (2009) recently associated the sexes using distributional and morphological data. Further taxonomic description of this species can also be found in Pitts *et al.* (2009).

***Odontophotopsis mamata* Schuster, 1958**

(Fig. 3.5)

Odontophotopsis (Periphotopsis) mamata Schuster, 1958: 60, ♂. Holotype: Arizona, Ehrenberg (UMSP).

Diagnosis. MALE. This species can be easily recognized by the distinct mesosternal processes, which are made up of large glabrous longitudinal swellings located on either side of the midline. Genitalia are illustrated in Fig. 3.5 with the paramere having a characteristic bend at approximately 2/3 the free length from the base, and the mandibles can be viewed in Pitts *et al.* (2010a: Fig. 10). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. mamata*: Arizona, Ehrenberg, 12 June 1935, F.H. Parker (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 3 ♂, LT, 26-28.V.2009, 2 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 16-18.X.2009, NFB; Non-dune site 2: 19 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, 4 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 4 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 58 ♂, LT, 23-25.VI.2009, 5 ♂, LT, 6-8.VII.2009, 19 ♂, LT, 21-23.VII.2009, 8 ♂, LT, 1 ♂, PT, 4-6.VIII.2009, 7 ♂, LT, 17-19.VIII.2009, 7 ♂, LT, 4-6.IX.2009, 14 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 3 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & DAT, 12 ♂, LT, 23-25.VI.2009, 6 ♂, LT, 6-8.VII.2009, 23 ♂, LT, 21-23.VII.2009, 11 ♂, LT, 17-19.VIII.2009, 7 ♂, LT, 1 ♂, PT, 4-6.IX.2009, 8 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 16-17.X.2009, NFB; Sand dune site 1: 5 ♂, LT, 26.VI.2008, NFB, DAT & JPP, 3 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 2: 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 4: 1 ♂, LT, 8-15.VI.2009, NFB & DAT; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP; Non-dune site 5: 4 ♂, LT, 13.VI.2008, 1 ♂, LT, 23.VII.2008, NFB &

DAT, 1 ♂, LT, 26-28.V.2009, NFB, 4 ♂, LT, 8-15.VI.2009, NFB & DAT, 4 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 9 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB; Copeland site: 12 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, PT, 5.VIII.2008, NFB.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active from late spring through mid-autumn (late May through mid-October).

Remarks. *Odontophotopsis mamata* were collected significantly more often in non-sand dune habitats than in sand dune habitats ($U=25$, $p=0.01$). Three hundred three *O. mamata* males were collected from May through October at light and pitfall traps. One hundred fifty-one *O. mamata* males were found at the NTS from June through September via light trapping, pitfall trapping and net collecting (Ferguson 1967; Allred 1973). The taxonomy of this species is discussed in further detail in Pitts *et al.* (2009).

***Odontophotopsis melicausa* (Blake, 1871)**

Agama melicausa Blake, 1871: 261, ♂. Holotype: Texas (ANSP).

Mutilla brevicornis Fox, 1899: 255, ♂. Lectotype (designated here): Texas (ANSP).

Odontophotopsis mellicornis Baker, 1905: 96, ♂. Holotype: Nevada, Ormsby County (CUIC).

Diagnosis. MALE. This species has a head that is quadrate posteriorly, deeply excised mandibles that are distinctly dilated apically (see Pitts *et al.* 2009: Fig. 33), lacks a tubercle situated posteromedially on the clypeus, has a pair of denticulate mesosternal processes, and has a shiny glabrous pygidium. Genitalia are illustrated by Pitts *et al.*

(2009: Fig. 13). FEMALE. The female of this species can be diagnosed by having dense appressed setae on the dorsum that obscures the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically. Also the ventral margin of the mandible is excised and has a rounded tooth, flagellomere 1 is longer than flagellomere 2, the lateral margins of the posterior half of the mesosoma are parallel in dorsal view, the first segment of the metasoma is petiolate with the second, the second metasomal segment is of normal length being $\sim 1 \times$ as long as anterior width or just slightly greater, and the pygidium is strongly striate.

Material examined. Type material. **Holotypes:** *A. melicausa*: Texas, Belfrage (ANSP); *O. mellicornis*: Nevada, Ormsby County, (CUIC). **Lectotype** of *M. brevicornis*: Texas, Type no. 4681 (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 21-23.VII.2009, 1 ♀, PT, 1 ♂, LT, 4-6.IX.2009, 17 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 2: 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 6 ♂, LT, 6-8.VII.2009, 6 ♂, LT, 21-23.VII.2009, 9 ♂, LT, 17-19.VIII.2009, 5 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 3: 10 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 18-23.IX.2009, 1 ♂, PT, 3.X.2009, NFB; Non-dune site 4: 3 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 2 ♀, PT, 9.VII.2008, 3 ♀, PT, 22.VII.2008, NFB & DAT, 3 ♀, PT, 2-3.IX.2008, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 12 ♂, LT, 6-8.VII.2009, 5 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 8 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 18-23.IX.2009, 1 ♂, PT, 3.X.2009, NFB; Sand dune site 1: 4 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 3 ♀, PT, 5.VIII.2008, NFB, 1 ♀, PT, 17-18.X.2008, NFB & SDB, 2 ♂, LT, 26-

28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 8 ♂, LT, 23-25.VI.2009, 10 ♂, LT, 6-8.VII.2009, 18 ♂, LT, 21-23.VII.2009, 7 ♂, LT, 17-19.VIII.2009, 3 ♂, LT, 4-6.IX.2009, 7 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 2: 5 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 3 ♀, PT, 9.VII.2008, 2 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♂, LT, 6-8.VII.2009, 23 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 10 ♂, LT, 17-19.VIII.2009, 6 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 1 ♂, PT, 2-4.X.2009, NFB; Sand dune site 3: 5 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 2 ♀, PT, 22.VII.2008, NFB & DAT, 3 ♀, PT, 2-3.IX.2008, NFB, 4 ♀, 1 ♂, PT, 17-18.X.2008, NFB & SDB, 1 ♂, LT, 26-28.V.2009, 4 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 6-8.VII.2009, 26 ♂, LT, 21-23.VII.2009, 13 ♂, LT, 4-6.VIII.2009, 5 ♂, LT, 17-19.VIII.2009, 3 ♂, PT, 4.IX.2009, 6 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-17.X.2009, NFB; Sand dune site 4: 20 ♂, LT, 9.VI.2008, NFB & DAT, 1 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 5 ♂, LT, 8-15.VI.2009, NFB & DAT, 18 ♂, LT, 23-25.VI.2009, 54 ♂, LT, 2 ♂, MT, 6-9.VII.2009, 45 ♂, LT, 21-23.VII.2009, 1 ♂, PT, 6.VIII.2009, 5 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 1 ♂, PT, 4-6.IX.2009, 17 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB; Sand dune site 5: 1 ♀, PT, 12 ♂, LT, 24-26.VI.2008, NFB, DAT & JPP, 6 ♂, LT, 10.VII.2008, 2 ♂, LT, 24.VII.2008, NFB & DAT, 1 ♀, 1 ♂, PT, 5-6.VIII.2008, 1 ♀, 1 ♂, PT, 2-3.IX.2008, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 6-8.VII.2009, 26 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 4-6.VIII.2009, 12 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 4 ♂, PT, 4-6.IX.2009, NFB; Non-dune site 5: 2 ♂, LT, 13.VI.2008, NFB & DAT, 2 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 9 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, NFB, 9 ♀, PT, 17-18.X.2008, NFB & SDB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 20 ♂, LT, 6-8.VII.2009, 19 ♂, LT, 21-

23.VII.2009, 1 ♂, PT, 6.VIII.2009, 1 ♂, LT, 4-6.IX.2009, 5 ♂, LT, 18-23.IX.2009, NFB;
 Copeland site: 1 ♂, LT, 14.V.2008, NFB & DAT, 1 ♂, LT, 30.V.2008, NFB & DAT, 3
 ♂, LT, 13.VI.2008, NFB & DAT, 2 ♀, 1 ♂, PT, 24-26.VI.2008, NFB, DAT & JPP, 2 ♀,
 PT, 22.VII.2008, NFB & DAT, 2 ♀, PT, 5.VIII.2008, NFB; Spring meadows site: 7 ♀,
 PT, 26.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 9.VII.2008, 2 ♀, PT, 22.VII.2008, NFB &
 DAT, 2 ♀, PT, 5.VIII.2008, 1 ♀, PT, 2-3.IX.2008, NFB; Mesquite site 1: 6 ♀, PT,
 26.VI.2008, NFB, DAT & JPP, 3 ♀, PT, 9.VII.2008, 2 ♀, PT, 22.VII.2008, NFB & DAT,
 1 ♀, PT, 5.VIII.2008, 3 ♀, PT, 2-3.IX.2008, NFB, 3 ♀, PT, 17-18.X.2008, NFB & SDB;
 Mesquite site 2: 10 ♀, PT, 26.VI.2008, NFB, DAT & SDB, 3 ♀, PT, 9.VII.2008, 4 ♀,
 PT, 22.VII.2008, NFB & DAT, 2 ♀, PT, 5.VIII.2008, 1 ♀, 1 ♂, PT, 2-3.IX.2008, NFB, 6
 ♀, 3 ♂, PT, 17-18.X.2008, NFB & SDB; Mesquite site 3: 7 ♀, PT, 26.VI.2008, NFB,
 DAT & JPP, 2 ♀, PT, 9.VII.2008, 3 ♀, PT, 22.VII.2008, NFB & DAT, 2 ♀, PT,
 5.VIII.2008, 11 ♀, PT, 2-3.IX.2008, NFB, 9 ♀, 3 ♂, PT, 17-18.X.2008, NFB & SDB.

Distribution. USA (Arizona, California, Montana, Nevada, New Mexico, Texas and Utah), Mexico, Canada (British Colombia).

Activity. Males were active from late spring through mid-autumn (late May through mid-October). Females were collected throughout the summer (late June through October 2008 and September 2009).

Remarks. *Odontophopsis melicausa* were collected significantly more often in sand dune habitats than in non-sand dune habitats ($U=23$, $p=0.05$). This is an interesting result given that this species is commonly found throughout the Southwest as far east as

Arkansas and as far north as Canada. Presumably, it is not restricted to dunes in these other areas.

Five hundred eighty-eight male and one hundred sixty-six female *O. melicausa* were collected throughout the course of this study. Males were collected from May through October at light traps and females were collected from June through October in pitfall traps. Thirty-two *O. melicausa* males were found at the NTS (Ferguson 1967). The taxonomy of this species is discussed in further detail in Pitts *et al.* (2009).

For this study I have designated a lectotype from the available syntypes. The lectotype was selected based on the quality of the specimen. The label data are as follows [TEX.] [Type no. 4681] [*M. brevicornis* Fox] [*Odontophotopsis (Odontophotopsis) melicausa* ssp. *melicausa* (Blake) ♂ Det. C.E. Mickel 1975]. The genitalia are extruded and clearly visible.

***Odontophotopsis microdonta* Ferguson, 1967**

(Figs 3.6, 3.14)

Odontophotopsis (Odontophotopsis) microdonta Ferguson, 1967: 22, ♂. Holotype:

Nevada, Nye County, 5 mi. NNW Mercury (NMNH).

Diagnosis. MALE. This species has a head that is rounded posteriorly, deeply excised mandibles that are slightly dilated apically (Fig. 3.14), has a transverse clypeus that is slightly depressed below mandibular margins, but lacks a tubercle situated posteromedially on the clypeus, has a pair of denticulate mesosternal processes situated more laterally and posteriorly than in *O. clypeata*, has a shiny glabrous pygidium and the

metasoma is usually castaneous, at least around the felt lines. Genitalia are illustrated in Fig. 3.6. FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. microdonta*: Nevada, Nye County, 5 mi. NNW Mercury, 25 Aug 1964, W. E. Ferguson (NMNH). Other material. **Nevada,** Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Non-dune site 2: 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 3: 17 ♂, LT, 23-25.VI.2009, 8 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 4 ♂, LT, 17-19.VIII.2009, 7 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 1 ♂, PT, 23.VII.2008, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 13 ♂, LT, 21-23.VII.2009, 4 ♂, LT, 17-19.VIII.2009, 4 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 1 ♂, PT, 2-4.X.2009, NFB; Sand dune site 1: 1 ♂, LT, 4-6.VIII.2009, NFB; Sand dune site 4: 2 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 5: 2 ♂, LT, 13.VI.2008, 1 ♂, LT, 23.VII.2008, NFB & DAT, 1 ♂, LT, 12-14.V.2009, 2 ♂, LT, 26-28.V.2009, 11 ♂, LT, 23-25.VI.2009, 13 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 4-6.IX.2009, 8 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2-4.X.2009, 1 ♂, LT, 16-18.X.2009, NFB.

Distribution. USA (California and Nevada).

Activity. Males were active from mid-spring through mid-autumn (May through mid-October).

Remarks. *Odontophotopsis microdonta* were collected significantly more often in non-sand dune habitats than in sand dune habitats ($U=24$, $p=0.02$). One hundred and nineteen *O. microdonta* males were collected from May through October at light and pitfall traps. One hundred twelve *O. microdonta* males were found at the NTS via light

and pitfall traps (Ferguson 1967). This species was first described by Ferguson (1967) from the NTS and is most abundant in the Mojave Desert.

***Odontophotopsis parva* Schuster, 1958**

Odontophotopsis (Odontophotopsis) parva Schuster, 1958: 55, ♂. Holotype: Arizona, Arlington (UMSP).

Diagnosis. MALE. This species possesses the following combination of characters: the mandible is excised ventrally forming an angle, but does not taper towards the apex (see Pitts *et al.* 2009: Fig. 35), the mesosternum has only one pair of large distinct spines that have a posterior face that is longitudinally sulcate, the metasternum is bidentate, and the pygidium is granulate and is defined laterally by carinae. The genitalia are illustrated by Pitts *et al.* (2009: Figs 16, 17). FEMALE. The female of this species can be recognized by the ventral margin of the mandible having a distinct angulation (see Pitts *et al.* 2009: Fig. 35), flagellomere 1 being only slightly longer than flagellomere 2, the lateral margins of the posterior half of the mesosoma being parallel in dorsal view, the first segment of the metasoma being sessile with the second, the second metasomal segment being of normal length, $\sim 1 \times$ as long as anterior width or just slightly greater, the pygidium being longitudinally striate, and by the dense appressed setae present on the dorsum that obscure the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically.

Material examined. Type material. *Holotype* of *O. parva*: Arizona, Arlington, 17 June 1919, A. Wetmore (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Sand dune site 1: 2 ♀, PT, 26.VI.2008, DAT, NFB & JPP; Sand dune site 4: 1 ♀, PT, 5-

6.VIII.2008, NFB; Copeland site: 1 ♀, PT, 5-6.VIII.2008, NFB, 2 ♀, PT, 17-18.X.2008, NFB & SDB; Mesquite site 1: 1 ♀, PT, 5-6.VIII.2008, 1 ♀, PT, 2.IX.2008, NFB, 2 ♀, PT, 17-18.X.2008, NFB & SDB; Mesquite site 3: 1 ♀, PT, 17-18.X.2008, NFB & SDB.

Distribution. USA (Arizona, California and Nevada).

Activity. No males were collected. Females were collected throughout the summer (late June through October 2008).

Remarks. *Odontophotopsis parva* were too rarely encountered to determine their habitat preference. Eleven *O. parva* females were collected throughout the course of this study. These could be the females of *O. acmaea*, *O. aufidia*, or *O. mamata*, which could account for the reason no males were collected. The specimens were collected from August through October via pitfall trapping. *Odontophotopsis parva* was not found at the NTS.

***Odontophotopsis piute* Mickel in Mickel & Clausen, 1983**

(Figs 3.7, 3.15)

Odontophotopsis (Odontophotopsis) piute Mickel in Mickel & Clausen 1983: 550, ♂.

Holotype: California, Needles (UMSP).

Diagnosis .MALE. This species can be recognized by the slender mandibles that are narrowed medially by a broad, shallow emargination, and lack a ventral tooth (Fig. 3.15). Additionally, the tuberculate anterior margin of the clypeus, the presence of a pair of small, widely spaced tubercles on the mesosternum, and paucity of plumose hairs distinguish this species from other species. Genitalia are illustrated in Fig. 3.7. **FEMALE.** Unknown.

Material examined. Type material. *Holotype* of *O. piute*: California, Needles, 900 ft, 22 June 1931, H.A. Scullen (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 3: 1 ♂, LT, 12-14.V.2009, NFB; Non-dune site 4: 1 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 1: 1 ♂, LT, 26.VI.2008, NFB, DAT & JPP; Sand dune site 4: 11 ♂, LT, 9.VI.2008, NFB & DAT, 12 ♂, LT, 1 ♂, MT, 12-15.V.2009, 8 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 5 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, 3 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP; Non-dune site 5: 1 ♂, LT, 26-28.V.2009, 2 ♂, LT, 6-8.VII.2009, NFB.

Distribution. USA (California and Nevada).

Activity. Males were active from mid-spring through mid-summer (May through July).

Remarks. *Odontophotopsis piute* were distributed uniformly over sand dune and non-dune habitats ($U=18$, $p>0.2$). Fifty-two *O. piute* males were collected from May through July at light traps. Four *O. piute* males were found at the NTS in June and July, but were not published in Ferguson (1967) or Allred (1973), because it remained undescribed until Mickel & Clausen (1983).

***Odontophotopsis quadrispinosa* Schuster, 1958**

Odontophotopsis quadrispinosa Schuster, 1958: 51, ♂. Neotype (designated by Pitts *et al.* 2009): California, Palm Springs (UMSP).

Diagnosis. MALE. The male of this species can easily be recognized by having the marginal cell much shorter than the stigma as measured along the costal vein, and two

pair of mesosternal processes forming a square, with the anterior pair much more obvious than the posterior pair. Also, the mandibles are deeply emarginate along the ventral margin, but the mandible narrows towards the apex (see Pitts 2007: Fig. 67). Genitalia are illustrated by Pitts *et al.* (2009: Fig. 18). FEMALE. Unknown.

Material examined. Type material. *Neotype* of *O. quadrispinosa*: California, Palm Springs, 1 May 1933, at light, Theo. Zschokke (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 5: 2 ♂, LT, 13.VI.2008, NFB and DAT, 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, NFB.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active in late spring (late May through June).

Remarks. *Odontophotopsis quadrispinosa* were too rarely encountered to determine their habitat preference. Four *O. quadrispinosa* males were collected in May and June at light traps. Thirty-five *O. quadrispinosa* males were found at the NTS via light traps, mammal trap and berlese funnel (Ferguson 1967).

This species is rare throughout its range and the taxonomy of this species is discussed in Pitts *et al.* (2009). This species can be difficult to identify, because the mesosternal processes are weak and sometimes difficult to observe. As such, this species could be confused as a species of *Sphaerophthalma* Blake, 1871, but the genitalia are distinct.

***Odontophotopsis serca* Viereck, 1904**

(Figs 3.8, 3.16)

Odontophotopsis sercus Viereck, 1904: 87, ♂. Holotype: Mexico, Lower California (ANSP).

Diagnosis. MALE. This species can be recognized by the lack of a clypeal tubercle, by having deeply excised mandibles with a vertical apex (Fig. 3.8), by having simple but prominent mesosternal processes, and by lacking a sternal felt line. Genitalia are illustrated in Fig. 3.16. FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. sercus*: Mexico, Lower California, type no. 4979 (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 26-28.V.2009, 3 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 2: 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 5 ♂, LT, 23-25.VI.2009, 5 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 1 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 4: 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 4: 1 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 5: 4 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, LT, 4-6.IX.2009, NFB.

Distribution. USA (Arizona, California and Nevada), Mexico (Baja California).

Activity. Males were active throughout the summer and into mid-autumn (June through mid-October).

Remarks. *Odontophotopsis serca* were collected significantly more often in non-sand dune habitats than in sand dune habitats ($U=24$, $p=0.02$). Thirty-seven *O. serca* males were collected from May through October at light traps. Sixteen *O. microdonta* males were found at the NTS via light and mammal traps (Ferguson 1967).

Odontophotopsis serca unlike *O. armata* lacks a felt line on the second metasomal sternite and can be easily confused with this species. The clypeal tubercle, however, is distinct in *O. armata*. This species, along with *O. melicausa*, has a tendency to develop a

slight secondary mesosternal tubercle posterior to the primary one. Sometimes this can be unilateral (Ferguson 1967). The taxonomy is discussed in more detail in Pitts *et al.* (2009).

***Odontophotopsis setifera* Schuster, 1952**

(Fig. 3.17)

Odontophotopsis (Odontophotopsis) setifera Schuster, 1952: 47, ♂. Holotype:

California, Riverside County, Palms to Pines Highway (UMSP); 1958: 56, ♂.

Diagnosis. MALE. This species can be recognized by its unique mandibular morphology. The mandible has the apex vertical and has four teeth with the dorsal tooth separated from the remaining teeth by a deep sinus (Fig. 3.17). Other potentially useful characters are listed in Pitts (2007) and Pitts *et al.* (2009). Genitalia are illustrated by Pitts (2007: Figs 30, 31). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *O. setifera*: California, Riverside County, Palms to Pines Highway, 28 May 1940, R.M. Bohart (UMSP). Other material. Nevada, Nye Co., AMNWR: Non-dune site 3: 1 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 2: 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 5: 1 ♂, LT, 17-19.VIII.2009, NFB; Non-dune site 5: 1 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 21-23.VII.2009, NFB; Copeland site: 1 ♂, LT, 13.VI.2008, NFB.

Distribution. USA (Arizona, California and Nevada), Mexico (Baja California).

Activity. Males were active throughout the summer (June through August).

Remarks. *Odontophotopsis setifera* were too rarely encountered to determine their habitat preference. Seven *O. setifera* males were collected from June through August at

light traps. Two *O. setifera* males were found at the NTS in July via light trapping (Ferguson 1967; Allred 1973).

***Odontophotopsis sonora* Schuster, 1958**

Sphaerophthalma (Micromutilla) sonora Schuster, 1958: 16, ♂. Holotype: Arizona, Tucson (UMSP).

Diagnosis. MALE. This species can be recognized by the lack of a tooth on the ventral margin of the mandible, the mandibular apex is tridentate and oblique (see Pitts 2007: Fig. 32), and by the clypeus being elongate and projecting over the dorsal margins of the mandibles. Also, this species lacks mesosternal armature, even though it is placed in the genus *Odontophotopsis*. Genitalia are illustrated by Pitts *et al.* (2009: Figs 20, 21).

FEMALE. Unknown, but will possibly be similar to the females of the *O. melicausa* species-group based on male morphology.

Material examined. Type material. *Holotype* of *S. sonora*: Arizona, Tucson, 10 Sep 1935. Bryant (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 4: 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 1: 7 ♂, LT, 26-28.V.2009, NFB, 4 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 2: 1 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 3: 1 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 4: 1 ♂, LT, 26-28.V.2009, NFB, 19 ♂, LT, 8-15.VI.2009, NFB & DAT, 10 ♂, LT, 23-25.VI.2009, 6 ♂, LT, 6-8.VII.2009, 21 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-

19.VIII.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Non-dune site 5: 2 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 6-8.VII.2009, NFB; Spring meadows site: 1 ♂, PT, 26.VI.2008, NFB, DAT & JPP, 1 ♂, PT, 24.VII.2008, NFB & DAT, 4 ♂, PT, 5.VIII.2008, 3 ♂, PT, 2-3.IX.2008, NFB.

Distribution. USA (Arizona, California, Nevada and Utah).

Activity. Males were active from late spring through late summer (late May through early September).

Remarks. *Odontophotopsis sonora* were distributed uniformly over sand dune and non-dune habitats ($U=18$, $p>0.2$). One hundred six *O. sonora* males were collected from late May through early September at light traps. One hundred thirty-six *O. sonora* males were found at the NTS from June to August via pan trapping, light trapping and net collecting (Ferguson 1967; Allred 1973).

***Sphaerophthalma amphion* (Fox, 1899)**

Mutilla amphion Fox, 1899: 263, ♂. Lectotype (designated here): Nevada (ANSP).

Photopsis abstrusa Baker, 1905: 113, ♂. Holotype: California (CUIC).

Photopsis nudata Baker, 1905: 114, ♂. Holotype: Clairmont, California (CUIC).

Diagnosis. MALE. The male of this species can be recognized by having the mandible with a somewhat tapered apex and with the dorsal carina becoming obsolete distally such that the distal portion of mandible is oblique (see Pitts *et al.* 2010a: Fig. 15). Also, the marginal cell length is short being $0.5-0.9 \times$ length of stigma, and this species lacks a sternal felt line. In addition to the mandibular morphology, the genitalia are diagnostic. The cuspis is elongate ($0.7-0.8 \times$ free length of paramere) and is dilated towards its apex

and has the ventral portion, especially at the apex and inner margin, clothed with long dense setae that have their apices plumose. Genitalia are illustrated by Pitts *et al.* (2010a: Fig. 52). FEMALE. The female of this species can be recognized by the following characters: the dorsum lacks dense appressed setae obscuring the integumental sculpture, the first segment of the metasoma is sessile with the second segment, the antennal scrobes have dorsal carinae, the mandible has a slightly developed ventral basal tooth and lacks a dorsal tooth at the termination of the dorsal carina, flagellomere 1 is almost $2 \times$ as long as the pedicel, the legs are concolorous with mesosoma, or at most slightly darker or lighter than mesosoma, the propodeum length in lateral view is subequal to $0.5 \times$ maximum height, the metasomal segments have sparse to dense plumose pubescence apically, the apical metasomal segments are concolorous with the basal segments, T2 is coarsely confluent punctate laterally and on basal ~ 0.66 , apical ~ 0.33 with sparse indiscernible punctures, the pygidium undefined laterally by carinae, and plumose setae are present on the metasomal fringes.

Material examined. Type material. *Lectotype* of *M. amphion*: Nevada, Type no. 4654 (ANSP). *Holotypes*: *Ph. abstrusa*: California (CUIC); *Ph. nudata*: Clairmont, California (CUIC). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 3: 1 ♂, LT, 29-31.X.2009, NFB and SDB.

Distribution. USA (Arizona, California, Colorado, Nevada, New Mexico and Utah), Mexico (Baja California).

Activity. One male was collected in late October 2009. No females were collected.

Remarks. *Sphaerophthalma amphion* were too rarely encountered to determine their habitat preference. Only one *S. amphion* male was collected in late October at a light trap. Ten *S. amphion* males were found at the NTS in August at light traps and a mammal trap (Ferguson 1967). This species is widespread throughout much of the western United States (Pitts *et al.* 2004). Host data and taxonomy for this species is presented in Pitts *et al.* (2004).

For this study I have designated a lectotype from the available syntypes. I selected the lectotype from the only specimen available. The label data are as follows [Nev.] [Type no. 4654] [M. *amphion* Fox]. The metasoma is broken off, but is still with pinned portion of the specimen.

***Sphaerophthalma angulifera* Schuster, 1958**

Sphaerophthalma (Photopsis) angulifera Schuster, 1958: 32, ♂. Holotype: California, Kern County, Bakersfield (CASC).

Diagnosis. MALE. The male of this species can be recognized by having mandibles that are weakly excised ventrally with a distinct angulate basal tooth and an apex that is tridentate and oblique, but most importantly the dorsal carina of the mandible is angulate at the midpoint of the mandible coinciding with the ventral tooth (see Pitts *et al.* 2010a: Fig. 54), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia also help to diagnose this species; the cuspis is a uniform diameter from the base to the apex (see Pitts *et al.* 2010a: Fig. 53). FEMALE. The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered

with moderately dense erect pale golden brachyplumose setae that do not obscure the integument; the ventral margin of the mandible has a slight excision followed by a distinct angulate tooth and lacks a dorsal tooth at the termination of the dorsal carina; the head below the eyes widens towards the mandibular insertions; the first metasomal segment is sessile with the second; the pygidium is granulate; and the apical margins of the tergites have dense fringes of white plumose setae.

Material examined. Type material. *Holotype* of *S. angulifera*: California, Kern County, Bakersfield (CASC). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 5: 1 ♀, PT, 8.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT; Copeland site: 1 ♀, PT, 24.VI.2008, NFB, DAT & JPP; Mesquite site 1: 1 ♀, PT, 8.VII.2008, NFB & DAT; Mesquite site 2: 1 ♀, PT, 24.VI.2008, NFB, DAT & JPP.

Distribution. USA (California and Nevada).

Activity. No males were collected. Females were collected in early through mid-summer (late June through July 2008).

Remarks. *Sphaerophthalma angulifera* were too rarely encountered to determine their habitat preference. Five *S. angulifera* females were collected from late June through July in pitfall traps. Nine female and twelve male *S. angulifera* were found at the NTS via pitfall traps (Ferguson 1967; Allred 1973). Female were found from May through July and males were found from late June through early September.

Sphaerophthalma angulifera is morphologically similar to *S. unicolor* and *S. mendica*, but can be differentiated from these two species by mandibular morphology (Wilson & Pitts 2009). Although this species is found throughout the Mojave and western Sonoran

deserts, it is extremely rare. Wilson and Pitts (2009) diagnosed the female based on associations made from similarities of the female to that of *S. mendica* and distributional data.

***Sphaerophthalma arota* species-complex (Cresson, 1875)**

Mutilla Arota Cresson, 1875: 120, ♀. Holotype: California, San Diego (UMSP).

Mutilla helicaon Fox, 1899: 254, ♂. Holotype: Nevada (UMSP).

Photopsis lingulatus Viereck, 1903: 737, ♂. Holotype: California, San Diego County, La Jolla (UMSP).

Sphaerophthalma (Photopsis) carinata Schuster, 1958: ♂. Holotype: Baja California, Purissima (NMNH).

Sphaerophthalma (Photopsis) helicaon coahuilae Schuster, 1958: 34, ♂. Holotype: lost.

Sphaerophthalma (Photopsis) helicaon diegueno Schuster, 1958: 35, ♂. Holotype: Arizona, S. Carlos (CUIC).

Diagnosis. MALE. This species is easily recognized by the weak excision and slight angulate tooth on the ventral margin of the mandible (see Pitts *et al.* 2009: Fig. 102), the apex of the mandible is oblique, the clypeus being carinate at base, but sometimes delicately so or gibbous, the lack of mesosternal processes or a sternal felt line, and the ventral margin of the paramere having dense setae that are directed inward toward the cuspis (see Pitts *et al.* 2009: Fig. 100). FEMALE. The female of this species can be diagnosed by the following combination characters: the mandible has only a weak angulate basal tooth on the ventral margin and lacks a dorsal tooth at the termination of

the dorsal carina (Fig. 40 and Pitts *et al.* 2009: Fig. 40), the mesosoma and second tergite of the metasoma is covered in brachyplumose orange setae surrounded by white setae along the margins (see Pitts *et al.* 2009: Figs 97, 98), the dorsum lacks dense appressed setae obscuring the integumental sculpture, the metasoma is petiolate, and the pygidium is granulate.

Material examined. Type material. *Holotypes*: *M. arota*: California, San Diego, G.R. Crotch, Type no. 1873 (UMSP); *M. helicaon*: Nevada, Type no. 4642 (UMSP); *Ph. lingulatus*: California, San Diego County, La Jolla (UMSP); *S. carinata*: Baja California, Purissima (NMNH); *S. helicaon diegueno*: Arizona, S. Carlos, 12-13 May 1918, J. Ch. Bradley (CUIC). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 2 ♂, LT, 26-28.V.2009, 3 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 16-18.X.2009, NFB; Non-dune site 2: 2 ♂, LT, 12-14.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 3 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 2 ♂, LT, 12-14.V.2009, 1 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 1 ♂, LT, 12-14.V.2009, 6 ♂, LT, 26-28.V.2009, NFB, 4 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 18-23.IX.2009, 3 ♂, LT, 16-17.X.2009, NFB; Sand dune site 1: 5 ♂, LT, 12-14.V.2009, 4 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 21-23.VII.2009, 4 ♂, LT, 4-6.IX.2009, 5 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB; Sand dune site 2: 1 ♂, LT, 29.V.2008, NFB & DAT, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 1 ♂, LT, 26-28.V.2009, NFB;

Sand dune site 4: 5 ♂, LT, 9.VI.2008, NFB & DAT, 1 ♂, PT, 25.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 12-14.V.2009, NFB, 15 ♂, LT, 8-15.VI.2009, NFB & DAT, 11 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 7 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 7 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 16-18.X.2009, NFB; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 5: 2 ♂, LT, 13.VI.2008, 1 ♂, LT, 23.VII.2008, NFB & DAT, 9 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, NFB, 7 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, 12 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2-4.X.2009, 8 ♂, LT, 16-18.X.2009, NFB; Copeland site: 4 ♂, LT, 5.V.2008, DAT, 4 ♂, LT, 14.V.2008, 8 ♂, LT, 30.V.2008, 5 ♂, LT, 13.VI.2008, NFB & DAT; Wash site: 13 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California, Nevada, New Mexico and Texas), Mexico (Baja California).

Activity. Males were active from mid-spring through mid-autumn (May through mid-October). No females were collected.

Remarks. *Sphaerophthalma arota* were distributed uniformly over sand dune and non-dune habitats ($U=16$, $p>0.2$). Two hundred twelve *S. arota* males were collected from May through October in light and pitfall traps. Only one *S. arota* male was found at the NTS in June via light trapping (Ferguson 1967).

Wilson *et al.* (2010) performed a phylogenetic analysis of this species. The study concluded that *S. arota* is composed of four genetically distinct species that cannot be distinguished morphologically based on current methods and suggested that the members

of this group be identified as the *S. arota* species-complex. It is likely from this study that only one of the species occurs at AMNWR. Wilson *et al.* (2010) also used this species for a biogeographical study. They found that major diversification events in this species complex were linked to late Neogene mountain building and aridification events, specifically the uplift of the mountain ranges in southern California and the expansion of the Bouse Sea.

***Sphaerophthalma becki* Ferguson, 1967**

Sphaerophthalma (Micromutilla) becki Ferguson, 1967: 9, ♂. Holotype: Nevada, Nye County, Hillside, 0.85 mi NNW Mercury (NMNH).

Diagnosis. MALE. This species is recognized by the deeply excised mandible with the tooth forming an oblique angle (see Pitts *et al.* 2009: Fig. 45), the lack of mesosternal processes, the marginal cell shorter than the stigma, the first segment of the metasoma petiolate with the second segment, and the genitalia with a short cylindrical cuspis (see Pitts *et al.* 2009: Fig. 2). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *S. becki*: Nevada, Nye County, Hillside, 0.85 mi NNW Mercury, 23 Aug 1964, W.E. Ferguson (NMNH). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 26-28.V.2009, 1 ♂, PT, 7.VII.2009, 6 ♂, LT, 4-6.VIII.2009, NFB; Non-dune site 2: 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, NFB; Non-dune site 3: 2 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 10 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, 5 ♂, LT, 21-23.VII.2009, 19 ♂, LT, 4-6.VIII.2009, 13 ♂, LT, 17-19.VIII.2009, 1 ♂, PT, 4.IX.2009, NFB; Non-dune site 4: 9 ♂, LT, 8-15.VI.2009, NFB & DAT, 5 ♂, LT, 23-

25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 11 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 1: 8 ♂, LT, 26.VI.2008, NFB, DAT & JPP, 1 ♂, PT, 5.VIII.2008, NFB, 1 ♂, PT, 19.XII.2008, NFB & SDB, 99 ♂, LT, 26-28.V.2009, NFB, 15 ♂, LT, 1 ♂, PT, 8-15.VI.2009, NFB & DAT, 26 ♂, LT, 23-25.VI.2009, 10 ♂, LT, 6-8.VII.2009, 60 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 2 ♂, PT, 4-6.VIII.2009, 35 ♂, LT, 17-19.VIII.2009, 6 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 2: 2 ♂, LT, 26-28.V.2009, 3 ♂, LT, 6-8.VII.2009, 5 ♂, LT, 1 ♂, MT, 21-23.VII.2009, 2 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 3: 1 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 4: 2 ♂, LT, 23-25.VI.2009, 1 ♂, MT, 6-9.VII.2009, 10 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 5: 2 ♂, LT, 13.VI.2008, NFB & DAT, 7 ♂, LT, 24.VI.2008, NFB, DAT & JPP 2 ♂, LT, 23.VII.2008, NFB & DAT, 4 ♂, LT, 26-28.V.2009, 3 ♂, LT, 6-8.VII.2009, 6 ♂, LT, 21-23.VII.2009, 13 ♂, LT, 17-19.VIII.2009, 4 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 5: 6 ♂, LT, 26-28.V.2009, NFB, 4 ♂, LT, 8-15.VI.2009, NFB & DAT, 6 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, 15 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-8.VIII.2009, 4 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Copeland site: 1 ♂, LT, 13.VI.2008, 1 ♂, LT, 14.V.2008, NFB & DAT; Spring meadows site: 1 ♂, PT, 26.VI.2008, NFB, DAT & JPP, 1 ♂, PT, 5.VIII.2008, NFB.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active from late spring throughout the summer (June through September).

Remarks. *Sphaerophthalma becki* were distributed uniformly over sand dune and non-dune habitats (U=13.5, p>0.2). Four hundred eighty-eight *S. becki* males were collected from late May through September via light, pitfall and malaise trapping. Eighteen *S. becki* males were found at the NTS from July through August via light and pitfall trapping (Ferguson 1967).

***Sphaerophthalma blakeii* (Fox, 1893)**

Photopsis Blakeii Fox, 1893: 6, ♂. Lectotype (designated by Ferguson 1967): Baja California, San Jose del Cabo (ANSP).

Mutilla Gautschii Dalla Torre, 1897: 43. Unnecessary replacement name for

Photopsis blakeii Fox, 1893, nec *Mutilla blakei* Cameron, 1894.

Mutilla ceyx Fox, 1899: 262, ♂. Lectotype (designated by Ferguson 1967): Calmili Mines (ANSP).

Diagnosis. MALE. This species is easily recognized by the posterior margin of the head being quadrate, by the weakly excised mandible that is dilated apically (see Pitts *et al.* 2009: Fig. 37), by the large stigma that is slightly longer than the marginal cell, by the denticles on the internal margin of the hind coxa, by the lack of mesosternal processes, by the quadrate pygidium, and by the lobate dorsoventrally flattened condition of the cuspis, which has long setae along the internal margin that coalesce apically (see Pitts *et al.* 2009: Fig. 23). FEMALE. The female of this species can be diagnosed by the following combination characters: the dorsum of the body is covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible lacks an excision and lacks a dorsal tooth at the termination of the dorsal carina,

the head below eyes is parallel, the head evenly rounded in lateral view, the first metasoma segment is sessile with the second segment and the pygidium is granulate.

Material examined. Type material. *Lectotype* of *Ph. blakeii*: Baja California, San Jose del Cabo (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 18-23.IX.2009, 6 ♂, LT, 16-18.X.2009, NFB; Non-dune site 2: 2 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 18-23.IX.2009, 3 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 7 ♂, LT, 12-14.V.2009, 7 ♂, LT, 26-28.V.2009, NFB, 1 ♂, PT, 10.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 2-4.X.2009, 1 ♂, LT, 16-17.X.2009, NFB; Non-dune site 4: 1 ♀, PT, 7-8.VII.2008, NFB & DAT, 2 ♂, LT, 12-14.V.2009, 13 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 1: 1 ♀, PT, 15 ♂, LT, 12-14.V.2009, 14 ♂, LT, 26-28.V.2009, NFB, 1 ♀, PT, 1 ♂, LT, 1 ♂, PT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB, 1 ♂, LT, 29-31.X.2009, NFB & SDB; Sand dune site 2: 1 ♂, LT, 15.V.2008, 6 ♂, LT, 29-30.V.2008, NFB & DAT, 2 ♂, LT, 26-28.V.2009, 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 2 ♂, LT, 12-14.V.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 4: 2 ♂, LT, 9.VI.2008, NFB & DAT, 4 ♂, LT, 12-14.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, NFB; Sand dune site 5: 1 ♂, LT, 18.IV.2008, NFB & DAT, 3 ♂, LT, 24-26.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 5: 3 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-

23.VII.2009, 7 ♂, LT, 18-23.IX.2009, 4 ♂, LT, 16-18.X.2009, NFB; Copeland site: 6 ♂, LT, 5.V.2008, DAT, 19 ♂, LT, 14-15.V.2008, 4 ♂, LT, 30.V.2008, 1 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, PT, 24.VI.2008, NFB, DAT & JPP; Wash site: 15 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California, Nevada, and Utah), Mexico.

Activity. Males were active from early spring through mid-autumn (mid-April through late June through October). Females were collected from mid to late summer in 2008 and mid-spring to early summer in 2009 (July through August 2008, May through early June 2009).

Remarks. *Sphaerophthalma blakeii* were distributed uniformly over sand dune and non-dune habitats ($U=19$, $p>0.2$). Five female and 189 male *S. blakeii* were collected throughout the course of this study. The females were collected from May through early August in pitfall traps, and the males were collected from mid-April through October via light and pitfall trapping. Five *S. blakeii* males were found at the NTS in June and October via light and pitfall trapping (Ferguson 1967; Allred 1973). Pitts *et al.* (2009) recently associated the sexes of this species and discussed the taxonomy.

***Sphaerophthalma difficilis* (Baker, 1905)**

Photopsis difficilis Baker, 1905: 114, ♂. Holotype: California Claremont (CUIC).

Sphaerophthalma (Micromutilla) maricopella purismella Schuster, 1958: 17, ♂.

Holotype: Lost.

Sphaerophthalma (Micromutilla) maricopella maricopella Schuster, 1958: 17, ♂.

Holotype: Lost.

Sphaerophthalma (Micromutilla) maricopella castanea Schuster, 1958: 17, ♂.

Holotype: Lost.

Sphaerophthalma (Micromutilla) californiense californiense Schuster, 1958: 18, ♂.

Holotype: Lost.

Sphaerophthalma (Micromutilla) californiense fuscatella Schuster, 1958: 18, ♂.

Holotype: Lost.

Sphaerophthalma (Micromutilla) quijotoa quijotoa Schuster, 1958: 18, ♂. Holotype:

Lost.

Sphaerophthalma (Micromutilla) quijotoa parrasia Schuster, 1958: 18, ♂. Holotype:

Lost.

Diagnosis. MALE. This species is recognized by the deeply excised vertical mandible with the tooth forming an acute angle (see Pitts *et al.* 2009: Fig. 38), the lack of mesosternal processes, the marginal cell shorter than the stigma, the first segment of the metasoma petiolate with the second segment and densely punctate, the second sternite with an anteromedial tumid region, and the genitalia with a long cylindrical cuspis that is setose ventrally with the apex having longer denser setae and parameres with dense setae located medially, but internally directed, along the internal margin (see Pitts *et al.* 2009: Fig. 3). FEMALE. The female of this species can be diagnosed by the following combination characters: the dorsum of the body is covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible with a deep excision subtended by a large rounded tooth and lacks a dorsal tooth at the termination of the dorsal carina, the head below eyes is parallel, the head

evenly rounded in lateral view, the first metasoma segment is petiolate with the second segment and the pygidium is striate to granulate.

Material examined. Type material. *Holotype* of *Ph. difficilis*: California Claremont (CUIC). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 2: 1 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, 8 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 3: 8 ♂, LT, 12-14.V.2009, 15 ♂, LT, 26-28.V.2009, NFB, 10 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 6-8.VII.2009, 5 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 7 ♂, LT, 17-19.VIII.2009, 2 ♂, PT, 4.IX.2009, NFB; Non-dune site 4: 1 ♂, PT, 23.VII.2008, NFB & DAT, 2 ♂, LT, 12-14.V.2009, 15 ♂, LT, 26-28.V.2009, NFB, 8 ♂, LT, 8-15.VI.2009, NFB & DAT, 8 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 6-8.VII.2009, 11 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 1: 1 ♂, LT, 26.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 18.IV.2009, 5 ♂, LT, 1 ♂, PT, 12-14.V.2009, 13 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & SDB, 16 ♂, LT, 23-25.VI.2009, 5 ♂, LT, 21-23.VII.2009, 2 ♂, PT, 6.VIII.2009, 5 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 2: 1 ♀, 2 ♂, PT, 2-3.IX.2008, 8 ♂, LT, 12-14.V.2009, 10 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 13 ♂, LT, 6-8.VII.2009, 29 ♂, LT, 21-23.VII.2009, 9 ♂, LT, 17-19.VIII.2009, 3 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 1 ♂, PT, 17-18.X.2008, NFB & SDB, 1 ♂, LT, 28.IV.2009, 2 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, 8 ♂, LT, 23-25.VI.2009, 6 ♂, LT, 6-8.VII.2009, 4 ♂, LT, 21-

23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 1 ♂, PT, 4-6.IX.2009, 5 ♂, LT, 18-23.IX.2009, 1 ♂, PT, 3.X.2009, NFB; Sand dune site 4: 6 ♂, LT, 12-14.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 12 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 4-6.IX.2009, 4 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 5: 15 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 2 ♂, LT, 10.VII.2008, 5 ♂, LT, 24.VII.2008, NFB & DAT, 17 ♂, LT, 12-14.V.2009, 4 ♂, LT, 26-28.V.2009, NFB, 5 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 9 ♂, LT, 6-8.VII.2009, 19 ♂, LT, 21-23.VII.2009, 5 ♂, LT, 4-6.VIII.2009, 17 ♂, LT, 17-19.VIII.2009, 1 ♂, PT, 4.IX.2009, NFB, 1 ♂, PT, 30.X.2009, NFB & SDB; Non-dune site 5: 1 ♀, PT, 24.VI.2008, NFB, DAT & JPP, 3 ♂, LT, 23.VII.2008, NFB & DAT, 2 ♀, PT, 5.VIII.2008, 10 ♂, LT, 12-14.V.2009, 13 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & DAT, 15 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 1 ♂, PT, 6-8.VII.2009, 17 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 1 ♂, PT, 4-6.VIII.2009, 7 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB; Copeland site: 1 ♂, LT, 5.V.2008, DAT, 2 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, PT, 24.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 22.VII.2008, NFB & DAT, 2 ♀, PT, 5.VIII.2008, NFB; Spring meadows site: 1 ♂, PT, 26.VI.2008, NFB, DAT & JPP, 1 ♂, PT, 10.VII.2008, NFB & DAT, 3 ♀, PT, 5.VIII.2008, 1 ♀, PT, 2-3.IX.2008, NFB; Mesquite site 1: 1 ♀, PT, 2-3.IX.2008, NFB.

Distribution. USA (Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, Washington, and Wyoming), Mexico (Baja California), Canada (British Columbia).

Activity. Males were active from mid-spring through mid-autumn (May through October). Females were collected in late summer (July and August through September 2008).

Remarks. *Sphaerophthalma difficilis* were distributed uniformly over sand dune and non-dune habitats ($U=18$, $p>0.2$). Twelve female and 522 male *S. difficilis* were collected throughout the course of this study. The females were collected from late June through early September in pitfall traps, and the males were collected from mid-April through October via light and pitfall trapping. Five *S. difficilis* males were found at the NTS in June and October via light and pitfall trapping (Ferguson 1967).

Wilson and Pitts (2010) performed a phylogenetic analysis of *S. difficilis* and used this species to identify potential Pleistocene refugia in the North American cold deserts. Their research on this species provided evidence that in addition to desert-like conditions persisting through the ice age in parts of the Nearctic warm deserts, many areas maintained desert-like characteristics in the regional cold deserts. This species is closely related to *S. django*, which is restricted to the Algodones Sand Dunes (Pitts *et al.* 2009).

***Sphaerophthalma edwardsii* (Cresson, 1875)**

(Fig. 3.18)

Mutilla Edwardsii Cresson, 1875: 119, ♂. Holotype: Oregon (ANSP).

Sphaerophthalma (Photopsis) edwardsii edwardsii: Schuster 1958: 36, ♂.

Sphaerophthalma (Photopsis) edwardsii flammifera Schuster, 1958: 36, ♂. Holotype: California, Antioch (UMSP).

Diagnosis. MALE. The male of *S. edwardsii* can be separated from all other *Sphaerophthalma* species by its coloration. The pubescence varies from yellow to scarlet, while the integumental coloration varies from orange to piceous and the wings are dark brown to black. This species also has the following unique combination of characters. The mandible is diagnostic being moderately dilated, distally little or scarcely wider than at tooth, the ventral basal tooth of the mandible is small, and the apex is vertical (Fig. 3.18). Also, the clypeus is moderately depressed below the dorsal mandibular margin, the sternal felt line is absent, and the genitalic morphology is unique (see Pitts 2006: Figs 8-10). FEMALE. The female of this species is easily recognized by the unique combination of characters: a small ventral angulation is located basally on the mandible, but the mandible lacks a dorsal tooth at the termination of the dorsal carina, metasomal segment 1 distinctly petiolate with the second segment, the pygidium is granulate, plumose setae are present especially on the fringes of the metasomal tergites, and the dorsum is covered in dense long yellow setae that obscures the integumental sculpturing.

Material examined. Type material. **Holotypes:** *M. edwardsii*: Oregon (ANSP); *S. edwardsii flammifera*: California, Antioch, 14 September 1941, J.R. Fisher (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 5: 1 ♀, PT, 8.VII.2008, NFB & DAT.

Distribution. USA (Arizona, California, Idaho, Nevada and Oregon).

Activity. No males were collected. One female was collected in early July 2008.

Remarks. *Sphaerophthalma edwardsii* were too rarely encountered to determine their habitat preference. Only one *S. edwardsii* female was collected in July in a pitfall trap. *Sphaerophthalma edwardsii* was not found at the NTS.

***Sphaerophthalma macswaini* Ferguson, 1967**

Sphaerophthalma (*Micromutilla*) *macswaini* Ferguson, 1967: 12, ♂. Holotype:
Nevada, Nye County, 2.1 mi NE Mercury (NMNH).

Diagnosis. MALE. This species has distinctive tridentate mandibles that are deeply excised ventrally and the apex is vertical and greatly dilated, which is similar to species of *Acrophotopsis* and *Dilophotopsis*, but more so than other species at Deep Canyon (see Pitts *et al.* 2010a: Fig. 24). Additionally, the clypeus is distinctly elongate and projects anteriorly and the genitalia have a distinctively shaped curved cuspis that bears a large seta filled pit (see Pitts *et al.* 2010a: Fig. 58). This species sometimes has weak mesosternal processes located anteromedially. FEMALE. Unknown.

Material examined. Type material. *Holotype* of *S. macswaini*: Nevada, Nye County, 2.1 mi NE Mercury, 24 August 1964, W.E. Ferguson (NMNH). Other material. Nevada, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 6-8.VII.2009, NFB.

Distribution. USA (Arizona, California and Nevada).

Activity. One male was collected in early July 2009.

Remarks. *Sphaerophthalma macswaini* were too rarely encountered to determine their habitat preference. Only one *S. macswaini* male was collected in July in a light trap. Two *S. macswaini* males were found at the NTS in July and August (Ferguson 1967).

The clypeus of this species is diagnostic (Pitts *et al.* 2010a). However, it is elongate and the extreme apex overlies the greatly dilated and deeply excised mandibles, but does not obscure them. Additional taxonomy for this species is presented by Pitts *et al.* (2010a).

***Sphaerophthalma marpesia* (Blake, 1879)**

Mutilla Marpesia Blake, 1879: 247, ♀. Lectotype (designated here): Kansas (ANSP).

Sphaerophthalma [sic!] *luteola* Blake, 1886: 235, ♀. Lectotype (designated here): Utah (ANSP).

Sphaerophthalma (*Photopsis*) *imperialiformis* Viereck, 1906: 189, ♂. Holotype: Kansas, Morton Co. (SEMC).

Sphaerophthalma (*Photopsis*) *imperialiformis imperialiformis*: Schuster, 1958: 34, ♂.

Sphaerophthalma (*Photopsis*) *imperialiformis maricopae* Schuster, 1958: 34, ♂.

Holotype: Arizona, Phoenix (UMSP).

Diagnosis. MALE. The male of *S. marpesia* can be separated from all other nocturnal species by its lack of mesosternal processes and by its coloration; the integument is black throughout except metasomal segment 3–6 are orangish and by the setal coloration of the vertex, pronotum, mesonotum and metasomal segment 2 that varies from silver to orange. The mandible is moderately dilated, distally little or scarcely wider than at tooth, the ventral basal tooth of the mandible is small, and the apex is vertical (see Pitts, 2006: Fig. 6) Also, the head is quadrate posteriorly being long and parallel behind the eyes (see Pitts 2006: Fig. 2), the clypeus is deeply depressed below the dorsal mandibular margin, the sternal felt line is present, and by characteristic genitalic morphology (see Pitts 2006:

Figs 14–16). FEMALE. The female of this species is easily recognized by its unique color pattern (see Pitts 2006: Fig. 25). Other useful characters include the petiolate metasomal segment 1, the small ventral angulation located basally on the mandible, the granulate pygidium, and the presence of plumose setae especially on the fringes of the metasomal tergites.

Material examined. Type material. **Lectotypes:** *M. marpesia*: Kansas, Type no. 4542 (ANSP); *S. luteola*: Utah, Type no. 4543 (ANSP). **Holotypes:** *S. imperialiformis*: Kansas, Morton Co., 3200', June 1902, F.H. Snow (SEMC); *S. imperialiformis maricopae*: Arizona, Phoenix, 25 September 1935, R.H. Crandall (UMSP). Other material. **Nevada,** Nye Co., AMNWR: Non-dune site 1: 3 ♂, LT, 26-28.V.2009, 7 ♂, LT, 23-25.VI.2009, NFB; Non-dune site 2: 3 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, NFB; Non-dune site 3: 1 ♀, PT 12-14.V.2009, 1 ♂, LT, 23-25.VI.2009, NFB; Non-dune site 4: 2 ♂, LT, 26-28.V.2009, 4 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 1: 1 ♂, LT, 12-14.V.2009, 4 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 2: 1 ♂, LT, 12-14.V.2009, 5 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 7 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 3: 2 ♂, LT, 26-28.V.2009, 4 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, NFB; Sand dune site 4: 3 ♂, LT, 9.VI.2008, NFB & DAT, 1 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, NFB, 8 ♂, LT, 8-15.VI.2009, NFB & DAT, 8 ♂, LT, 23-25.VI.2009, NFB, 1 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 5: 4 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 17-19.VIII.2009, NFB; Copeland site: 1 ♂, LT, 30.V.2008, NFB

& DAT; Mesquite site 1: 1 ♂, PT, 24.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 2-3.IX.2008, NFB; Mesquite site 3: 1 ♀, 1 ♂, PT, 2-3.IX.2008, NFB.

Distribution. USA (Arizona, California, Colorado, Idaho, Kansas, Nevada, New Mexico, Oklahoma, Oregon, Texas, Utah and Washington), Mexico.

Activity. Males were active from mid-spring through late summer (May through early September). Two females were collected in early autumn (September 2008) and one was collected in early spring (May 2009).

Remarks. *Sphaerophthalma marpesia* were distributed uniformly over sand dune and non-dune habitats (U=20, p=0.2). Three female and ninety-two male *S. marpesia* were collected throughout the course of this study. The females were collected in May and September via pitfall trapping, and males were collected from May through early September via light and pitfall trapping. *Sphaerophthalma marpesia* was not found at the NTS. Pitts (2006) associated the females of this species and discussed the taxonomy.

The lectotypes of *Mutilla marpesia* and *Sphaerophthalma luteola* were selected based on the quality of the specimens. The label data for *Mutilla marpesia* are as follows [Kan. Snow] [Type no. 4542] [M. marpesia Blake] and the label data for *Sphaerophthalma luteola* are [Utah] [Type no. 4543] [luteola Blake].

***Sphaerophthalma megagnathos* Schuster, 1958**

Sphaerophthalma (Photopsis) megagnathos megagnathos Schuster, 1958: 36, ♂.

Holotype: Arizona, Ehrenberg (UMSP).

Sphaerophthalma (Photopsis) megagnathos aurifera Schuster, 1958: 36, ♂. Holotype:

Arizona, Tinajas Atlas Mountains (UMSP).

Diagnosis. MALE. The male of *S. megagnathos* can be separated easily from all other nocturnal species by mandibular morphology: the mandibles are very broadly dilated, especially ventral portion apically, distally much wider than width at ventral angulation, the ventral basal tooth of the mandible is small, and the apex is vertical (see Pitts 2006: Fig. 7). Also, the head is long and parallel posteriorly, the clypeus is deeply depressed below the dorsal mandibular margin, the mesosternum lacks tubercles, the wings are yellowish-hyaline, and the sternal felt line is absent. The genitalic morphology also is diagnostic (see Pitts 2006: Figs 17–19). In some specimens the coloration of the integument and setae are bright orange, while in others the setal coloration varies from orange to white and the integument is stramineous to castaneous. FEMALE. The female of this species is easily recognized by weak to non-existent ventral angulation located basally on the mandible while the mandible lacks an elongate tooth at the termination of the dorsal carina, distinctly petiolate metasomal segment 1, the granulate pygidium, presence of plumose setae especially on the fringes of the metasomal tergites, the sparse long orange setae that does not obscure the integumental sculpturing and the anterior raised areas just lateral of the midline on the second tergum that has tuberculate sculpturing.

Description of female (hitherto unknown). *Coloration and setal pattern.* Integument ferruginous, except segments 3-6 infuscated, and antenna and legs orange. Femur of hind leg sometimes infuscated. Pronotum, pleura, propodeum, and metasoma except T2 medially with sparse, erect, white to dirty yellow brachyplumose setae not obscuring integumental sculpture. Dorsum of mesosoma and T2 medially with sparse, erect reddish

orange brachyplumose setae not obscuring integumental sculpture. Posterior margin of head, pronotum, pleura, and T1 with short white plumose setae. Fringes of metasomal terga and sterna with dense white plumose setae.

Head. Rounded posteriorly, not as wide as mesosoma; coarsely punctate. Eyes round. Antennal tubercles slightly granulate. Scrobe with lateral carina beginning just below eye, becoming weaker above height of antennal tubercle but continuing to antennal tubercle. Mandible bidentate, with slight ventral angulation basally; dorsal carina continuing to internal tooth. Genal carina absent. Flagellomere 1 $\sim 2.0 \times$ pedicel length; flagellomere 2 $\sim 1.5 \times$ length of pedicel. Clypeus truncate with slight median emargination; tuberculate posteriorly, appearing longitudinally carinate from anterior margin to posterior tubercle.

Mesosoma. As wide as long. Humeral angles dentate. Dorsum with distinct lateral margin. Coarsely punctate. Propleuron coarsely to moderately punctate. Mesopleuron with medial area moderately punctate and produced outward from dorsal to ventral margin; otherwise glabrous and nitid. Metapleuron and lateral faces of propodeum glabrous and nitid. Propodeum with distinct vertical and dorsal faces; reticulate.

Metasoma. Segment 1 distinctly petiolate with segment 2. T1 moderately punctate. T2 coarsely confluent punctate. T2 with anterior raised ovate areas located just lateral of midline with conspicuous raised puncture margins; area with tuberculate sculpture. T3-T5 and S3-S5 micropunctate, appearing granulate. S2 similar in punctation to T2, with anterior medial tumid region. Pygidium laterally defined by carinae, granulate.

Material examined. Type material. *Holotypes:* *S. megagnathos megagnathos:*

Arizona, Ehrenberg, 27 April 1939, F.H. Parker (UMSP); *S. megagnathos aurifera:*

Arizona, Tinajas Atlas Mountains, 1905, W.J. McGee (UMSP). Other material. **Nevada,**

Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 3: 1 ♂, LT, 12-14.V.2009, 2 ♂, LT, 26-28.V.2009, NFB; Non-dune site 4: 6 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT; Sand dune site 1: 1 ♂, LT, 26-28.V.2009, NFB; Sand dune site 2: 2 ♂, LT, 29.V.2008, NFB & DAT; Sand dune site 4: 2 ♀, PT, 24.VI.2008, NFB, DAT & JPP, 3 ♀, PT, 8.VII.2008, 3 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, 1 ♀, PT, 16.IV.2009, NFB, 1 ♀, PT, 10.VI.2009, NFB & DAT, 1 ♂, LT, 21-23.VII.2009, NFB; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP; Non-dune site 5: 1 ♀, PT, 24.VI.2008, NFB, DAT & JPP, 2 ♀, PT, 8.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT, 2 ♀, PT, 2 ♂, LT 12-14.V.2009, 1 ♂, LT, 23-25.VI.2009, NFB; Copeland site: 5 ♂, LT, 14.V.2008, 1 ♂, LT, 30.V.2008, NFB & DAT, 2 ♀, PT, 24.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 8.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, NFB, 1 ♀, PT, 17-18.X.2008, NFB & SDB; Spring meadows site: 1 ♀, PT, 24.VI.2008, NFB, DAT & JPP; Mesquite site 1: 3 ♀, PT, 2.IX.2008, NFB, 2 ♀, PT, 17-18.X.2008, NFB & SDB; Wash site: 42 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active in late spring (May through June). Females were found from spring through mid-autumn (late June through October in 2008 and April through June in 2009).

Remarks. *Sphaerophthalma megagnathos* were distributed uniformly over sand dune and non-dune habitats (U=20.5, p>0.1). Twenty-eight female and sixty-eight male *S. megagnathos* were collected throughout the course of this study. The females were collected from April through October in pitfall traps, and the males were collected from May through July. *Sphaerophthalma megagnathos* was not found at the NTS.

Sphaerophthalma megagnathos is a member of the *S. imperialis* sp.-group, which is made up of four species, *S. imperialis*, *S. edwardsii*, *S. marpesia*, and *S. megagnathos* (Pitts 2006). Besides *S. megagnathos*, all other species in the *S. imperialis* sp.-group have associated females. The morphology of this female is similar to the other three species in this group and can, thus, be associated with the only male lacking an associated female, *S. megagnathos*. A key is provided here for females of the *S. imperialis* sp.-group.

***Sphaerophthalma mendica* (Blake, 1871)**

Agama mendica Blake, 1871: 259, ♂. Lectotype (designated here): Nevada (ANSP).

Mutilla aspasia Blake, 1879: 250, ♀. Holotype: Nevada (ANSP).

Photopsis nebulosus Blake, 1886: 275, ♂. Holotype: Nevada (ANSP).

Diagnosis. MALE. The male of this species can be recognized by having mandibles that are weakly excised ventrally with a indistinct basal tooth and an apex that is tridentate and oblique (see Pitts *et al.* 2010a: Fig. 55), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia of this species are quite similar to those of *S. angulifera*. Genitalia are illustrated by Pitts *et al.* (2010a: Fig. 60). FEMALE. The female of this species can be diagnosed by the following combination of characters: the dorsum

of the body is covered with dense erect red to pale orange brachyplumose setae that obscure the integument; the ventral margin of the mandible has a slight excision, but lacks a ventral tooth and a dorsal tooth at termination of dorsal carina; the head below the eyes widens towards the mandibular insertions; the first metasoma segment is sessile with the second segment; and the pygidium is longitudinally striate and granulate between the striae; the eyes are larger than the distance from the posterior margin of the eye to the vertex of the head (the eye is from 1.2 to 1.4 times as big as the length from the margin of the eye to the vertex of the head); and the apical margins of the tergites have dense fringes of white plumose setae.

Material examined. Type material. *Lectotype* of *A. mendica*: Nevada, type no. 4551 (ANSP). *Holotypes*: *M. aspasia*: Nevada, type no. 4574 (ANSP); *Ph. nebulosus*: Nevada, type no. 4549 (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 4 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 2: 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, 5 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009, NFB; Non-dune site 3: 1 ♀, PT, 16.IV.2009, 1 ♀, PT, 1 ♂, LT, 12-14.V.2009, 16 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 21-23.VII.2009, 29 ♂, LT, 18-23.IX.2009, 2 ♂, LT, 16-17.X.2009, NFB, 1 ♂, LT, 29-31.X.2009, NFB & SDB; Non-dune site 4: 1 ♀, PT, 23.VII.2008, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 8 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 8 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 17-19.VIII.2009, 20 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 1: 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 4: 1 ♂, LT, 12-14.V.2009, NFB; Sand dune site 5: 1 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 5: 2 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 21-

23.VII.2009, 4 ♂, LT, 18-23.IX.2009, NFB; Mesquite site 1: 1 ♀, PT, 8.VII.2008, NFB & DAT.

Distribution. USA (Arizona, California, Colorado, Idaho, Nevada, New Mexico and Utah).

Activity. Males were active from mid-spring through mid-autumn (May through October). Two females were collected, one in July 2009 and one in April 2009.

Remarks. *Sphaerophthalma mendica* were collected significantly more often in non-sand dune habitats than in sand dune habitats ($U=24$, $p=0.02$). Three female and 122 male *S. mendica* were collected throughout the course of this study. The females were collected in April and July via pitfall trapping, and males were collected from May through October via light trapping. One hundred fifty-seven females and 58 males of *S. mendica* were found at the NTS (Ferguson 1967; Allred 1973). The female specimens were collected from April through November via pitfall trapping and the males were collected from July through August via pitfall, light trapping and net collecting.

There is a wide array of integumental coloration in this species (Wilson & Pitts 2010). Specimens range from nearly black integument to a more reddish-brown color characteristic of most nocturnal velvet ants. Female integumental coloration has a range similar to the males. At AMNWR, only the reddish-brown color form was collected.

For this study I have designated a lectotype from the available syntypes. I selected the lectotype from the only specimen available. The label data are as follows [Nev.] [Type no. 4551] [*mendica*].

***Sphaerophthalma nana* (Ashmead, 1896), stat. resurr.**

(Fig. 3.9)

Photopsis nanus Ashmead, 1896: 181, ♂. Lectotype (designated here): Arizona, Tucson (NMNH); Pitts *et al.* 2004: 224, ♂ (as type species of *Micromutilla* Ashmead).

Mutilla acontius Fox, 1899: 266, ♂. Lectotype (designated here): New Mexico, Las Cruces (ANSP), **syn. nov.** .

Mutilla ashmeadii Fox, 1899: 289. Replacement name for *Photopsis nanus* Ashmead, 1896, nec *Mutilla nana* Smith 1879.

Micromutilla ashmeadii (Fox): Krombein 1951: 752, ♂.

Sphaerophthalma (*Micromutilla*) *nana* (Ashmead): Schuster 1958: 16, ♂.

Sphaerophthalma (*Micromutilla*) *acontius* (Fox): Schuster 1958: 16, ♂.

Sphaerophthalma (*Micromutilla*) *acontia* (Fox): Krombein 1979: 1288, ♂.

Photopsis nana Ashmead: Lelej, Brothers 2008: 35, ♂ (as type species of *Micromutilla* Ashmead).

Diagnosis. MALE. This species can be recognized by its small size, the moderately emarginate mandibles (see Pitts 2007: Fig. 27), the small marginal cell, which is shorter than the stigma measured along the costal margin, the lack of mesosternal processes, the genitalia with an extremely short cuspis that barely surpasses the penial valve in lateral view, and the lack of plumose setae even along the margins of the metasomal tergites. Genitalia are illustrated in Fig. 3.9. FEMALE. Unknown.

Material examined. Type material. **Lectotypes:** *Ph. nanus*: Arizona, Tucson, type no. 3279 (NMNH); *M. acontius*: New Mexico, Las Cruces, type no. 3279 (ANSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 26-28.V.2009, NFB; Non-dune site 3: 2 ♂, LT, 4-6.VIII.2009, NFB; Non-dune site 4: 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 1: 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB.

Distribution. USA (Arizona, California, Nevada and New Mexico).

Activity. Males were active from mid-summer through late-summer (late July through September).

Remarks. *Sphaerophthalma nana* were too rarely encountered to determine their habitat preference. Seven *S. nana* males were collected from late May through September at light traps. Twenty *S. nana* males were found at the NTS from July through August via light trapping (Ferguson 1967).

For this study I have designated lectotypes from the available syntypes. I selected the lectotype of *Photopsis nanus* from the only specimen available. The label data are as follows [Tucson Ariz] [collection Ashmead] [Type No. 3279 U.S.N.M.]. The metasoma is broken off, but glued to point and genitalia extruded. The lectotype of *Mutilla acontius* was selected based on having extruded genitalia and the quality of the specimen. The label data are as follows [Ckll. 2297 Las Cruces] [Type no. 4644] [acontius]. The genitalia are extruded and clearly visible.

According to article 59.3 of ICZN (1999), *Photopsis nana* Ashmead, 1896 (misspelled as *nanus*) is valid name, because the replacement name, *Mutilla ashmeadii* Fox, 1899,

has been used before 1961 only by Krombein in the catalogue (Krombein 1951).

Furthermore, *Ph. nana* is the type species of *Micromutilla* Ashmead, 1899. Lastly, using the other available name, *Mutilla ashmeadii* Fox, 1899, could be confused with *Morsyma ashmeadii* Fox, 1899, the type species of related genus *Morsyma* Fox, 1899. For stability and to lessen potential confusion, *Photopsis nana* is reinstated here.

***Sphaerophthalma orestes* (Fox, 1899)**

(Figs 3.10, 3.19)

Mutilla orestes Fox, 1899: 256, ♂. Holotype: no locality data (ANSP).

Mutilla Pattersonae Melander, 1903: 309, ♂. Holotype: California, Fort Washington, 3 October 1895, R. Patterson (NMNH).

Photopsis indigens Baker, 1905: 112, ♂. Holotype: King's Canon, Ormsby Co., Nevada (CUIC).

Photopsis uniformis Baker, 1905: 113, ♂. Holotype: California, Clairmont (CUIC).

Photopsis pedatus Baker, 1905: 115, ♂. Holotype: California, Clairmont (CUIC).

Photopsis ingenuus Baker, 1905: 116, ♂. Holotype: California, Clairmont (CUIC).

Photopsis salmani Mickel, 1938: 178, ♂. Holotype : California, Eagle Lake, 30 July 1936, C.E. Mickel (UMSP).

Sphaerophthalma (Photopsis) salmani fresnoensis Schuster, 1958: 30, ♂. Holotype: lost.

Sphaerophthalma (Photopsis) salmani oregano Schuster, 1958:31, ♂. Holotype: lost.

Diagnosis. MALE. The male of this species can be recognized by having mandibles that are strongly excised ventrally, have a vertical face, have a distinct basal tooth and an apex

that is tridentate and oblique (Fig. 3.19), the posterior margin of the head is rounded, the mesosternum lacks processes, the second metasomal sternite lacks a distinct felt line, the pygidium is glabrous and the cuspis of the genitalia spatulate and lack plumose setae.

Genitalia are illustrated in Fig. 3.10. FEMALE. The female of this species can be diagnosed by the following combination characters: the dorsum of the body is covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible bears a large ventral basal tooth but lacks a dorsal tooth at the termination of the dorsal carina, the head below eyes is parallel, the head evenly rounded in lateral view, the first metasoma segment is petiolate with the second segment and the pygidium is granulate.

Material examined. Type material. *Holotypes*: *M. orestes*, no locality data (ANSP); *M. pattersonae*: California, Fort Washington, 3 October 1895, R. Patterson (NMNH); *Ph. uniformis*: California, Clairmont (CUIC); *Ph. pedatus*: California, Clairmont (CUIC); *Ph. ingenuus*: California, Clairmont (CUIC); *Ph. salmani*: California, Eagle Lake, 30 July 1936, C.E. Mickel (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, MT, 13-15.V.2009, 2 ♂, LT, 26-28.V.2009, NFB; Non-dune site 3: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Non-dune site 4: 5 ♀, PT, 25.VI.2008, NFB, DAT & JPP, 3 ♀, PT, 7-8.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♀, PT, 1 ♂, LT, 12-14.V.2009, 8 ♂, LT, 26-28.V.2009, NFB, 9 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 1 ♀, PT, 7.VII.2009, 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 1: 6 ♀, PT, 3 ♂, LT, 25-26.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 22.VII.2008, NFB & DAT, 2 ♀, PT,

5.VIII.2008, NFB, 3 ♀, PT, 17-18.X.2008, NFB & SDB, 1 ♀, PT, 18-19.II.2009, 1 ♀, PT, 16.IV.2009, 6 ♀, PT, 58 ♂, LT, 12-14.V.2009, 121 ♂, LT, 26-28.V.2009, NFB, 27 ♀, 2 ♂, PT, 10 ♂, 8-15.VI.2009, NFB & DAT, 31 ♂, LT, 23-25.VI.2009, 1 ♀, 2 ♂, PT, 2 ♂, LT, 6-8.VII.2009, 4 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 4-6.IX.2009, 3 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 2: 5 ♂, LT, 15.V.2008, NFB & DAT, 8 ♀, 5 ♂, PT, 25.VI.2008, NFB, DAT & JPP, 4 ♀, PT, 7-8.VII.2008, 7 ♀, 1 ♂, PT, 22-23.VII.2008, NFB & DAT, 3 ♀, PT, 5.VIII.2008, 7 ♀, PT, 2-3.IX.2008, 2 ♀, PT, 16.IV.2009, 1 ♀, PT, 1 ♂, MT, 12 ♂, LT, 12-15.V.2009, 1 ♂, MT, 25 ♂, LT, 26-28.V.2009, NFB, 2 ♀, 1 ♂, PT, 5 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♀, 1 ♂, PT, 3 ♂, LT, 6-8.VII.2009, 33 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 11 ♂, LT, 17-19.VIII.2009, 2 ♂, PT, 1 ♂, LT, 4-6.IX.2009, 3 ♂, LT, 18-23.IX.2009, NFB, 1 ♂, PT, 28.X.2009, NFB & SDB; Sand dune site 3: 5 ♀, PT, 25.VI.2008, NFB & DAT, 2 ♀, PT, 7-8.VII.2008, 3 ♀, PT, 22.VII.2008, NFB & DAT, 2 ♀, 1 ♂, PT, 5.VIII.2008, 4 ♀, PT, 2-3.IX.2008, 2 ♂, LT, 12-14.V.2009, 36 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & DAT, 7 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 6-8.VII.2009, 20 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 6 ♂, LT, 4-6.IX.2009, 8 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 4: 21 ♂, LT, 9.VI.2008, NFB & DAT, 7 ♀, 1 ♂, PT, 25.VI.2008, NFB, DAT & JPP, 1 ♀, 1 ♂, PT, 7-9.VII.2008, 3 ♀, PT, 22.VII.2008, NFB & DAT, 3 ♀, PT, 5.VIII.2008, 1 ♀, PT, 16.IV.2009, 1 ♀, PT, 24 ♂, LT, 12-14.V.2009, 1 ♂, MT, 13 ♂, LT, 26-28.V.2009, NFB, 1 ♀, PT, 72 ♂, LT, 8-15.VI.2009, NFB & DAT, 55 ♂, LT, 23-25.VI.2009, 2 ♀, PT, 5 ♂, LT, 6-8.VII.2009, 18 ♂, LT, 21-23.VII.2009, 4 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 4-6.IX.2009, 9 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-18.X.2009,

NFB; Sand dune site 5: 1 ♀, PT, 96 ♂, LT, 24-25.VI.2008, NFB, DAT & JPP, 7 ♂, LT, 1 ♀, 7-10.VII.2008, 1 ♀, PT, 8 ♂, LT, 22-24.VII.2008, NFB & DAT, 4 ♂, LT, 12-14.V.2009, NFB, 21 ♂, LT, 26-28.V.2009, NFB, 2 ♀, PT, 5 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 5 ♂, LT, 6-8.VII.2009, 28 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 5 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 4-6.IX.2009, 1 ♂, LT, 22-23.IX.2009, NFB; Non-dune site 5: 7 ♂, LT, 13.VI.2008, NFB & DAT, 5 ♀, PT, 25.VI.2008, NFB, DAT & JPP, 2 ♀, PT, 7-8.VII.2008, 4 ♀, PT, 1 ♂, LT, 22-23.VII.2008, NFB, 1 ♀, PT, 5.VIII.2008, 1 ♀, 1 ♂, PT, 2-3.IX.2008, NFB, 3 ♀, PT, 17-18.X.2008, NFB & SDB, 4 ♂, LT, 12-14.V.2009, 22 ♂, LT, 26-28.V.2009, NFB, 1 ♀, PT, 11 ♂, LT, 8-15.VI.2009, NFB & DAT, 10 ♂, LT, 23-25.VI.2009, 1 ♀, PT, 1 ♂, LT, 6-8.VII.2009, 3 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Copeland site: 2 ♂, LT, 14.V.2008, NFB & DAT, 4 ♀, PT, 25.VI.2008, NFB, DAT & JPP, 1 ♀, PT, 2-3.IX.2008, NFB; Spring meadows site: 8 ♀, PT, 25.VI.2008, NFB, DAT & JPP, 2 ♀, PT, 7-8.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, 1 ♀, PT, 2-3.IX.2008, NFB; Mesquite site 1: 1 ♀, PT, 7-8.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT; Mesquite site 2: 6 ♀, 2 ♂, PT, 24-25.VI.2008, NFB, DAT & JPP, 7 ♀, PT, 7-8.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♂, PT, 5.VIII.2008, NFB, 5 ♀, 1 ♂, PT, 17-18.X.2008, NFB & SDB; Mesquite site 3: 6 ♀, 4 ♂, PT, 24-25.VI.2008, NFB, DAT & JPP, 1 ♀, 1 ♂, PT, 7-8.VII.2008, 2 ♀, 1 ♂, PT, 22.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, 4 ♀, 4 ♂, PT, 2-3.IX.2008, NFB, 5 ♀, 2 ♂, PT, 17-18.X.2008, NFB & SDB.

Distribution: USA (Arizona, California, Idaho, Nevada, Oregon, Utah and Washington), Mexico.

Activity. Males were active from mid-spring through mid-autumn (May through October). Females were collected from spring through mid-autumn (late June through October of 2008 and April through July of 2009).

Remarks. *Sphaerophthalma orestes* were collected significantly more often in sand dune habitats than in non-sand dune habitats ($U=25$, $p=0.01$). One hundred ninety-eight female and 965 male *S. orestes* were collected throughout the course of this study. The female specimens were collected from April through October via pitfall trapping. The male specimens were collected from May through October via light and pitfall trapping. *Sphaerophthalma orestes* was not found at the NTS. The absence of *S. orestes* at the NTS is odd because the species is known to be abundant throughout its range, which extends west of the Rocky Mountains from mainland Mexico to southern Canada. The absence of *S. orestes* at the NTS is also not due to mis-identification as Dr. W.E. Ferguson was clearly familiar with *S. orestes* with the description of *S. orestes* biology in Ferguson (1962).

***Sphaerophthalma pallida* (Blake, 1871)**

Agama pallida Blake, 1871: 263, ♂. Holotype: Texas (ANSP).

Sphaerophthalma (*Micromutilla*) *arizonae* Schuster, 1958: 16, ♂. Holotype: Arizona, Tucson (UMSP).

Diagnosis. MALE. This small species can be recognized by the deeply excised mandibles that are oblique apically (see Pitts *et al.* 2010a: Fig. 27), a marginal cell that is

approximately the same length as the stigma, the mesosternum lacks processes, the first metasomal segment is sessile with the second, plumose setal fringes are absent on the metasoma, and the cuspis of the genitalia is very short just barely surpassing the free length of the penis valve (see Pitts *et al.* 2010a: Fig. 61). FEMALE. Unknown.

Material examined. Type material. **Holotypes:** *A. pallida*: Texas, type no. 4552 (ANSP); *S. arizonae*: Arizona, Tucson, 5 June 1935, Bryant (UMSP). Other material. **Nevada,** Nye Co., AMNWR: Non-dune site 1: 5 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 2: 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 9 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Non-dune site 4: 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 1: 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 4 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 2: 1 ♂, LT, 17-19.VIII.2009, NFB; Sand dune site 4: 2 ♂, LT, 23-25.VI.2009, NFB; Sand dune site 5: 1 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 17-19.VIII.2009, NFB.

Distribution. USA (Arizona, California, Nevada, New Mexico, Oklahoma and Texas).

Activity. Males were active from late spring through late summer (June through August).

Remarks. *Sphaerophthalma pallida* were distributed uniformly over sand dune and non-dune habitats ($U=15.5$, $p>0.2$). Forty-two *S. pallida* males were collected from June

through August via light trapping. Seven *S. pallida* males were found at the NTS in August (Ferguson 1967).

***Sphaerophthalma parkeri* Schuster, 1958**

(Figs 3.11, 3.20)

Sphaerophthalma (Photopsis) parkeri Schuster, 1958: 28, ♂. Holotype: Arizona, Ehrenberg (UMSP).

Diagnosis. MALE. The male of this species can be recognized by having mandibles that are vertical and are strongly excised ventrally with a distinct basal tooth and an apex that is tridentate and oblique (Fig. 3.20), the posterior margin of the head is rounded, the mesosternum lacks processes, the second metasomal sternite with a distinct tuft-like felt line, S2 with a anteromedial carinate tumid region, the pygidium is glabrous and the cuspis of the genitalia spatulate and lack plumose setae. Genitalia are illustrated in Fig. 3.11. FEMALE. Unknown.

Material examined. Type material. Holotype of *S. parkeri*: Arizona, Ehrenberg, 27 April 1939, F.H. Parker (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 2: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, NFB; Sand dune site 1: 1 ♂, LT, 8-15.VI.2009, NFB & DAT; Sand dune site 2: 1 ♂, LT, 12-14.V.2009, 1 ♂, LT, 26-28.V.2009, NFB; Sand dune site 5: 2 ♂, LT, 24.VI.2008, NFB, DAT & JPP; Non-dune site 5: 1 ♂, LT, 8-15.VI.2009, NFB & DAT; Copeland site: 1 ♂, LT, 14.V.2008, 2 ♂, LT, 13.VI.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada).

Activity. Males were active from mid-spring into early summer (May through June).

Remarks. Individuals of *S. parkeri* were too rarely encountered to determine their habitat preference. Eleven *S. parkeri* males were collected in May and June via light trapping. *Sphaerophthalma parkeri* was not found at the NTS.

***Sphaerophthalma triangularis* (Blake, 1871)**

Agama triangularis Blake, 1871: 262, ♂. Holotype: Nevada (ANSP).

Diagnosis. MALE. The male of this species is easily recognized by the lobe-like projections on the hind coxae. Other useful characters include the triangular shaped posterior margin of the head, the weakly excised mandible (see Pitts *et al.* 2009: Fig. 40), the lack of mesosternal processes, and the unique triangulate posterior projection of the apex of the hind tibia. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 26). FEMALE. The female of this species has the following combination characters: the dorsum of the body is covered with sparse erect brachyplumose setae, but the integument is not obscured; the ventral margin of the mandible has a slight excision, but lacks a long erect tooth at the termination of the dorsal carina; the head below eyes is parallel; the head evenly rounded in lateral view; the first metasomal segment is sessile with the second segment; and the pygidium is longitudinally striate.

Material examined. Type material. *Holotype* of *A. triangularis*: Nevada (ANSP).

Other material. Nevada, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 1 ♂, MT, 26-28.V.2009, NFB, 1 ♀, PT, 10.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 4-6.IX.2009, NFB; Non-dune site 2: 9 ♂, LT, 26-28.V.2009, NFB, 7 ♂, LT, 8-15.VI.2009, NFB & DAT, 8 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 21-23.VII.2009, 6 ♂, LT, 17-19.VIII.2009, 7 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 3: 1 ♂, LT, 12-

14.V.2009, 5 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 1 ♂, PT, 4.IX.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 2 ♂, LT, 12-14.V.2009, 5 ♂, LT, 26-28.V.2009, NFB, 1 ♀, PT, 13 ♂, LT, 8-15.VI.2009, NFB & DAT, 18 ♂, LT, 23-25.VI.2009, 1 ♀, 1 ♂, PT, 3 ♂, LT, 6-8.VII.2009, 7 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 5 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 1: 1 ♀, 2 ♂, PT, 5.VIII.2008, NFB, 1 ♀, 1 ♂, PT, 19.XII.2008, NFB & SDB, 1 ♀, PT, 3 ♂, LT, 12-14.V.2009, 16 ♂, LT, 26-28.V.2009, NFB, 5 ♂, LT, 8-15.VI.2009, NFB & DAT, 5 ♂, LT, 23-25.VI.2009, 13 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 3 ♂, PT, 4-6.VIII.2009, 3 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 4-6.IX.2009, NFB; Sand dune site 2: 1 ♀, PT, 9.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♀, PT, 1 ♂, LT, 12-14.V.2009, 7 ♂, LT, 26-28.V.2009, NFB, 1 ♀, PT, 10.VI.2009, NFB & DAT, 1 ♀, PT, 2 ♂, LT, 6-8.VII.2009, 8 ♂, LT, 21-23.VII.2009, 4 ♂, LT, 17-19.VIII.2009, 4 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 1 ♀, PT, 17-18.X.2008, NFB & SDB, 10 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 6 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 6-8.VII.2009, 5 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 4 ♂, LT, 17-19.VIII.2009, 3 ♂, LT, 4-6.IX.2009, 4 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 4: 2 ♂, PT, 9.VII.2008, 1 ♀, PT, 22.VII.2008, NFB & DAT, 1 ♀, 4 ♂, PT, 5-6.VIII.2008, 1 ♀, LT, 13.V.2009, 2 ♂, LT, 26-28.V.2009, NFB 2 ♀, PT, 23 ♂, LT, 8-15.VI.2009, NFB & DAT, 10 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 6-8.VII.2009, 23 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 2 ♂, LT, 4-6.IX.2009, 3 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 5: 2 ♀, PT, 5 ♂, LT, 24-26.VI.2008, NFB, DAT & JPP, 2 ♂, LT, 10.VII.2008, 8 ♂,

LT, 24.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, 1 ♀, PT, 6 ♂, LT, 12-14.V.2009, 2 ♂, LT, 26-28.V.2009, NFB, 2 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♀, PT, 7.VII.2009, 12 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 6 ♂, LT, 17-19.VIII.2009, NFB, 1 ♀, PT, 30.X.2009, NFB & SDB; Non-dune site 5: 1 ♂, LT, 13.VI.2008, 2 ♀, PT, 3 ♂, LT, 22-23.VII.2008, NFB & DAT, 1 ♀, 1 ♂, PT, 2-3.IX.2008, 9 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 5 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 2 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Copeland site: 1 ♂, LT, 13.VI.2008, 6 ♂, LT, 14.V.2008, 4 ♂, LT, 30.V.2008, NFB & DAT, 2 ♀, LT, 26.VI.2008, NFB, DAT & JPP, 1 ♀, 1 ♂, PT, 22.VII.2008, NFB & DAT, 1 ♀, 4 ♂, PT, 5.VIII.2008, NFB; Spring meadows site: 1 ♀, PT, 26.VI.2008, NFB, DAT & JPP, 3 ♀, PT, 9.VII.2008, NFB & DAT, 1 ♀, PT, 5.VIII.2008, NFB; Mesquite site 2: 1 ♀, PT, 2-3.IX.2008, NFB; Mesquite site 3: 1 ♀, PT, 17-18.X.2008, NFB & SDB; Wash site: 1 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California, Nevada, New Mexico and Texas), Mexico (Baja California).

Activity. Males were active from mid-spring through late summer (May through early September). Females were collected from spring through mid-autumn (late June through October in 2008 and May through July, and October 2009).

Remarks. *Sphaerophthalma triangularis* were distributed uniformly over sand dune and non-dune habitats ($U=18$, $p>0.2$). Thirty-seven female and 395 male *S. triangularis* were collected throughout the course of this study. The females were collected from May through December via light and pitfall trapping, and males were collected from May

through September via light, pitfall and malaise trapping. *Sphaerophthalma triangularis* was not found at the NTS.

***Sphaerophthalma uro* (Blake, 1879)**

(Fig. 3.21)

Agama uro Blake, 1879: 253, ♂. Lectotype (designated here): Texas (ANSP).

Photopsis melanderi Baker, 1905: 112, ♂. Holotype: Texas, Coryell Co. (CUIC).

Sphaerophthalma (Photopsioides) uro stenognatha Schuster, 1958: 38, ♂. Holotype: Arizona, St. Carlos (UMSP).

Diagnosis. MALE. The male of this species can be recognized by the mandible, which is slightly to very broadly dilated apically, has a sharp dorsal carina that is blade-like to apex of mandible such that the mandible vertical throughout, but has a weak ventral emargination and tooth (Fig. 21). Also, the clypeus strongly depressed, anterior margin hidden below dorsal mandibular rims, the head is quadrate posteriorly, the marginal cell is $0.75-1.0 \times$ the length of the stigma, S2 lacks a felt line and the cuspis of the genitalia are broadly spatulate and bear plumose setae (Pitts *et al.* 2004: Figs 19-21). FEMALE. The female of this species can be recognized by the following characters: the dorsum lacks dense appressed setae that obscures the integumental sculpture, the first segment of the metasoma is sessile with the second segment, the antennal scrobes have dorsal carinae, the mandible has a slightly developed ventral basal tooth and lacks a dorsal tooth at the termination of the dorsal carina, flagellomere 1 is almost $2 \times$ as long as the pedicel, the legs are concolorous with mesosoma or at most slightly infuscated or lighter than mesosoma, the propodeum length in lateral view is subequal to $0.5 \times$ maximum height,

the metasomal segments have sparse plumose pubescence apically and the apical metasomal segments are concolorous with basal metasomal segments, T2 is coarsely punctate throughout with the interstitial distance less than a puncture width and the pygidium is undefined laterally by carinae.

Material examined. Type material. *Lectotype* of *A. uro*: Texas, Type no. 4547 (ANSP). *Holotypes*: *Ph. melanderi*: Texas, Coryell Co., Birkman (CUIC). *S. uro stenognatha*: Arizona, St. Carlos, 27 August 1935, F.H. Parker (UMSP). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 2 ♂, LT, 26-28.V.2009, 7 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 17-19.VIII.2009, 7 ♂, LT, 18-23.IX.2009, 5 ♂, LT, 16-18.X.2009, NFB; Non-dune site 2: 4 ♂, LT, 12-14.V.2009, 4 ♂, LT, 26-28.V.2009, NFB, 6 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 7 ♂, PT, 21-23.VII.2009, 1 ♂, LT, 4-6.VIII.2009, 3 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 3: 2 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 5 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 4: 6 ♂, LT, 26-28.V.2009, NFB, 4 ♂, LT, 8-15.VI.2009, NFB & DAT, 6 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-17.X.2009, NFB; Sand dune site 1: 1 ♀, PT, 19.XII.2008, NFB & SDB, 4 ♂, LT, 12-14.V.2009, 26 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 3 ♂, LT, 23-25.VI.2009, 10 ♂, LT, 21-23.VII.2009, 4 ♂, LT, 17-19.VIII.2009, 3 ♂, LT, 4-6.IX.2009, 3 ♂, LT, 18-23.IX.2009, 4 ♂, LT, 16-18.X.2009, NFB; Sand dune site 2: 2 ♂, LT, 15.V.2008, NFB & DAT, 7 ♂, LT, 12-14.V.2009, 13 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 6-8.VII.2009, 11 ♂, LT, 21-23.VII.2009, 1

♂, LT, 17-19.VIII.2009, 4 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 1 ♂, LT, 1 ♂, MT, 17-18.IV.2009, 3 ♂, LT, 12-14.V.2009, 10 ♂, LT, 26-28.V.2009, 8 ♂, LT, 23-25.VI.2009, 3 ♂, LT, 6-8.VII.2009, 15 ♂, LT, 21-23.VII.2009, 3 ♂, LT, 4-6.VIII.2009, 2 ♂, LT, 17-19.VIII.2009, 15 ♂, LT, 18-23.IX.2009, 1 ♂, LT, 16-17.X.2009, NFB, 1 ♀, PT, 17.XII.2009, NFB & TB Frank; Sand dune site 4: 4 ♂, LT, 9.VI.2008, NFB & DAT, 1 ♀, PT, 2 ♂, LT, 12-14.V.2009, 3 ♂, LT, 26-28.V.2009, NFB, 45 ♂, LT, 8-15.VI.2009, NFB & DAT, 12 ♂, LT, 23-25.VI.2009, 1 ♀, MT, 6-9.VII.2009, 18 ♂, LT, 21-23.VII.2009, 8 ♂, LT, 18-23.IX.2009, 7 ♂, LT, 16-18.X.2009, NFB; Sand dune site 5: 1 ♂, LT, 18.IV.2008, NFB & DAT, 1 ♂, LT, 24.VI.2008, NFB & DAT, 3 ♂, LT, 26-28.V.2009, 1 ♂, LT, 6-8.VII.2009, 10 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 5: 1 ♂, LT, 13.VI.2008, NFB & DAT, 1 ♂, PT, 17-18.X.2008, NFB & SDB, 11 ♂, LT, 26-28.V.2009, NFB, 3 ♂, LT, 8-15.VI.2009, NFB & DAT, 4 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 4-6.IX.2009, 2 ♂, LT, 18-23.IX.2009, NFB; Copeland site: 2 ♂, LT, 5.V.2008, DAT, 2 ♂, LT, 14.V.2008, NFB & DAT; Spring meadows site: 1 ♂, PT, 2.IX.2008, NFB; Mesquite site 1: 1 ♂, PT, 2.IX.2008, NFB; Wash site: 1 ♂, LT, 30.V.2008, NFB & DAT.

Distribution. USA (Arizona, California, Colorado, Kansas, Nevada, Oklahoma, New Mexico, Texas and Utah).

Activity. Males were active from early spring through mid-autumn (mid-April through October). Females were collected year round (one in Dec. 08, one in May 09, one in July 09, one in Dec. 09).

Remarks. *Sphaerophthalma uro* were distributed uniformly over sand dune and non-dune habitats (U=21, p=0.1). Four female and 393 male *S. uro* were collected throughout

the course of this study. The females were collected in May, July and December via pitfall and malaise trapping, and males were collected from April through October via pitfall, malaise and light trapping. *Sphaerophthalma uro* was not found at the NTS.

For this study I have designated a lectotype from the available syntypes. The lectotype was selected based on having extruded genitalia and the quality of the specimen. The label data are as follows [Tex.] [Type no. 4547] [uro]. The genitalia are extruded and clearly visible.

***Sphaerophthalma yumaella* Schuster, 1958**

Sphaerophthalma (Micromutilla) yumaella Schuster, 1958: 19, ♂. Holotype: Arizona, Yuma County, Wellton (CUIC).

Diagnosis. MALE. This species is recognized by the strongly excised mandible (see Pitts *et al.* 2010a: Fig. 31), the lack of mesosternal processes, the marginal cell being shorter than the stigma, the first segment of the metasoma sessile with the second segment, and the genitalia with a long thick cylindrical cuspis that tapers apically and has a large basal pit on the internal margin (see Pitts *et al.* 2009: Fig. 6). FEMALE. Unknown.

Material examined. Type material. *Holotype* of *S. yumaella*: Arizona, Yuma County, Wellton (CUIC). Other material. **Nevada**, Nye Co., AMNWR: Non-dune site 1: 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 2: 1 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 4 ♂, LT, 23-25.VI.2009, 2 ♂, LT, 21-23.VII.2009, 2 ♂, LT, 4-6.VIII.2009, 1 ♂, LT, 17-19.VIII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Non-dune site 3: 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Non-dune site 4: 1 ♂, LT, 26-28.V.2009, 1 ♂, LT, 4-6.VIII.2009, NFB; Sand dune site 1: 19 ♂, LT,

26-28.V.2009, NFB, 2 ♂, LT, 1 ♂, PT, 8-15.VI.2009, NFB & DAT, 2 ♂, LT, 23-25.VI.2009, 4 ♂, LT, 6-8.VII.2009, 5 ♂, LT, 21-23.VII.2009, 1 ♂, LT, 18-23.IX.2009, NFB; Sand dune site 3: 1 ♂, LT, 26-28.V.2009, NFB; Sand dune site 4: 1 ♂, LT, 9.VI.2008, NFB & DAT, 2 ♂, LT, 12-14.V.2009, 14 ♂, LT, 26-28.V.2009, NFB, 1 ♂, LT, 8-15.VI.2009, NFB & DAT, 1 ♂, LT, 23-25.VI.2009, 1 ♂, LT, 6-8.VII.2009, NFB; Sand dune site 5: 3 ♂, LT, 24.VI.2008, NFB, DAT & JPP, 2 ♂, LT, 21-23.VII.2009, NFB; Non-dune site 5: 9 ♂, LT, 6-8.VII.2009, 2 ♂, LT, 21-23.VII.2009, NFB; Copeland site: 1 ♂, LT, 5.V.2008, DAT, 2 ♂, LT, 14.V.2008, NFB & DAT.

Distribution. USA (Arizona, California and Nevada), Mexico (Baja California).

Activity. Males were active from mid-spring through late summer (May through mid-September).

Remarks. *Sphaerophthalma yumaella* were distributed uniformly over sand dune and non-dune habitats ($U=13$, $p>0.2$). Ninety-two *S. yumaella* males were collected from May through September via light trapping. *Sphaerophthalma yumaella* was not found at the NTS.

This species is widespread (Pitts *et al.* 2009). Based on mandibular and genitalic morphology, along with wing venation similarities, this species is closely related to *S. brachyptera* Schuster, *S. noctivaga* (Melander), *S. sublobata* Schuster, and *Odontophotopsis piute* Mickel. Additional taxonomic description for this species can be found in Pitts *et al.* (2009).

Key to the male velvet ants of Ash Meadows National Wildlife Refuge

(Males of *Dasymutilla pseudopappus* are unknown.)

1. Axillae spinose or triangulate; diurnal forms: integument usually dark, from black to ferruginous; apical fringe of T2–6 without plumose setae 39
 - Axillae indistinct; nocturnal forms: integument brown, testaceous or stramineous (except in *S. marpesia* and some individuals of *S. mendica* which have integument black or dark ferruginous and the apical fringe of T2–6 with obvious plumose setae); apical fringe of T2–6 usually with plumose setae 2
2. Mesosternum with large glabrous longitudinal swellings located on either side of the midline *Odontophotopsis mamata* Schuster
 - Mesosternum with spine-like processes, ridges or lacking processes 3
3. Hind coxae with lobes or denticles 4
 - Hind coxae unmodified 5
4. Hind coxae with denticles; hind tibia without lateral expansion
 - *Sphaerophthalma blakeii* (Fox)
 - Hind coxae with lobes; hind tibia with lateral expansion
 - *Sphaerophthalma triangularis* (Blake)
5. Clypeus elongate, but not overlapping mandibles; mandible greatly dilated apically and ventrally excised *Sphaerophthalma macswaini* Ferguson
 - Clypeus not elongate; mandible moderately dilated to not dilated apically 6

6. Hypopygidium flattened; lateral margins of hypopygidium with longitudinal carinae basally; cuspis of genitalia elbowed 7
- Hypopygidium convex; lateral margins of hypopygidium without longitudinal carinae; cuspis of genitalia straight or slightly curved 8
7. Dorsoventrally flattened and elbowed cuspis with a dorsal carina in elbowed region *Dilophotopsis concolor* (Cresson)
- Dorsoventrally flattened and elbowed cuspis lacks a dorsal carina in elbowed region *Dilophotopsis paron* (Cameron)
8. Mesosternum armed with spines or ridges 9
- Mesosternum unarmed, lacking spines or ridges 22
9. Mandible quadridentate, with three apical teeth and a fourth tooth along internal margin that overhangs clypeus; cuspis of genitalia knobbed apically.....
- *Acanthophotopsis falciformis* Schuster
- Mandible apex bidentate, tridentate, or quadridentate, but without a fourth tooth along internal margin that overhangs clypeus; cuspis of genitalia tapering apically 10
10. Mandible greatly dilated with large dorsal tooth separated from other teeth by a deep, wide sinus 11
- Mandible moderately dilated or not dilated, but without a deep, wide sinus 12
11. Clypeus with dense, short, even-length brush of stiff, subclavate setae; clypeus without horseshoe-shaped tubercle posteromedially process; mandibles quadridentate distally (fig. 17) *Odontophotopsis setifera* Schuster

- Clypeus virtually glabrous; clypeus with horseshoe-shaped tubercle posteromedially that overhangs the clypeus as a slight hood-like or nasutiform process; mandibles tridentate distally *Odontophotopsis biramosa* Schuster
- 12. Ventral margin of mandible with deep excision subtended by a large rounded tooth ...
..... 13
- Ventral margin of mandible with weak excision subtended by angulation or small rounded tooth 19
- 13. Pygidium granulate; mesosternal processes bifid *Odontophotopsis bellona* Mickel
- Pygidium glabrous; mesosternum with either only a single tooth on each side of the midline, or with two teeth on each side of the midline separated by a distance greater than their height and forming a square 14
- 14. Marginal cell approximately $0.5 \times$ length of stigma; mesosternum with two teeth on each side of the midline separated by a distance greater than their height and forming a square *Odontophotopsis quadrispinosa* Schuster
- Marginal cell approximately equal to or longer than, the length of stigma; mesosternum with only a single tooth on each side of the midline 15
- 15. Clypeus posteromedially tuberculate *Odontophotopsis armata* Mickel
- Clypeus lacking posteromedial tubercle 16
- 16. S2 lacking a felt line *Odontophotopsis serca* Viereck
- S2 with a felt line 17
- 17. Posterior margin of head quadrate; clypeus depressed below dorsal margin of mandible, appearing concave *Odontophotopsis melicausa* (Blake)

- Posterior margin of head rounded; clypeus level with dorsal margin of mandible or slightly below it 18
18. Apex of mandible slightly less than vertical (fig. 13); mesosternal processes anteromedially situated *Odontophotopsis clypeata* Schuster
- Apex of mandible obviously not vertical, half way between vertical and horizontal (45°) to 60° (fig. 14); mesosternal processes situated more lateral and slightly more posterior than for previous species *Odontophotopsis microdonta* Ferguson
19. Mandible lacking distinct ventral excision (fig. 15); pygidium glabrous
..... *Odontophotopsis piute* Mickel
- Mandible with distinct ventral excision, although excision may be shallow or weak; pygidium granulate 20
20. Mandible broadly dilated apical to ventral excision; metasternum tridentate; sternal felt lines absent; head with posterior margin quadrate
..... *Odontophotopsis inconspicua* (Blake)
- Mandible parallel to slightly dilated apical to ventral excision; metasternum bidentate; sternal felt lines present; head with posterior margin rounded 21
21. Mesosternal processes tall and conspicuous; distal third of mandible dilated
..... *Odontophotopsis acmaea* Viereck
- Mesosternal processes low and indistinct; distal third of mandible attenuated
..... *Odontophotopsis aufidia* Mickel
22. Clypeus overhangs closed mandibles and mandibles with a weak or nonexistent ventral excision *Odontophotopsis sonora* Schuster

| | |
|---|---|
| - Clypeus does not overhang closed mandibles or mandibles with distinct ventral excision | 23 |
| 23. S2 lacking felt line | 24 |
| - S2 with distinct felt line | 29 |
| 24. Mandible with a weak ventral excision and small ventral tooth | 25 |
| - Mandible with a strong ventral excision and large ventral tooth (fig. 19) | |
| <i>Sphaerophthalma orestes</i> (Fox) | |
| 25. Cuspis of genitalia cylindrical, setae simple throughout | 26 |
| - Cuspis of genitalia dorsoventrally flatten, spatulate, with ventral setae plumose towards apex | 28 |
| 26. Clypeus lacking medial raised area or longitudinal carina posteriorly; mandibles broadly dilated, especially ventral portion apically, distally much wider than width at ventral angulation, apex vertical (see Pitts 2006: Fig. 7); clypeus deeply depressed below mandibular rims; parameres lacking large tuft of inward directed setae along ventral margin at base of paramere (see Pitts 2006: Fig. 19) | 27 |
| - Clypeus with medial raised area or longitudinal carina present posteriorly; mandibles not dilated apically, apex oblique; clypeus not depressed below mandibular rims; parameres with inward directed setae along ventral margin at base of paramere; head rounded posteriorly | <i>Sphaerophthalma arota</i> (Cresson) |
| 27. Mandibles very broadly dilated, especially ventral portion apically, distally much wider than width at ventral angulation (Fig. 7); clypeus very deeply depressed below mandibular rims; wings yellowish-hyaline | <i>Sphaerophthalma megagnathos</i> Schuster |

- Mandibles moderately dilated, distally little or scarcely wider than at tooth (fig. 18);
 clypeus moderately depressed; wings dark brown to black
*Sphaerophthalma edwardsii* (Blake)
28. Mandibles with dorsal carina sharp, blade-like to apex of mandible, mandible vertical
 throughout (fig. 21); length of clypeal apical truncation greater than $0.6 \times$ width
 *Sphaerophthalma uro* (Blake)
- Mandibles with dorsal carina becoming obsolete distally, distal portion of mandible
 oblique; length of clypeal apical truncation less than $0.5 \times$ width
 *Sphaerophthalma amphion* (Fox)
29. Cuspis of genitalia cylindrical without setae plumose; S2 usually not tumid basally (if
 second sternite of metasoma is tumid, marginal cell is shorter than stigma); S2 with well-
 developed felt lines (if felt lines are tuft-like, integument is dark) 30
- Cuspis of genitalia dorsoventrally flattened, spatulate, apex with ventral setae plumose; S2
 tumid basally, protuberant, strongly carinate on the tumidity; S2 with tuft-like felt lines ...
 *Sphaerophthalma parkeri* Schuster
30. Sternal felt line tuft-like; mandibles weakly excised ventrally; mandibles vertical and
 broadly dilated, especially ventral portion apically, distally much wider than width at
 ventral angulation (see Pitts 2006: Fig. 6); second metasomal segment and mesosoma
 black or blackish and second segment with pubescence variable from orange to silver
 (see Pitts 2006: Fig. 28) *Sphaerophthalma marpesia* (Blake)
- Sternal felt line well-developed; mandibles weakly to strongly excised ventrally;
 mandibles oblique, not dilated apically; integument stramineous to castaneous (some

- specimens of *S. mendica* can have darken integument but mandibles are obviously oblique) 31
31. Mandibles with the dorsal ridge angulately produced about half-way between base and apex, the dorsal carina suddenly becoming obsolete
 *Sphaerophthalma angulifera* Schuster
- Mandibles without the dorsal ridge anguliform-produced about half-way between base and apex, the dorsal carina gradually becomes obsolete 32
32. Pygidium granulate; apex of mandible oblique; marginal cell longer than stigma as measured along costal margin; mandible with a weak ventral excision and small ventral tooth *Sphaerophthalma mendica* (Blake)
- Pygidium glabrous; apex of mandible vertical; marginal cell longer than stigma as measured along costal margin; mandible with a strong ventral excision and large ventral tooth 33
33. Cuspis of genitalia $\sim 0.5 \times$ free length of paramere; marginal cell $\sim 1.25 \times$ length of stigma; metasoma with dense white plumose fringes, integument usually castaneous around felt lines *Odontophotopsis microdonta* Ferguson
- Cuspis of genitalia length various; marginal cell length equal to or shorter than that of stigma; metasoma with weak white plumose fringes or lacking them altogether 34
35. Angle formed by ventral mandibular excision (obtuse) greater than 90 degrees; cuspis of genitalia $\sim 0.5 \times$ free length of paramere *Sphaerophthalma becki* Ferguson
- Angle formed by ventral mandibular excision (acute) less than 90 degrees; cuspis of genitalia much longer or much shorter 36

36. T2–6 lacking fringes of plumose setae; cuspis of genitalia in lateral view slightly surpassing the apex of the penis valve (cuspis less than $0.25 \times$ the free length of the paramere) *Sphaerophthalma nana* (Ashmead)
- At least T2 fringe with plumose setae medially; cuspis of genitalia in lateral view greatly surpassing the apex of the penis valve (cuspis $\sim 0.75 \times$ the free length of the paramere) 37
37. First segment of metasoma sessile with second segment; setae of cuspis of similar length throughout *Sphaerophthalma yumaella* Schuster
- First segment of metasoma petiolate with second segment; apex of cuspis with a ventral tuft of setae that is longer than at the base of the cuspis 38
38. Apex of mandible attenuated; S2 not tumid basally; cuspis of genitalia with dense straight setae mostly along internal margin; marginal cell $\sim 1 \times$ length of stigma
 *Sphaerophthalma pallida* (Blake)
- Apex of mandible parallel; S2 tumid basally, protuberant, strongly carinate on the tumidity; cuspis of genitalia with dense apical tuft of downward directed setae that are curled at the tips; marginal cell $\sim 0.75 \times$ length of stigma or less
 *Sphaerophthalma difficilis* (Blake)
39. S2 having median pit filled with setae 40
- S2 lacking median pit *Dasymutilla arenivaga* Mickel
40. Setae on dorsum of mesosoma orange to yellow
 *Dasymutilla gloriosa* (de Saussure)
- Setae on dorsum of mesosoma black 41

41. Pronotum emarginate anteromedially; yellow/orange setae covering apical margin of T2 *Dasymutilla chisos* Mickel
- Pronotum not emarginate anteromedially; yellow/orange setae covering apical half of T2 *Dasymutilla satanus* Mickel

A key for the female velvet ants of AMNWR is not presented, because nearly half of all velvet ant females remain unknown. Specifically, the female of *Acanthophotopsis falciformis*, *Dasymutilla chisos*, *Dilophotopsis paron*, *Odontophotopsis acmaea*, *O. armata*, *O. aufidia*, *O. bellona*, *O. biramosa*, *O. microdonta*, *O. piute*, *O. quadrispinosa*, *O. serca*, *O. setifera*, *O. sonora*, *Sphaerophthalma nana*, *S. becki*, *S. macswaini*, *S. pallida*, *S. parkeri* and *S. yumaella* are unknown.

Key to the females of the *Sphaerophthalma imperialis* species-group

1. T2 of metasoma without distinct tubercles located anteriorly just lateral of the midline and pubescence dense on T2 at least along anterior margin 2
- T2 of metasoma with distinct tuberculate sculpturing located anteriorly near margin just lateral of midline and pubescence sparse on T2 ... *Sphaerophthalma megagnathos* Schuster
2. Mesosoma as broad as long; flagellomere 1 less than $2 \times$ length of pedicel, subequal in length to flagellomere 2; pubescence of head, mesosoma and metasoma not concolorous 3
- Mesosoma longer than broad; flagellomere 1 more than $2 \times$ length of pedicel, noticeably longer than flagellomere 2; pubescence of head, mesosoma and metasoma

- reddish to orange or yellow, concolorous except plumose fringes on metasomal tergites whitish *Sphaerophthalma edwardsii* (Blake)
3. Mesosoma with yellow setae; T2 not concave anteromedially; antennal scrobe having a well-developed dorsal carina *Sphaerophthalma marpesia* (Blake)
- Mesosoma with black to reddish setae; T2 appearing concave antero-medially; antennal scrobe lacks a well-developed dorsal carina *Sphaerophthalma imperialis* (Blake)

Discussion

Collecting at AMNWR revealed 42 species of velvet ants based on 8843 specimens. Because our estimated species richness derived from the species accumulation curve was 45 total species, I believe that additional sampling may reveal further species.

Given that only a single complete year of sampling was completed, only one species displayed a distinct pattern of activity out of all 36 species. *Dasymutilla arenivaga* became active much later in the year than all other species. This temporal differentiation from the average activity pattern exhibited by the velvet ant community likely indicates resource specialization in *D. arenivaga*. Our results are similar to a report on 19 velvet ant species in southern Florida that revealed that only two of the 19 total species examined exhibited a temporal separation from the average activity patterns of the community (Deyrup & Manley 1990). There is little support, however, here or in Deyrup & Manley (1990) for phenological niche partitioning or reduced flight intervals due to the dependence on a single host or other such variables.

While I observed little support for phenological niche partitioning, the identification of habitat preference for each species provides evidence that there may be some spatial niche partitioning among velvet ants. *Dasymutilla arenivaga*, *Odontophotopsis melicausa* and *Sphaerophthalma orestes* were found to be most abundant in sand dune habitats. As potential aculeate hosts such as sand wasps (Crabronidae: Bembicinae) are sand obligate species, it is likely that these three velvet ant species could specialize on the variety of hosts occupying the distinct sand dune habitats. This finding is unexpected for *O. melicausa* and *S. orestes* given that *O. melicausa* is found throughout the United States west of the Mississippi River and is highly abundant throughout its range even in non-dune areas, and *S. orestes* has a distribution including the Mojave and Sonoran deserts and extending north along the Pacific coast and into Washington and British Columbia. Both *O. melicausa* and *S. orestes* are not likely to be restricted to sand dune habitats throughout their range as both species have a wide distribution encompassing biomes that are not considered deserts and do not have sand dune habitats. *Odontophotopsis melicausa* and *S. orestes* preference for sand dune habitats in a desert biome could simply be an attribute of prey availability as many desert bee species have a preference for nesting in sandy soils and those sand obligate species such as sand wasps are also nesting in sandy soils there would be an abundance of aculeate hosts in sand dune habitats (Cane 1991).

Four other species, *Odontophotopsis mamata*, *O. microdonta*, *O. serca*, and *Sphaerophthalma mendica*, were found to be significantly less abundant in sand dune habitats than in the non-sand dune habitats. Such exclusion may indicate a competitive

interaction between those species prevalent on sand dunes and those more abundant in non-sand dune habitats. Future morphological investigations comparing species with opposing habitat preferences may reveal adaptations for the specific habitat. Adaptations exemplified by other sand obligate insects include lamellate spines (or a pecten) on the foretarsi of most sand wasps (Crabronidae: Bembicinae) (Evans & O'Neill 2007) and the elongated dorsolateral spines on the hind tibia of the Great Sand Treader Camel cricket (*Daihinibaenetes giganteus* Tikhman) (Weissmann 1997). These characteristics would be displayed in the female sex. However, the female of only one of these species, *S. mendica*, is known. Thus morphological comparisons cannot be made at this time.

While habitat type appears to be an important variable for multiple velvet ant species, 18 species at AMNWR were collected homogeneously in sand dune and non-sand dune habitats. These species may be extreme generalists in their host preference and do not target a specific habitat for host use, or the habitats being used by these species are not dictated by soil type, but by other biotic or abiotic factors such as vegetation type and density, slope, and soil moisture. One of the species listed as a uniformly distributed species, *Sphaerophthalma uro*, is known to target multiple cavity-nesting species as hosts (Pitts *et al.* 2004). Identifying the biotic and abiotic factors associated with the presence or absence of velvet ants in a habitat will aid in the identification of the suites of their host species. Future studies, like this, to help identify niche partitioning in velvet ants can provide clues into what types of prey may be targeted by each species.

Comparison of the velvet ants from NTS and AMNWR showed that six species found at the NTS were not collected at AMNWR. Some of these six species may account

for the estimated 4 ± 2 additional velvet ant species predicted by the first order jackknife species richness estimator to occur at AMNWR. Based on collection records for five of the six species found at NTS, *Acrophotopsis dirce*, *Dasymutilla monticola*, *Sphaerophthalma ferruginea*, *S. parapenalis*, and *O. obliqua* are expected to occur at AMNWR and they may be found with additional sampling. The sixth species, *O. cassia*, is endemic to the Great Basin region and likely does not occur at AMNWR. While none of the 42 velvet ant species found at AMNWR are endemic to AMNWR, 15 species that were found at AMNWR were absent at the NTS. As the NTS is located at the transition zone between the Great Basin and Mojave deserts the reduced velvet ant diversity at the NTS, when compared to AMNWR, is likely due to the changing environment and climate accompanying the transition from a hot to a cold desert.

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CHAPTER 4

SUMMARY AND CONCLUSIONS

The objective of this thesis was to determine if sand dune habitats with varying plant diversity and soil stability differ from each other and from non-sand dune habitats in the richness, diversity and abundance of their insect communities. The insects examined in this thesis were selected because they are typically diverse in arid regions and they each fulfill unique and important for ecosystem processes and may impact the known endemic and endangered species at AMNWR. The insects include antlions, bees, darkling beetles and velvet ants. As the impact and interactions of velvet ants are largely unknown within any ecosystem, this thesis will also include a faunal study of velvet ants at AMNWR and their spatial and temporal variation.

Through the comparison of the species richness, diversity, and abundance of each insect group between the stabilized and unstabilized sand dune habitats and the non-sand dune habitats, each insect group was found to be uniquely distributed between the three habitats. This indicates that each habitat supports a unique insect community. Sand dune habitats were especially important for all groups as both sand dune habitats hosted diversity equal to, or greater than, the diversity of non-sand dune habitats.

While both sand dune habitats supported equally greater species richness and abundance than non-sand dune habitats, the stabilized sand dune habitat was the most important habitat for most antlion species at AMNWR as it hosted greater diversity than the unstabilized sand dune habitat. Of the literature dealing with the biotic and abiotic factors that influence the distribution of Nearctic antlion species only species of the pit-

building genera, *Myrmeleon*, are considered (Simberloff *et al.* 1978; Boake *et al.* 1984; Marsh 1987; Lucas 1989; Gotelli 1993; Van Zyl *et al.* 1996; Gatti & Farji-Berner 2002). Therefore, little is known about the biotic and abiotic factors that influence the distribution of the majority of antlion species in the Nearctic. Our results suggest that habitat preferences for most sand-obligate antlions may be similar to the preferences of pit-building species, as the pit-building antlion species at AMNWR only occur in the stabilized sand dune habitats.

All habitats were equally important for bees. Bee species richness and diversity were the same across all habitats, but bee species composition and the large proportion of unique species in each of the habitats revealed that each habitat supported a unique assemblage of bee species. Other studies on bee distributions have similarly found that bee communities can vary widely in species composition between habitats and even between sampling locations within the same habitat (Herrera 1988; Minkely *et al.* 1999; Williams *et al.* 2001; Brosi *et al.* 2007; 2008; Wilson *et al.* 2009).

Unstabilized sand dune habitats were most important for darkling beetles. While stabilized sand dune habitats did not significantly differ from unstabilized sand dune habitats in richness, diversity or abundance, the stabilized habitats also did not differ from non-sand dune habitats which supported significantly fewer beetles species than the non-sand dune habitats. The sand-obligate darkling beetle species, *Edrotes ventricosus*, *Eussatus muricatus*, *Trogloderus constatus*, and *Chilometopon pallidum*, were found in both sand dune habitats, but were more abundant in unstabilized sand dune habitats.

Many sand-obligate species are detritivorous and typically occupy less stable soils in sand dunes (Crawford & Seely 1987; Seely & Louw 1980; Seely 1991).

Overall, velvet ants were largely indifferent to habitat type and were nearly equally distributed across all habitat types. This supports the current opinion that velvet ants are generalist in their host choice (Brothers 1989; Pitts *et al.* 2004). Differences in species richness and abundance did occur and revealed that velvet ants were least speciose and abundant in unstabilized sand dune habitats. This indicates that most velvet ant species are indifferent to soil type and may be influenced by other variables such as plant cover or diversity. In our comparison of velvet ants at the species level between sand dune and non-sand dune habitats, habitat preferences were observed for seven of 42 velvet ant species. Three of the seven species with habitat preferences preferred sand dune habitats over non-sand dune habitats. The three species included *Dasymutilla arenivaga*, *Odontophotopsis melicausa* and *Sphaerophthalma orestes*. The finding is unexpected for *O. melicausa* and *S. orestes* given that *O. melicausa* is found throughout the United States west of the Mississippi River and is highly abundant throughout its range even in non-dune areas, and *S. orestes* has a distribution including the Mojave and Sonoran deserts and extending north along the Pacific coast and into Washington and British Columbia. Both *O. melicausa* and *S. orestes* are not likely to be restricted to sand dune habitats throughout their range as both species have a wide distribution encompassing biomes that are not considered deserts and do not have sand dune habitats. As only one velvet ant species at AMNWR, *Dasymutilla arenivaga*, may actually be restricted to sand dune habitats, the impact of soil type on the velvet ant assemblage is

very small. Temporal segregation in habit was also investigated for velvet ants at AMNWR and *Dasymutilla arenivaga*, again, was the only species to vary from the other species at AMNWR. The variation of *Dasymutilla arenivaga* from all other species may be due to the partial diurnal activity this species exhibits, which is different from all other species collected as they are nocturnal in habit. Velvet ant life history is still poorly understood and more research is needed to explain their distributions. A similar lack in research on the factors influencing the diversity, distribution and abundance of all desert adapted predaceous arthropods exists as it is largely unstudied (Polis & Yamashita 1991).

The basic inventory of antlions, bees, darkling beetles, and velvet ants at AMNWR identified a total of 189 species from 8382 specimens consisting of 25 antlion species from 1092 specimens, 96 bee species from 870 specimens, 34 darkling beetle species from 2155 specimens, and 34 velvet ant species from 4265 specimens. Eight additional species of velvet ants were identified with the inclusion of two other sampling localities in Chapter 3. None of the terrestrial insects found in either study were endemic to AMNWR. The number of antlion, darkling beetle, and velvet ant species were similar to the number of species found in other studies (Thomas 1983; Güsten 2002; Saji & Whittington 2008; Pitts *et al.* 2009; 2010). The number of bee species found at AMNWR, however, was much lower than other studies in similar areas. As bees are very diverse within and between habitats, the restriction of sampling to select sand dune and non-sand dune habitats at AMNWR excluded many other habitats that are likely occupied by unique bee communities. The species accumulation curve also indicates more species are

expected to occur at the refuge. With additional sampling in other habitats more bee species are expected to be found.

AMNWR was created for the protection of endemic and endangered species. Several of the endemic and endangered species at the refuge include terrestrial plants, which inevitably share an interaction with terrestrial insects. Our study has increased the number of known terrestrial invertebrates at the refuge and has provided a comparison of terrestrial insect distribution and habitat use at AMNWR. Through these investigations I have contributed to the goals and objectives of the U. S. Fish and Wildlife Service to obtain basic inventories and understand the terrestrial habitat use of invertebrates at AMNWR (U.S. Fish and Wildlife Service 2009). Further investigations into the interactions of those endemic and endangered species with insects will provide more focus to the insect species of greatest concern.

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APPENDICES

APPENDIX A

Table A.1. List of common plant species found in each of the habitat types surveyed at Ash Meadows National Wildlife Refuge. List excludes species of concern.

| Plant | Non-sand dune | Stabilized sand dune | Unstabilized sand dune |
|---|---------------|----------------------|------------------------|
| Alkali sacaton (<i>Sporobolus airoides</i>) | X | | |
| Creosote bush (<i>Larrea tridentata</i>) | X | | |
| Death Valley ephedra (<i>Ephedra funerea</i>) | X | | |
| Desert isocoma (<i>Isocoma acradenia</i>) | X | | |
| Desert-thorn (<i>Lycium andersonii</i>) | X | | |
| Emory baccharis (<i>Baccharis emoryi</i>) | X | X | |
| Fivehook bassia (<i>Bassia hyssopifolia</i>) | | X | |
| Fourwing saltbrush (<i>Atriplex canescens</i> spp. <i>canescens</i>) | | X | X |
| Honey mesquite bush (<i>Prosopis glandulosa</i> var. <i>torreyana</i>) | X | X | |
| Leather-leaf ash (<i>Fraxinus velutina</i>) | X | | |
| Mojave thistle (<i>Cirsium mohavense</i>) | X | | |
| Quailbrush (<i>Atriplex lentiformis</i> ssp. <i>torreyi</i>) | X | X | |
| Rubber rabbitbrush (<i>Ericameria nauseosus</i>) | X | X | |
| Salt grass (<i>Distichlis spicata</i>) | X | | |
| Sandpaper plant (<i>Petalonyx thurberi</i>) | | | X |
| Scratch grass (<i>Muhlenbergia asperifolia</i>) | X | | |
| Spiny menodora (<i>Menodora spinescens</i>) | X | | |
| Spiny milkwort (<i>Polygala acanthoclada</i>) | X | | |
| Spiny saltbrush (<i>Atriplex confertifolia</i>) | X | X | X |
| Threadleaf matchweed (<i>Gutierrezia microcephala</i>) | X | | |
| Torrey's sea-blite (<i>Suaeda moquinii</i>) | X | X | |
| White bursage (<i>Ambrosia dumosa</i>) | X | | |
| Wire-lettuce (<i>Stephanomeria pauciflora</i>) | X | X | X |
| White ratany (<i>Krameria grayi</i>) | X | | |
| Whiteflower rabbitbrush (<i>Chrysothamnus albidus</i>) | | X | |
| Wormwood (<i>Oxytenia acerosa</i>) | X | | |
| Yellow cryptantha (<i>Cryptantha confertiflora</i>) | X | | |

* List obtained with permission from Bio-West, Inc. (2011) Ash Meadows National Wildlife Refuge vegetation mapping and rare plants survey final report. Las Vegas (NV): U.S. Fish and Wildlife Service, Desert National Wildlife Refuge Complex, Ash Meadows National Wildlife Refuge.

APPENDIX B

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By the power vested in me, a power that has been fought for under duress and at the cost of blood, sweat, and tears by myself and countless indentured students; I, with this power granted by the General Academy of Scholars, grant permission to the most noble and studious Nicole Boehme, a sister with a bond tempered and forged by the heat and filth of Pahrump Nevada, permission to use the manuscript 'Faunal study of velvet ants (Hymenoptera: Mutillidae) and their activity patterns and habitat preference at Ash Meadows National Wildlife Refuge, Nye County, Nevada, USA' as a chapter in her thesis.

Humblly and with greatest respect and adoration,



David Tanner

21 February, 2013

Nicole Boehme has my permission to include the following paper, of which I was a co-author, in her thesis.

N.F. Boehme, K.A. Williams, and J.P. Pitts. 2012. Faunal study of velvet ants (Hymenoptera: Mutillidae) and their activity patterns and habitat preference at Ash Meadows National Wildlife Refuge, Nye County, Nevada, USA. *Zootaxa*, 2587: 1-45.

A handwritten signature in black ink, appearing to read 'Kevin Williams', with a stylized, cursive script.

Kevin A. Williams