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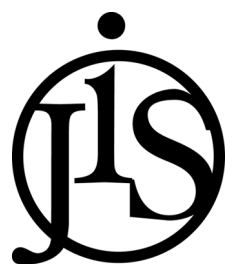
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Evidence for community structure and habitat partitioning in coastal dune stiletto flies at the Guadalupe-Nipomo dunes system, California

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Abstract

This study provides empirical evidence for habitat selection by North American species of stiletto flies (Diptera: Therevidae), based on local distributions of adults and immatures, and the first hypothesis of community assemblages proposed for a stiletto fly community. Sites at three localities within the Guadalupe-Nipomo dune system were sampled for stiletto flies in 1997 and 2001 by sifting sand, malaise trapping, and hand netting. Nine species were collected from four ecological zones and three intermediate ecological zones: *Acrosathe novella* (Coquillett), *Brachylinga baccata* (Loew), *Nebritus powelli* (Webb and Irwin), *Ozodiceromyia* sp., *Pherocera* sp., *Tabudamima melanophleba* (Loew), *Thereva comata* Loew, *Thereva elizabethae* Holston and Irwin, and *Thereva fucata* Loew. Species associations of adults and larvae with habitats and ecological zones were consistent among sites, suggesting that local distributions of coastal dune stiletto fly species are influenced by differences in habitat selection. In habitats dominated by the arroyo willow, *Salix lasiolepis*, stiletto fly larvae of three species were collected in local sympatry, demonstrating that *S. lasiolepis* stands along stabilized dune ridges can provide an intermediate ecological zone linking active dune and riparian habitat in the Guadalupe-Nipomo dune system. Sites dominated by European beach grass, *Ammophila arenaria*, blue gum, *Eucalyptus globulus*, and Monterey cypress, *Cupressus macrocarpa*, are considered unsuitable for stiletto flies, which emphasizes the importance of terrestrial habitats with native vegetation for stiletto fly species. The local distributions of stiletto fly species at the Guadalupe-Nipomo dune system allow the community to be divided into three assemblages; active dune, pioneer scrub, and scrub-riparian. These assemblages may be applicable to other coastal dune stiletto fly communities, and may have particular relevance to stiletto fly species collected in European coastal dunes. The results from this study provide a descriptive framework for studies testing habitat selection in coastal dune stiletto fly species and inform conservation of threatened dune insects.

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Introduction

North American stiletto flies (Insecta: Diptera: Therevidae) rank among the better-known groups of Diptera found in semiarid ecosystems due to a recent increase in taxonomic revisions (Irwin, 1977a-b; Webb and Irwin, 1989, 1991a-b, 1995, 1999; Gaimari and Irwin, 2000; Hauser and Irwin, 2003; Holston and Irwin, 2005; Webb and Metz, 2000; Webb, 2003). Over 1000 species of stiletto flies have been described worldwide; and more than 200 species of stiletto flies can be found in subtropical, desert, temperate, and boreal habitats of North America. Adults have been observed drinking from wet soil or sand and occasionally visiting flowers (Cole, 1923; Winterton et al., 1999; Irwin, 2001; Holston and Niehuis, 2002). Stiletto fly species can be locally common (Lyneborg and Spitzer, 1974; Irwin, 2001; Holston and Niehuis, 2002), but many species in this cosmopolitan family of Diptera are considered rare due to poor representation in insect collections (Lyneborg and Spitzer, 1974; Holston, 2004). Colored pan traps are not particularly effective (Barkenmeyer, 1994, 1995; Grootaert et al., 2001; Keil, 2003), but malaise traps have yielded diverse samples and numerous specimens of stiletto flies. This is especially apparent near intermittent streams and rivers where adults are intercepted as they search for water (Irwin, 2001; Holston and Niehuis, 2002). Taxonomic and ecological research on stiletto fly species has been promoted by the widespread use of malaise traps in collecting insects, and a corresponding influx of stiletto fly specimens.

Stiletto fly larvae are prominent and easily recognizable members of the invertebrate soil fauna (Honczarenko, 1976; Kaplin, 1977; Krivokhatskii, 1982; Straka, 1982), but most studies of stiletto fly species have focused on the morphologically diverse adults. Sexual dimorphism in adults of most stiletto fly species is apparent in the head and abdomen: males have larger compound eyes that meet at the midline of the head and a less tapered abdomen that is often clothed with white or silvery white hair and other vestiture (e.g., *Tabudamima* and *Acrosathe*) (Figs 1-3). Unusually long antennae are found in both males and females of *Nebritus* species, which have similar eye morphology and abdominal vestiture patterns (Fig. 4). Stiletto fly larvae are active predators with a well-sclerotized head capsule and a snakelike body (Fig. 5) that allows them to move rapidly through sand and

friable soils where they prey on lepidopteran and beetle immatures (Irwin and Lyneborg, 1981a-b). Prey records are scarce but include the lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Smith and Johnson, 1989) and the red sunflower seed weevil, *Smicronyx fulvus* LeConte (Pinkham and Oseto, 1987a-b) in agroecosystems. Local distributions of immatures are likely to reveal well-defined patterns of habitat utilization that could be obscured by trivial movements of the adults. The immatures of most stiletto fly species are undescribed or unknown (English, 1950; Irwin and Lyneborg, 1981a-b), but they have a great potential to address fundamental issues concerning stiletto fly diversity and distributions.

The majority of immature stiletto flies have been collected and reared from dune localities where the sand can be easily sieved and expose stiletto fly larvae and pupae. Stiletto flies are known from adults and larvae collected from coastal sand dunes in Australia (English, 1950; Lyneborg, 2001), New Zealand (Lyneborg, 1992), North Africa (Lyneborg, 1987), South Africa (Irwin, 1972; Lyneborg, 1976, 1980), Japan (Nagatomi and Lyneborg, 1988, 1989), Europe (Barkenmeyer, 1994, 1995; Stubbs and Drake, 2001), central America (Webb and Irwin, 1991b), and western North America (Irwin and Lyneborg, 1981a; Webb and Irwin, 1991, 1995, 1999; Webb, 2003; Hauser and Irwin, 2003; Holston and Irwin, 2005). Species in four of the 30 North American stiletto fly genera (*Acrosathe*, *Megalinga*, *Nebritus*, and *Thereva*) have been collected only in coastal sand dunes, and an additional 10 genera (*Ammonaios*, *Brachylinga*, *Chromolepida*, *Litolinga*, *Ozodiceromyia*, *Penniverpa*, *Pherocera*, *Rhagioforma*, *Tabuda*, and *Tabudamima*) include species collected at both coastal and inland localities. Studies of forest habitats have examined local distributions of stiletto fly species in Illinois (Hartman et al., 1995) and the Czech Republic (Keil, 2003), but spatial structuring has only been reported for stiletto fly communities at coastal dune localities (English, 1950; Barry and Schlinger, 1977; Irwin, 1972; Barkenmeyer, 1993, 1994). This emphasizes the suitability of coastal dune ecosystems for studies of stiletto fly community structure and spatial partitioning.

Studies of the stiletto fly community at the Guadalupe-Nipomo dune system add substantially to the scarce ecological data on stiletto fly species, support ongoing research of an ecosystem with high

Fig 1-4. Three stiletto fly species found in the Guadalupe-Nipomo Dunes System. **Figure 1:** *Acrosathe novella*, male. **Fig. 2:** *A. novella*, female. **Fig. 3:** *Tabudamima melanophleba*, male. **Fig. 4:** *Nebritus powelli*, female.

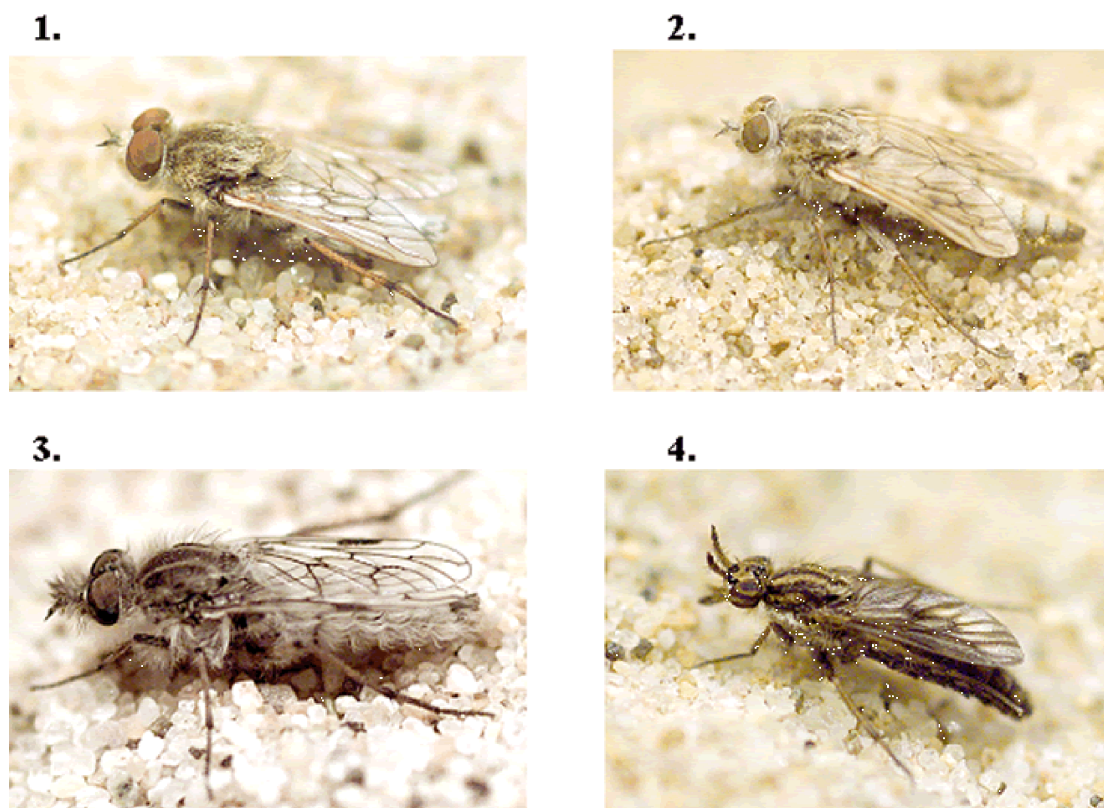
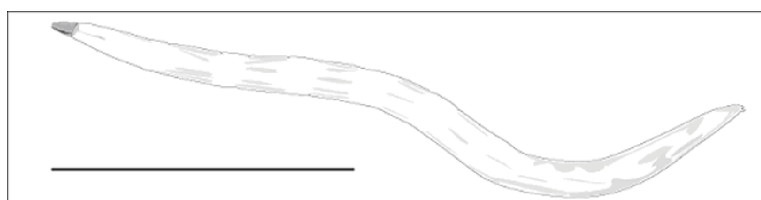


Fig 5. Habitus of a stiletto fly larva, showing the dark sclerotized head capsule and internal metacephalic rod (left) and snakelike body. Scale bar = 1.0 cm.



conservation value (Holland et al., 1995; USFWS, 2000; IPM, 2001), and provide data for comparative studies of stiletto fly communities. Detailed ecological characterizations for stiletto fly communities are an important step towards assessing the conservation status of North American species, which has led to the placement of 11 stiletto fly species on lists of rare and threatened European insects (Shirt, 1987; Gärdenfors, 2000). Seven of the 14 genera associated with North American coastal sand dunes (including *Acrosathe*, *Nebritus*, and *Thereva*) are represented by adults and larvae collected from the

Guadalupe-Nipomo dune system, a 12,000-acre coastal dune complex in central California, but ecological studies have not been conducted of this diverse stiletto fly community. Holland et al. (1995), however, identified six plant communities in the Guadalupe-Nipomo dune system, which encompasses the highest level of endemism among California coastal dunes (Cooper, 1967; Holland et al., 1995).

The objectives of the present study were to provide an inventory of the stiletto fly species found in the Guadalupe-Nipomo dune system, describe the local

Fig 6. View westward across Guadalupe Nipomo dune system south of Rancho Guadalupe-Nipomo County Park, showing the diversity of ecological zones within the “Central coast dune scrub with Active interior dunes” Holland et al., 1995)



distributions of stiletto fly adults and immatures, examine these local distributions for evidence of habitat selection within and among ecological zones, and to use local distributions for developing an hypothesis of spatial structuring in the stiletto fly community.

Materials and Methods

Ecological zones

The rate of sand accumulation is a fundamental characteristic of coastal dune habitats in which stiletto flies are found that contributes to ecological zonation of dune flora and fauna. According to the classification of dune types by Boedeker et al. (1998), white dunes experience continuous accumulation of sand, green dunes accumulate sand at low levels, and grey dunes are no longer accumulating sand (brown dunes are sheltered grey dunes with the highest level of organic soil content). Plant distributions in dunes reflect this succession, with pioneer species of plants found in white dunes and late succession plants found in older, stabilized brown dunes (Holland et al., 1995). Studies that describe local species distributions of stiletto flies at European coastal dunes (Ardö, 1957) and North Sea sand islands (Barkenmeyer, 1994, 1995) used dune types and plant distributions to identify different habitats or ecological zones. Similarly, dune type was used in combination with

plant community distributions to define ecological zones for the present study.

The following ecological zones have close equivalents to the zones of Ardö (1957) and Barkenmeyer (Barkenmeyer, 1994, 1995) and are based on the three terrestrial and three wetland plant communities defined by Holland et al. (1995): Zone 1, Coastal strand and active coastal dunes; Zone 2, Central coast foredunes (pioneer dunes); Zone 3a, Active interior dunes; Zone 3a, Central coast dune scrub; Zone 4, Coastal dune riparian woodland; Zone 5, Coastal dune swale; and Zone 6, Coastal dune freshwater marsh and ponds (Table 1). Holland et al. (1995) noted that “Central coast dune scrub with Active interior dunes” is a “mosaic” of active and stabilized dunes and that pioneer plant species begin a succession that culminates with the stabilized dune scrub community (Fig. 7). The distinctions among green, grey, and brown dunes can be subtle within this dune “mosaic,” whereas open dunes and dune hummocks that actively recruit sand (white dunes) are distinguished from stabilized dunes (grey or brown dunes) by of scrub vegetation. The “Central coast dune scrub with Active interior dunes” of Holland et al. (1995) was divided into Zone 3a (Active interior dunes) and Zone 3b (Central coast dune scrub).

Fig 7-8. Spatial relationships among stiletto fly community assemblages, illustrating the direct link between Active dune and scrub-riparian habitats via dune forms stabilized by *Salix lasiolepsis*. Differentiation among ecological zones and community assemblages decreases from the top (complete differentiation) to the bottom (complete overlap); sand dune and plant community development advances from the left (early succession stages) to the right (late succession).

Fig. 7. Ecological zones.

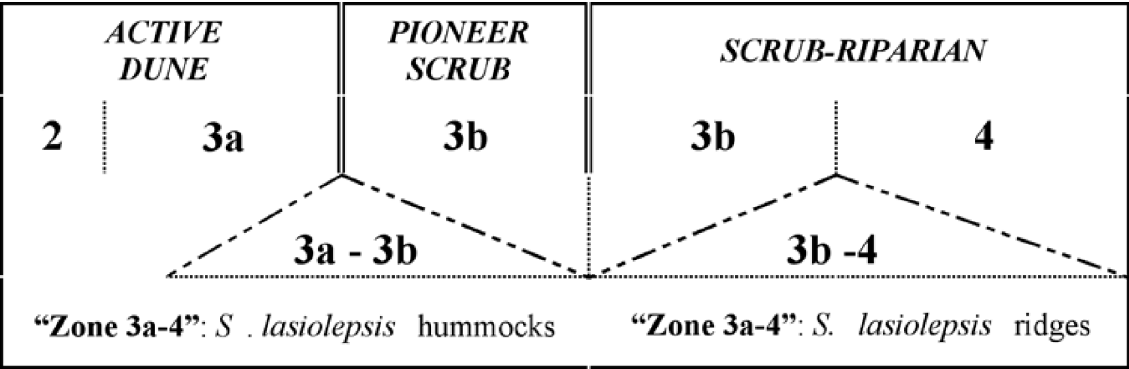
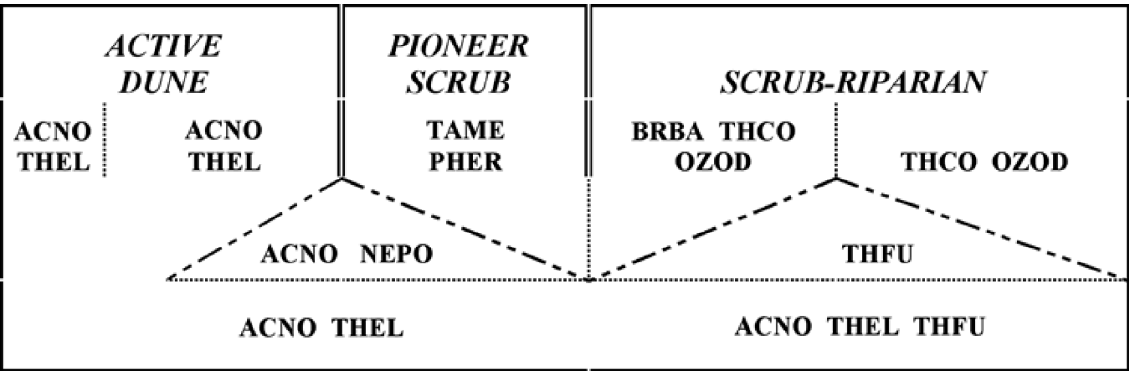


Fig 8. Stiletto fly distributions. Species name abbreviations follow Table 3).



Because the transition between dune types and plant communities varies from gradual to abrupt (Boedeker et al., 1998; Holland et al., 1995), dominant plant species and dune forms were noted to allow comparisons of sites within zones (Table 2). This resulted in the recognition of two intermediate zones between temporally adjacent zones, according to the linear sequence of plant and dune succession, Zones 3a-3b and 3b-4. The dominance of *Salix lasiolepsis* (arroyo willow) in foredunes, dune scrub, and riparian habitats (Holland et al., 1995) warranted the recognition of a third intermediate zone, Zone 3a-4. Isolated *S. lasiolepsis* bushes form dune hummocks (usually considered “Zone 3a” in this study); these bushes increase in size and density along dune slopes and ridges (“Zone 3b”) and may establish riparian habitats (“Zone 4”). In this regard, the “Arroyo willow series” of the *Manual of California Vegetation* (Sawyer and Keeler-Wolf, 1995) lacks precision with respect to the different *S. lasiolepsis*

habitats identified in this study. Similarly, the “sand-verbena - beach bursage series” encompasses both Pioneer and Active interior dune habitats distinguished in this study (Table 1). Vegetation series are widely used in conservation management, and have close correspondence to sites in Zones 3a and 4 (Tables 1 and 2), but the Californian vegetation series do not account for differences among sites in dune geomorphology. This is a particularly important distinction for this study because substrate type is a probably a more accurate predictor of stiletto fly larval habitat than plant species, due to the generalist predatory ecology of the larvae.

Localities and sites sampled

Zones 2, 3a, 3b, 4, and 5 were sampled for immature or adult stiletto flies (29 sites) at three localities (Table 2). At RGNCP, foredune sites (Zone 2) were sampled in 1997, and sites within a 200-m2 backdune area located 1.5 km from the shore were sampled in 1997 and 2001 (Table 2).

Table 1. List of the six ecological zones within the Guadalupe-Nipomo dune system recognized in the present study and the corresponding ecological zones identified by Holland et al. (1995), Barkemeyer (1994, 1995), and Ardö (1957).

	Zone 1	Zone 2	Zone 3a	Zone 3b	Zone 4	Zone 5	Zone 6
	Coastal Strand and Active Coastal Dunes	Central Coast Foredunes (Pioneer Dunes)	Active Interior Dunes	Central Coast Dune Scrub	Coastal Dune Riparian Woodland	Coastal Dune Swale	Coastal Dune Freshwater Marsh and Ponds
Holland et al., 1995	Coastal Strand and Active Coastal Dunes	Central Coast Foredunes (Pioneer Dunes)	Central Coast Dune Scrub with Active Interior Dunes	Central Coast Dune Scrub with Active Interior Dunes	Coastal Dune Riparian Woodland	Coastal Dune Swale	Coastal Dune Freshwater Marsh and Ponds
Barkemeyer, 1993, 1994, 1995	Strand	Primärdüne, "Strandwall"	Secondärdünen, Weißendünen	Tertiärdünen, Graudünen, "Ruderal- <i>Calluna</i> -Fäche"	"Waldnähe," "Baumgruppen"	"langgestrecktes Dünenital," "feuchten Dellen" (Kibitzdelle, Waterdelle)	Süßwasserteich
Ardö, 1957	Fore Shore + High Beach, High Shore	Fore Dune ("white dune," "dune vivante")	Dune Ridge (First Dune Range, Sea Dune)	Dune Heath	Dune Wood	Dune Heath, depression	dune lakes
Sawyer and Keeler-Wolf, 1995	Sand-verbena - beach bursage series			Dune lupine - goldenbush series, Coyote brush series	Arroyo willow series, Aspen Series, Coast live oak series	Sedge series	Bullrush - cattail series

Table 2. List of sites sampled for stiletto flies at three localities within the Guadalupe-Nipomo dune system.

A. Rancho Guadalupe-Nipomo County Park.				
Zone	Site	Site Description	Coordinates	Date(s) Sampled
2	1	Hummock (Ammophila arenaria)	34° 57' 57" N 120° 39' 02" W	21.VI.1997
	2	Hummocks with prostrate vegetation (Ambronia sp., Ambrosia chamissonis)	" "	" "
3a	1	Open dune plain adjacent to Zone 3a-4	34° 57' 32" N 120° 38' 27" W	17, 19, 21, 25.VI.1997 [14.V., 1-2, 17.VI.2001]
	2	Hummocks with prostrate vegetation (Ambrosia chamissonis)	" "	21,25.VI.1997
	3	Crest of retention ridge with erect, herbaceous vegetation (Senecio blochmaniae)	" "	25.VI.1997
3b	1	Sheltered dune plain with woody scrub cover (Lupinus chamissonis, Ericameria ericoides)	" "	17, 19, 21, 25.VI.1997 [14.V., 1-2, 17.VI.2001]
3a-4	1	Crest of retention ridge under Salix lasiolepis	" "	25.VI.1997 [2.VI.2001]
4	1	Slipface of retention ridge (Salix lasiolepis, Quercus agrifolia)	" "	[2.VI.2001]
B. Backdunes, west of Teixeira Farms.				
Zone	Site	Site Description	Coordinates	Date(s) Sampled
3a	1	Open dune ridge adjacent to Zone 3b, Site 1 (sand mixed with straw from straw plugs)	35° 02' 00" N 120° 36' 54" W	19, 20.VI.1997
	2	Open dune plain adjacent to Zone 3a, Site 4 (sand without straw)	35° 01' 39" N 120° 36' 40" W	20.VI.1997
	3	Open dune slope adjacent to Zone 3b, Site 2 (sand without straw)	" "	24.VI.1997
	4	Hummock with prostate vegetation (Ambrosia chamissonis) (sand without straw)	" "	" "
	5	Crest of retention ridge (Lupinus chamissonis) (sand mixed with straw from straw plugs)	" "	19, 20, 24.VI.1997
3b	1	Sheltered dune plain with woody scrub cover (Lupinus chamissonis) (sand without straw)	35° 02' 00" N 120° 36' 54" W	20.VI.1997
	2	Sheltered dune plain with woody scrub cover (Lupinus chamissonis) (sand mixed with straw from straw plugs)	35° 01' 39" N 120° 36' 40" W	24.VI.1997, (malaise traps: 19-25.VI.1997)
3a-4	1	Crest of retention ridge under Salix lasiolepis (sand without straw)	" "	" "
	2	Hummock under Salix lasiolepis (sand without straw)	" "	" "
C. Backdunes, west of Mills Farms.				
Zone	Site	Site description	Coordinates	Date(s) sampled
3a	1	Open dune ridge	35° 01' 33" N 120° 37' 16" W	22.VI.1997
	2	Dune plain north of stabilized dune hill with herbaceous prostate vegetation	35° 01' 19" N 120° 37' 24" W	" "
	3	Open dune plain adjacent to Zone 3b, Site 2	35° 01' 03" N 120° 37' 24" W	" "
3a-3b	1	Dune slope (north face) of stabilized dune hill (Artemisia californica, Lotus scoparius)	35° 01' 19" N 120° 37' 24" W	" "
3b	1	Sheltered dune plain with woody scrub cover (Lupinus chamissonis, Ericameria ericoides)	35° 01' 03" N 120° 37' 24" W	" "
	2	Sheltered dune plain (Ammophila arenaria)	35° 01' 05" N 120° 37' 36" W	" "
	3	Extensive dune plateau with scrub cover (Artemisia californica, Baccharis pilularis), sand bound by a surface layer of moss and lichen in many areas	35° 01' 19" N 120° 36' 56" W	" "
3b-4	1	Sparsely forested (Quercus agrifolia) slope northeast of dune plain under woody scrub (Artemisia californica, Baccharis pilularis)	35 01.311N 120 36.929W	24.VI.1997
4	1	Forested northeast border of dune plateau (Populus trichocarpa)	35° 01' 19" N 120° 36' 56" W	22.VI.1997
	2	Forested northeast border of dune plateau (Cupressus macrocarpa)	" "	24.VI.1997
	3	Forested northeast border of dune plateau (Eucalyptus globulus)	" "	" "
5	1	Swale thicket (Salix lasiolepis, Lupinus chamissonis, Toxicodendron diversilobum) with grassy undergrowth (Carex spp.)	35° 01' 03" N 120° 37' 24" W	" "

The paved road to the RGNCP beach parking lot intersects this backdune area through a sheltered dune plain dominated by *Lupinus chamissonis* (silver lupine) and *Ericameria ericoides* (mock heather) (Zone 3b) bordered to the south by unvegetated sand and dune hummocks stabilized by prostate vegetation (Zone 3a) and bordered to the north by a retention ridge that drops abruptly to the Santa Maria River floodplain. This retention ridge is stabilized by *Salix lasiolepis* (Zone 3a-4), which expands eastward into a riparian area dominated by larger specimens of *S. lasiolepis* and *Quercus agrifolia* (coast live oak) (Zone 4). *Lupinus chamissonis* and *E. ericoides* were also found at backdune sites west of Teixeira Farms and Mills Farms (Zone 3b) although *Artemisia californica* (California sagebrush) and *Baccharis pilularis* (coyote bush) were dominant in these areas (Holland et al., 1995). In many areas of the stabilized dune plateau west of Mills Farms (Zone 3b), the surface layer of sand between plants is bound by moss and lichen. Sites at Teixeira Farms and RGNCP are similar in plant composition although the surface layer of sand at sites closest to the border of Teixeira Farms is mixed with straw from dune stabilization with straw plugs (Table 2). Riparian zones at all three localities are characterized by *Q. agrifolia* (Zone 4), with *S. arenaria* found on active dune ridges and hummocks west of Teixeira Farms (Zone 3a-4) and *Populus balsamifera* ssp. *trichocarpa* (black cottonwood) at the western border of Mills Farms (Zone 4). A thicket of *S. lasiolepis* and *L. chamissonis*, with *Toxicodendron diversilobum* (poison oak) and *Carex* spp. (sedges) in the undergrowth, represents the single dune swale sampled during this study (Zone 5) and is located west of Mills Farms (Table 2).

Four sites examined during this study were dominated by plant species not native to the Guadalupe-Nipomo Dunes System. Stands of *Cupressus macrocarpa* (Monterey cypress) and *Eucalyptus globulus* (blue gum) at the western border of Mills Farms, and foredunes at RGNCP (Zone 2) and backdunes west of Mills Farms (Zone 3b) dominated by *Ammophila arenaria* (European beach grass) were sampled for stiletto fly immatures and adults (Table 2). Studies of *E. globulus* and *A. arenaria* indicate that these plant species decrease the native coastal floral or arthropod diversity (Slobodchikoff and Doyen, 1977; Gordon, 1992; Holland et al., 1995; Chestnut, 1999), so these non-native plants were not expected

to provide primary habitats for stiletto fly species. Habitats dominated by these plant species have not been sampled for stiletto flies during previous studies, and the data obtained would be directly applicable to coastal dune preservation and restoration efforts in the Guadalupe-Nipomo dune system (USFWS, 2000; IPM, 2001).

Sampling protocol

Adults observed on the ground or vegetation were collected by hand net and sampling for stiletto fly immatures involved sifting through the substrate primarily under vegetation in relatively cool sand at depths up to 10 centimeters. Four two-meter Sharkey malaise traps were also run from 19-25 June 1997 at Teixeira Farms, placed in Zone 3b backdunes (Table 2). Sifting sand on the windward side of sand hummocks, in sand of open dunes, and in bare patches of sand at RGNCP yielded no insect immatures (Table 2, A.), and no subsequent sampling was conducted in the bare sand of Zone 3a. Because stiletto fly larvae frequently attack and kill each other when placed in the same rearing container (English, 1950; Irwin, 1972), larvae and pupae were placed separately into 10-dram plastic vials with sand from the collecting site.

Rearing protocol

Immatures were reared following protocols described by Irwin (1972), except for the use of covered plastic cups instead of glass vials, and adults were determined to species. The contents of each collecting vial were transferred to a 1-oz. transparent plastic cup covered with a cardboard lid. Four drops of water were added every two to three days, and four to five larvae of the confused flour beetle, *Tribolium confusum*, were added to the rearing chambers every three to five days. After stiletto fly larvae pupated, any remaining *T. confusum* specimens were removed from the rearing container (feeding damage by beetle larvae and adults will kill stiletto fly pupae). Hydration of the rearing chambers was continued after pupation, and the emerged adults were collected and pinned after the chamber was placed in a freezer. Rearing containers were kept in an environmentally controlled room at 26° to 32° C or at room temperature. Most of the surface sand can remain loose in plastic cups, whereas a hard surface plug can form and prevent stiletto fly larvae from reaching prey or adults from emerging from the sand in the relatively narrow glass vials.

Species identifications and specimen data

Identification keys and taxonomic descriptions for North American stiletto flies and a collection of comparative material (including type specimens) were used for species determinations. Published taxonomic and distribution data was available for *Nebritus powelli* (Webb and Irwin, 1991b), *Tabudamima melanophleba* (Webb and Irwin, 1999), and *Thereva* species (Holston and Irwin, 2005); additional taxonomic data on stiletto fly species was available in Cole (1923) and Irwin and Lyneborg (1981a-b). Unpublished specimen-level data was available through the MandalaTM Systematic Database of Therevidae (Kampmeier et al., 2003, <http://www.inhs.uiuc.edu/cee/therevid>), which has supported taxonomic work on North American stiletto flies since 1996. Database record identification numbers consist of a prefix followed by a 6-digit number (e.g., “MEI 006369”), which can be used to obtain additional information on specimens.

Results

Species inventory

The nine species of stiletto flies known from the Guadalupe-Nipomo dune system were collected during this study by sifting sand for immatures or by using malaise traps and hand nets for adults. The species collected included *Acrosathe novella* (Coquillett), *Brachylinga baccata* (Loew), *Nebritus powelli* Webb and Irwin, *Ozodiceromyia* sp., *Pherocera* sp., *Tabudamima melanophleba* (Loew), *Thereva comata* Loew, *Thereva*

elizabethae Holston and Irwin, and *Thereva fucata* Loew (Table 3). This stiletto fly community is diverse at the genus-level (seven genera), with eight species classified in the subfamily Therevinae (*Pherocera* sp. belongs to the subfamily Phycinae) (Irwin and Lyneborg, 1981a). The species of *Ozodiceromyia* and *Pherocera* are undescribed, but specimens examined and database records indicate that one species in each of these genera is present at the Guadalupe-Nipomo dune system. The most diverse genus within the Guadalupe-Nipomo dune system is *Thereva* (three species), which includes the majority of species described in ecological studies of European stiletto flies (Ardö, 1957; Barkenmeyer, 1994, 1995; Grootaert et al., 2001; Holston and Niehuis, 2002; Keil, 2003). The majority of specimens collected and observed, however, were *A. novella* (31 larvae, and over 70 adults) (Table 2).

Stiletto fly species found in the Guadalupe-Nipomo dune system range from completely to marginally distributed in coastal dune systems. *Acrosathe novella*, *N. powelli*, and *Th. elizabethae* occur only at coastal localities in western North America. *Tabudamima melanophleba* and *Th. comata* have been found at inland localities as far north as Oregon (*Th. comata*) and Washington (*Ta. melanophleba*) (Webb and Irwin, 1991b, 1999; Holston and Irwin, 2005). *Brachylinga baccata* and *Th. elizabethae* are distributed eastward to Utah with most specimens from California collected at inland localities (Holston and Irwin, 2005).

Table 3. Collecting summary per site for total field collection of immatures and for identified specimens (immatures, adults). Hyphenated numbers for ecological zones are intermediate zones. Legend: ACNO = *Acrosathe novella*, THEL = *Thereva elizabethae*, NEPO = *Nebritus powelli*, PHER = *Pherocera* sp., THFU = *Thereva fucata*, TAME = *Tabudamima melanophleba*, THCO = *Thereva comata*, OZOD = *Ozodiceromyia* sp., BRBA *Brachylinga baccata*; “-” = no specimens collected; “*” = specimens reared from pupae; “***” = specimens collected by malaise trap. Square brackets indicate data from 2001.

A. Rancho Guadalupe-Nipomo County Park.												
Zone	Site	larva	pupa	ACNO	THEL	NEPO	PHER	THFU	TAME	THCO	ODOD	BRBA
2	1	-	-	-	-	-	-	-	-	-	-	-
	2	7	-	4, 1	3, 0	-	-	-	-	-	-	-
3a	1	-	-	0, 14	-	-	-	-	-	-	-	-
	2	20	-	10, 4	-	-	-	-	-	-	-	-
	3	5	-	1, 3	-	-	-	-	-	-	-	-
3b	1	1	3 [3]	0, 5	-	0, [6]	0, 2 [5]	-	3 [3]*, 7 [16]	0, [4]	0, 1	-
3a-4	1	9 [2]	-	3, 4	2, 0	-	-	3, 0	-	-	-	-
4	1	-	[1]	-	-	-	-	-	-	[0, 2]	[1*, 0]	-
B. Backdunes, west of Teixeira Farms.												
Zone	Site	larva		ACNO	THEL	NEPO	PHER	THFU	TAME	THCO	ODOD	BRBA
3a	1	n/a		n/a, 7	-	-	-	-	-	-	-	-
	2	n/a		n/a, 10	-	-	-	-	-	-	-	-
	3	n/a		n/a, 8	-	-	-	-	-	-	-	-
	4	7		2, 2	-	-	-	-	-	-	-	-
3b	5	-		0, 6	-	-	-	-	-	-	-	-
	1	n/a		-	-	-	n/a, 1	-	n/a, 1	-	-	-
	2	-		0, 5	-	-	-	-	-	-	0, 2**	0, 1**
3a-4	1	4		3, n/a	-	-	-	-	-	-	-	-
	2	3		1, n/a	1, n/a	-	-	-	-	-	-	-

Other North American species in the genera *Acrosathe* and *Thereva* are restricted to coastal dunes (Irwin and Lyneborg, 1981a, Holston and Irwin, 2005), but other species of *Nebritus* have been collected only at inland localities (Webb and Irwin, 1991b). *Ozodiceromyia* sp. and *Pherocera* sp. are known only from specimens collected from the Guadalupe-Nipomo dune system, but a survey of nearby inland localities is needed to confirm this possible endemism.

Distribution and intraspecific variation of two species of *Thereva* demonstrate that the dune system harbors unique fauna at the transition between northern and southern coastal populations. The Guadalupe-Nipomo dune system encompasses the most northern collecting localities for *A. novella* and *N. powelli* and the most southern localities for *Th. elizabethae* (Webb and Irwin, 1991b; Holston and Irwin, 2005). *Coreopsis gigantea* (giant coreopsis) is a species of the stabilized dune scrub plant community that also has the northern limit of its range at the Guadalupe-Nipomo dune system (Holland et al., 1995). Vestiture patterns indicate that populations of *Th. comata* can be divided into a northern and southern group, with the southern group found within and south of the Guadalupe-Nipomo dune system (Holston and Irwin, 2005). Intraspecific variation in *Th. elizabethae* follows a similar north-south division, but the southern group can be further divided with the specimens from the Guadalupe-Nipomo dune system representing a small central Californian coastal population (Holston and Irwin, 2005).

Local species distributions

Adult stiletto flies were collected at the Guadalupe-Nipomo dune system from Zones 2, 3a, 3b, and 4 (Table 3 and 4) with five species distributed in different areas of Zone 3b, the zone

that encompasses the most heterogenous plant community (Holland et al., 1995). Most specimens of *A. novella* were observed at Zone 3a sites, with 10 adults observed on bare sand in Zone 3b and one adult observed in Zone 2 (Table 2). Aggregations of *A. novella* males were observed in wind-sheltered dune plains (Zone 3a) at all three localities where males flew up from the sand and intercepted conspecific males and other low-flying insects. *Pherocera* sp. and *T. melanophleba* were found only at Zone 3b sites in association with *L. chamissonis* and *E. ericoides* (Table 2), which are plant species of the pioneer (or early successional) dune scrub community (Holland et al., 1995). Specimens of *Pherocera* sp. were observed crawling on sand underneath *L. chamissonis* and *E. ericoides* bushes, whereas *Ta. melanophleba* perched on the leaves and upper branches of *L. chamissonis* bushes. *Tabudamima melanophleba* males flew after passing conspecifics from their perches on *L. chamissonis* bushes, similar to males of *A. novella* in dune plains. The few specimens of *B. baccata*, *N. powelli*, and *Ozodiceromyia* sp. were collected in Zone 3b, with *N. powelli* collected from bare sand and the single observed adult of *Ozodiceromyia* sp. flying above Zone 3b scrub (*B. baccata* was not observed). Adults of *Th. comata* were found on low herbaceous vegetation and woody scrub in Zone 3b and on *S. lasiolepis* in Zone 4 adjacent to the Santa Maria floodplain (Zone 5). Adults of *Th. elizabethae* and *Th. elizabethae* were not collected.

Five stiletto fly species were collected as immatures in Zones 2, 3a, 3b, 4, and the four intermediate ecological zones (Zones 3a-3b, 3a-4, 3b-4) (Table 2 and 3) in close association with adult habitats. Pupae of *Ta. melanophleba* were the only immatures found under *L. chamissonis* bushes where adults of *Ta. melanophleba* were collected. The pupa of *Ozodiceromyia* sp. was the only

Table 4. Presence of stiletto fly species in ecological zones of the Guadalupe-Nipomo dune system based on immatures (I) and collected or observed adults (A).

Locality	Rancho Guadalupe-Nipomo County Park				Teixiera Farms		Mills Farms					
	2	3a	3b	3a-4	4	3a	3b	3a-4	3a	3a-3b	3b	3b-4
<i>Acrosathe novella</i>	I, A	I, A	A	I		I, A	A	I	I, A	I, A		
<i>Thereva elizabethae</i>	I	I		I				I				
<i>Nebritus powelli</i>			A									
<i>Pherocera</i> sp.			A				A				A	
<i>Thereva fucata</i>				I								I
<i>Tabudamima melanophleba</i>			I, A				A					
<i>Thereva comata</i>			A		A							
<i>Ozodiceromyia</i> sp.			A		I		A					
<i>Brachytinga baccata</i>							A					

immature collected from Zone 4 and was found in dry, organically rich sand underneath fallen branches at RGNCP in the *S. lasiolepis*-dominated thicket adjacent to the Santa Maria floodplain (Table 2A, Zone 4, Site 1). *Acrosathe novella* was reared from sites in active dunes, including a dune hummock stabilized by *Ambronia chamissonis* with numerous subterranean sand-covered silken tubes from lepidopteran larvae (Table 2A., Zone 3A, Site 2) and a stabilized dune hill under *A. californica* and *Lotus scoparis* (Table 2C., Zone 3a-3b, Site 1). In general, *A. novella* is distributed widely in the Guadalupe-Nipomo dune system, with adult males aggregating in dune plains adjacent to sites where larvae were collected. One larva from dark, organically rich sand in a hollow at the base of a *P. balsamiferus* tree (Table 2C: Zone 4, Site 1) was not successfully reared; but larvae from the nearest site, collected from a sparsely forested, stabilized dune slope under woody scrub (Table 2C., Zone 3b-4, Site 1), were *Th. fucata*. Although five sites yielded only one species of stiletto fly, all larvae of *Th. elizabethae* were collected with *A. novella* larvae (Zones 2, 3a, and 3a-4), and larvae of *A. novella*, *Th. elizabethae*, and *Th. elizabethae* were collected at one site in local sympatry underneath *S. lasiolepis* (Table 2A., Zone 3a-4, Site1). Immatures of *B. baccata*, *N. powelli*, *Pherocera* sp., and *Th. comata* were not reared.

Stiletto flies were not collected in habitats dominated by non-native plants or in the dune swale, and larvae were not found in sand underneath moss and lichen or sand mixed with straw. No insect larvae were found at the bases of *A. arenaria* in either Zone 2 or Zone 3a (Table 2). Although the microhabitat of dunes stabilized by *A. arenaria* was not examined in detail, a thin crust of sand was observed on these dunes that was not present on Zone 2 or 3a dunes stabilized by native vegetation. No larvae were collected from the pungent leaf litter under *E. globulus* trees, or the cool sand mixed with needles underneath *C. macrocarpa* trees (Zone 4) at Mills Farms, or in the loose sand within a dune swale (Zone 5) (Table 2). Although beetle larvae were found underneath the matrix of moss and lichen of the stabilized dune plateau (Table 2C: Zone 3b, Site 3), no stiletto fly larvae were found under this matrix or in the warm, loose sand between plants. Stiletto fly larvae were not found in sand mixed with straw at Teixeira Farms even when beetle larvae were present, but adjacent dune formations without straw contained

both beetle larvae and stiletto fly larvae (Table 2). Sand underneath *L. chamissonis* and *Salix arenaria* where stiletto fly larvae were collected was mixed with leaves and other plant debris, indicating that plant debris alone does not make dune habitats unsuitable for stiletto fly larvae.

Discussion

Efficiency of sampling methods

Although the majority of specimens collected or observed during this study were of *A. novella* (31 larvae and 83 adults), the absence of this species in malaise trap samples is noteworthy. Malaise traps have proven to be the most effective means of obtaining stiletto flies at most localities, but the success of these traps is dependent on the trivial movements of adult specimens (Irwin, 2001, Holston and Niehuis, 2002). In particular, specimens must fly or crawl up into the collecting chamber after encountering the middle partition of a malaise trap. Adults of *A. novella* were observed on bare sand and occasionally on low vegetation, and specimens invariably flew to the ground when encountering the middle partition of malaise traps. The low flight and grounding behavior renders malaise traps ineffective for sampling *A. novella*, and suggests that even long-term malaise trap sampling would insufficiently sample this coastal stiletto fly community. The use of malaise traps in Zone 3b yielded the only specimen of *B. baccata*, demonstrating the benefit of the three collecting methods (malaise trapping, hand netting, and sifting) during this short-term collecting.

Nebritus powelli adults have the earliest collecting dates of stiletto fly species found in the Guadalupe-Nipomo dune system, and final instar larvae of *N. powelli* may not have been present during field sampling for this study. *Nebritus powelli* adults have been collected from 15 February to 19 June within the Guadalupe-Nipomo dune system (Webb and Irwin, 1991b), suggesting that adults would be present at RGNCP in early June and that peak emergence of this species would be in early or late spring. On 02 June 2001, only adults of *A. novella*, *T. melanophleba*, and *Pherocera* sp. were observed in the backdunes of RGNCP although *A. novella*, *N. powelli*, *T. melanophleba*, and *T. comata* were observed in the same area on 14 May 2001. Larvae of *N. powelli* and *A. novella* were collected from RGNCP on 16 January 2002, indicating that final instar larvae of *N. powelli* should be collected by conventional

Table 5. Unique specimen identifiers and localities of stiletto fly specimens collected in the Guadalupe-Nipomo Dune System and Point Reyes National Seashore prior to this study. An exhaustive list of specimens collected from these localities may be obtained through the Mandala specimen database for Therevidae (<http://pherochera.inhs.uiuc.edu/index.html>) or from the author.

Species	Collecting Data	Specimen Identifiers
<i>A. novella</i>	California, San Luis Obispo Co. Guadalupe-Nipomo Dunes, SE of Guad.-Nipomo County Park 34° 57.528' N 120° 38.477' W 16.I.2002, M. E. Irwin	MEI 136554, MEI 136686, MEI 136792, MEI 136796, MEI 136804, MEI 136822, MEI 136827, MEI 136832, MEI 136834, MEI 136841, MEI 136843, MEI 138012, MEI 138032 – 138041, MEI 138073, MEI 138160 – 138166, MEI 138175
<i>N. powelli</i>	[same as above]	MEI 136553, MEI 136555, MEI 136586, MEI 136685
<i>N. powelli</i>	California, Ventura Co. Point Magu St. Park, 1 km. E. Pt. Magu, 34.09° N, 119.04° W 27.XII.1998, M. E. Irwin “sifted from hillside dunes”	MEI 146441
<i>N. powelli</i>	California, San Luis Obispo Co. Dune Lakes, 3 mi S Oceano, 15.II.74, Doyen & Powell, “on Salix”	MEI 006369, MEI 006370, MEI 006383
<i>B. baccata</i>	California, San Luis Obispo Co. Dune Lakes, 3 mi. S. Oceano, 20.V.1976, Doyen & Rude, “larvae coll. ex. berlese sample of misc. chaparral litter”	MEI 040909
<i>Th. comata</i>	California, Marin Co., Pt. Reyes Natl. Seashore, North Beach, <100' 23.V.1970, E. I. Schlinger	CIS 006661 – 006662, CIS 006664, CIS 006665 – 006667, CIS 006690, MEI 082010-11

sieving (Table 5). Additionally, larvae of *Pherocera* sp., the smallest stiletto fly species at the Guadalupe-Nipomo dune system (ranging from 5 to 7 mm), were also not collected. First instar larvae of *N. powelli* and the larvae of *Pherocera* sp. may not have been collected due to small size, suggesting a bias in sampling toward larger larvae. In contrast, adults of *Th. elizabethae* (August-September) and *Th. elizabethae* (September-October) emerge from August to October (Holston and Irwin, 2005), much later than all other species, and the well-developed larvae of these species were large and easily collected.

Evidence for habitat selection

Local distributions of adults and immatures at the Guadalupe-Nipomo dune system reveal spatial structuring of the stiletto fly community and specialization in dune habitats, particularly in ecological zones characterized by active sand or pioneer dune scrub (Table 3 and Table 4). *Acrosathe novella* and *Th. elizabethae* larvae are associated with active dune habitats in Zones 2 and 3a. The proximity of suitable oviposition sites to male aggregations of *A. novella* demonstrates that adults and immatures of this species can be found in the same active dune habitats. *Tabudamima melanophleba* adults were collected from the upper branches of Zone 3b pioneer dune scrub under which immatures of this species were collected, showing that males of *Ta. melanophleba* aggregate above suitable oviposition sites as in *A. novella*. Males of *Ta. melanophleba* and *A. novella* have white reflective vestiture (dustlike tomentum and hairs) on the abdomen that flashes during the short flights of males when the abdomen is not covered by the wings (Figs 1, 3). This reflective quality of the abdomen is enhanced in the exposed habitats where specimens of these two species are observed.

Males and females of *Pherocera* sp. were found on sand underneath Zone 3b pioneer scrub, and the exposed sand in Zone 3b pioneer scrub may represent a third area within Zone 3b that is utilized by *N. powelli*. A few individuals of *A. novella* were also collected on exposed sand in Zone 3b (Table 2), but were not observed with specimens of *N. powelli*.

Additional observations of *N. powelli* suggest that distributions of adults and larvae circumscribe the Zone 3a-3b transition and that adult morphology and behavior is adaptive in Zone 3b. Adults of *N. powelli* at McGrath State Beach (Ventura County, California) rested motionless on bare sand sheltered by dune scrub plants after short, hop-like flights and resembled dark bits of windblown plant debris. In comparison, specimens of *A. novella* at rest have an overall yellowish grey appearance that is much closer to the light sand of active dunes than the dark brown of *N. powelli* (Figs 1-2). The morphology and putative cryptic behavior of *N. powelli* is likely to be more effective in bare patches of Zone3b pioneer scrub than in Zone 3a habitats, where the wind is stronger and plant material is unable to accumulate in exposed areas of sand. Larvae of both *N. powelli* and *A. novella* were collected from the back-dune area of RGNCNP examined during this study (M. E. Irwin, personal communication), but the habitat of specimens was not recorded and larval distributions of *N. powelli* and *A. novella* may not overlap. The larva of *N. powelli* “sifted from hillside dunes” further suggests a Zone 3a-3b association for *N. powelli* (Table 5); Zone 3a habitats examined during this study were restricted to dune hummocks, crests of active retention ridges, and dune plains (Table 2).

The coexistence of *A. novella*, *Th. elizabethae*, and *Th. elizabethae* reveals an overlap in larval habitat use between Zones 3b and 4 provided by *S. lasiolepis*, a species tolerant to sand burial (Holland et al., 1995). Although *A. novella* and *Th. elizabethae* larvae were found in fore-dune hummocks stabilized by sprawling vegetation such as *Ambrosia chamissonis*, back-dune hummocks with larvae of these two species were stabilized by *S. lasiolepis*. Where *S. lasiolepis* formed a thicket along a retention ridge, *A. novella* and *Th. elizabethae* larvae were found with *Th. elizabethae* larvae on the active side of the dune crest adjacent to the riparian zone (Table 2A, Zone 3a-4, Site 1). The other site where *Th. elizabethae* larvae were collected was also on a dune ridge, but on the edge of a stabilized dune plateau in the intermediate scrub-riparian zone (Table 2C, Zone 3b-4, Site 1). The association of *N. powelli* adults with “*Salix*” (Table 5) also suggests utilization of Zone 3a-4 by the third active dune species. These observations indicate that *Th. elizabethae* larvae are associated with riparian edge dune habitats and that *S. lasiolepis* can provide larval habitat allowing the coexistence of active dune and riparian stiletto fly species habitats in the Guadalupe-Nipomo dune system. The ecological importance of *S. lasiolepis* stands, whose development bypasses succession of the dune plant community, has not been previously noted although *S. lasiolepis* is considered an important member of riparian and other wetland coastal dune plant communities (Ferren et al., 1995; Holland et al., 1995).

Habitat specificity in *Th. comata*, *B. baccata*, and *Ozodiceromyia* sp. is difficult to determine although additional observations of *Th. comata* and *B. baccata* suggest that these two species can be found in a wide range of habitats. Adults of *Th. comata* were distributed from low pioneer scrub plants in Zone 3b to *S. lasiolepis* trees adjacent to the Santa Maria floodplain in Zone 4. At McGrath State Beach, individuals and mating pairs of *Th. comata* were found in back-dunes dominated by plant species associated with Zones 4 and 5 (*Urtica dioica* ssp. *holosericea*, stinging nettle) or Zone 3b (*Salvia* spp., sagebrush) in the Guadalupe Nipomo dune system (Holland et al., 1995). *Thereva comata* were collected at many coastal dune localities dominated by *Carpobrotus* spp. (ice plants), including North Beach, Point Reyes National Seashore, where several larvae have also been collected (Table 5). Many specimens of *B. baccata* were found on *Carpobrotus* spp. at the

heavily disturbed dunes at Playa Del Rey, Los Angeles County, and a larva of *B. baccata* reared from “chaparral” provides a larval association with Zone 3b in the Guadalupe-Nipomo dune system (Table 5). Data on *Ozodiceromyia* sp. are limited to observations reported above, but the presence of a pupa of this species in Zone 4 and adults in Zone 3b indicates utilization of both scrub and riparian habitats. The few specimens of these three species indicate that Zones 3b and 4 warrant further sampling for a more detailed analysis of local distributions.

Hypothesis of community structure

Based on ecological associations for the nine species of stiletto flies, the Guadalupe-Nipomo Dunes fauna has been divided into three community assemblages; active dune, pioneer scrub, and scrub-riparian (Figs 7-8). The active dune assemblage is composed of the three stiletto fly species distributed only within coastal dunes, and adults of two species, *A. novella* and *N. powelli*, are known to inhabit exposed areas of active sand (Fig. 9). Because most adults of *N. powelli* were observed on bare sand in Zone 3b pioneer scrub and larval habitats were in Zone 3a in close association with Zone 3b habitats, this species is associated with the Zone 3a-3b transition. The pioneer scrub assemblage includes *Ta. melanophleba* and *Pherocera* sp., which are associated with sites dominated by *L. chamissonis* and *E. ericoides* (Fig. 10). Inland habitats where *Ta. melanophleba* have been collected are likely to be similar to pioneer dune scrub, in sandy areas with relatively high levels of substrate disturbance. The scrub-riparian assemblage is composed of the four species that have the strongest association with inland and riparian habitats: *B. baccata*, *Ozodiceromyia* sp., *Th. comata*, and *Th. elizabethae*. Regional and local distributions of *B. baccata*, *Th. comata*, and *Th. elizabethae* suggest that broad heterogeneity of Zones 3b and 4 and broad utilization of habitats by *Th. comata* contributes to the higher diversity of this assemblage in dune localities. *Thereva fucata* is one of the few species of *Thereva* collected in the Central Valley of California (Holston and Irwin, 2005), and the association of *Th. elizabethae* with riparian edge habitats at the Guadalupe-Nipomo dune system may be useful in determining larval habitat use for this species within this heavily disturbed agricultural region.

Fig 9-10. Stiletto fly habitats in the active dune zone at Rancho Guadalupe-Nipomo County Park. **Fig 9:** Zone 3a (vegetated hummocks). **Fig 10:** Zone 3b (sheltered dune plain).



Spatial partitioning by larvae of *A. novella* and *Th. elizabethae* was not observed, but two size classes of larvae were easily distinguished in sand where both species were present. Size differences in *A. novella* and *Th. elizabethae* larvae collected in June 1997 were appreciable, with larvae of *Th. elizabethae* ($n = 7$) 5 to 10 mm longer than larvae of *A. novella* ($n = 28$), corresponding to the larger size of *Th. elizabethae* adults. It is possible that different size classes of larvae, and, thus, the different species, feed on prey of different sizes, ecologically partitioning the prey resource base. An overlap in size classes between these species is expected for *A. novella* and early instars of *Th. elizabethae*, but determining the duration of size overlap will require data on rates of larval development. *Th. elizabethae* is a late summer species, in contrast to the spring and summer emergence of *A. novella* adults, so phenology may serve to exaggerate these size differences between the species. The earliest cohort of *N. powelli* larvae, which probably begins development in early spring, may similarly avoid direct competition for prey at Zone 3a-3b sites with the well-developed *A. novella* larvae produced during the previous year. The biology of these stiletto fly species as larvae is unknown, and significant differences in prey choice may or may not exist that are related to species or larval size. Nevertheless, size differences provide a metric useful in examining niche similarity from a morphological perspective (Arlettaz, 1999) and should be noted between *A. novella* and *N. powelli* larvae, and between *Pherocera* sp. and *Ta. melanophleba* larvae, if future sampling reveals local sympatry in these species.

Further evidence for habitat selection

Coastal dune habitats have been associated with stiletto fly species at several localities, but the empirical data underlying these associations was not made available and it is not clear that the assessments include the entire stiletto fly

communities at these localities. At beaches in New South Wales, Australia, English (1950) recorded adults of *Anabarhynchus latifrons* (Macquart) (as "*Platycarenum quinquevittata*") from "beach sand" and adults of *A. latifrons* and *A. maritimus* Hardy from "tall grasses on sand dunes behind the beach" although larvae of both species were found among spinifex roots "at the back of the beach." Irwin (1972) reported habitat differentiation in the coastal dunes at Umhlanga Rocks, South Africa, associating larvae and adults of *Microgephyra capricornis* (Lyneborg) with scrub vegetation dominated by *Senecio barbetonicus* Klatt on "humus-enriched sand on the leeward side of beach dunes" and larvae of "a new genus close to *Psilocephala*" with "the exposed, ocean side of the beach dunes...". Barry and Schlinger (1977) presented an annotated species checklist for Inglenook Fen, California, recording *Tabuda planiceps* Loew (as "*Metaphragmata planiceps*") from "Prairie Grassland," "*Chromolepida* sp." from the "Fen-Dune Ecotone," and two species identified as "*Thereva*" "sp. 1" and "sp. 2" from the "Dune" habitat. Inglenook Fen encompasses the greatest species and ecological diversity among these localities, but the "Dune" and "Prairie Grassland" categories allow only vague comparisons with zones recognized for the Guadalupe-Nipomo dune system.

Ecological studies of Diptera have also provided coastal dune habitat associations for European species of *Acrosathe*, *Dialineura*, and *Thereva*, with detailed notes on species providing links to ecological zones recognized in this study. Ardö (1957) noted that "an equal number" of *Acrosathe annulata* (Fabricius) specimens were "observed on the dune ridge [Zone 3a] and on the dune heath [Zone 3b]." Several authors have mentioned that *A. annulata* forms male aggregations in dune plains and ridges (Zone 3a) (Ardö, 1957; Barkenmeyer,

1995; Lyneborg, 1986), and Stubbs and Drake (2001) noted that *A. annulata* “may be swept from vegetation adjacent to likely sun-bathing spots [Zone 3a or 3a-3b].” *Dialineura anilis* (Linnaeus) has been associated with Zone 3b and 3a-3b habitats described as “sparsely vegetated areas” (Stubbs and Drake, 2001) and “sparse vegetation and bare sand on yellow dunes” (Howe, 2002, as opposed to “the bare sand [Zone 3a] chosen by *A. annulata*” (Stubbs and Drake, 2001). On the North Sea island Memmert, where *A. annulata* was not recorded, Barkenmeyer (Barkenmeyer, 1994) found *D. anilis* more frequently in “secondary dune” areas and the “south seawall” (Zone 3a) than *Th. nobilitata* (Fabricius), whereas *Th. nobilitata* far outnumbered *D. anilis* in grey dune areas characterized as a “Sambuchus-Hippophaë-bzw. Hippophaë-und Salix Gebürschen” zone (Zone 3b). On the North Sea island Norderney, *D. anilis* was found on dunes near *Betula* and *Alnus* stands (Zone 3a-3b) (Barkenmeyer, 1993). In Wales, *Thereva cinifera* (Meigen) has been associated with “large areas of bare and relatively unstable sand, and sparsely vegetated dunes [Zone 3a]” and *Thereva fulva* (Meigen) with “areas of fixed sand with well established vegetation and patches of bare substrate [Zone 3b or 3a-3b]” (Howe, 2002). Barkenmeyer (1993, 1995) found *Th. cinifera* in the “Ruderal-Calluna-Fäche” (Zone 3b) on Norderney and “grey dunes [Zone 3b]” on the North Sea island Borkum, whereas *Thereva unica* (Harris) was associated with “bewaldeten” areas (Zone 4) on Norderney and “tertiary dunes [Zone 3b]” on Borkum.

Conclusions

Associations of stiletto fly species with particular ecosystems have been reported in taxonomic revisions (Irwin and Lyneborg, 1981a; Irwin, 1977b; Hauser and Irwin, 2003; Holston and Irwin, 2005; Lyneborg, 2001) and faunistic studies (Lyneborg and Spitzer, 1974; Weinberg, 1985; Keil, 2003), suggesting ecological specialization in stiletto fly species at a regional geographic scale. Lyneborg and Spitzer (1974) reported ecological notes for 19 species of *Thereva* found in the Czech Republic and *A. annulata* and linked the distributions of species to lowland, steppe, mountainous, or boreoalpine biomes. Extending these results, Keil (2003) described ecological “trends” among 19 of the 26 stiletto fly species found the Czech Republic and concluded that species composition of lowland, warm steppe/xerothermic, and mountain localities was different. Weinburg (1985) similarly noted in a

study of Romanian stiletto flies that nine species “are specific to the sandy habitat...in the dunes from the Danube Delta and in the sand along the Danube River” and five species are found “in the Carpathian mountains from 800 - 2200 m.” Although distributions and inferred habitat preferences are useful aids for species determinations and will be relevant to studies of speciation (Hauser and Irwin, 2003; Holston and Irwin, 2005), studies of stiletto fly communities are needed to examine habitat selection at local geographic scales. Results from this study demonstrate that dune habitats within a larger geographic area are utilized by different stiletto fly species, which has strong relevance for further diversity and conservation assessments.

Habitat associations suggest that stiletto fly adults spatially partition European coastal dunes and that species can be classified ecologically using the assemblages described for the Guadalupe-Nipomo dune system. Probable members of the active dune assemblage are *A. annulata* and *Th. cinifera*, and observations of *D. anilis* suggest that it may occupy habitats in the intermediate active dune-pioneer scrub (Zone 3a-3b). Members of European pioneer scrub and scrub-riparian assemblages are likely to be species of *Thereva*, with *Th. nobilitata* and *Th. unica* prominent at many coastal dune localities. Unfortunately, local distributions and habitat associations for larvae in European coastal dunes have not been determined. A notable observation is that the putative active dune species of central and northern Europe, *A. annulata* and *Th. cinifera*, are also found at inland localities that include the sandy banks of rivers (Lyneborg and Spitzer, 1974; Lyneborg, 1986; Barkenmeyer, 1993; Grootaert et al., 2001; Holston and Niehuis, 2002; Howe, 2002). Inland riparian sites may be key localities for studying inland stiletto fly communities, for which spatial structuring has not been demonstrated (Hartman et al., 1995; Keil, 2003). Relative differences in reproductive success with respect to habitat type are, however, most crucial for determining habitat selection among species (Arlettaz, 1999), and the results from this study provide a descriptive framework for testing habitat selection in stiletto fly species associated with coastal dunes.

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