

Faunal Study of the Nocturnal Aculeate Wasps (Hymenoptera) of the Sonoran and Mojave Deserts of Joshua Tree National Park

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Abstract

Nocturnal aculeate wasps (Hymenoptera: Chyphotidae, Brachycistidinae [Tiphidae], and Mutillidae) are abundant in North America's deserts, yet their patterns of diversity are not well studied. Here we report on the diversity of these groups in Joshua Tree National Park (JTNP). On the basis of collection data from a transect of 14 sampling sites transitioning from the Mojave to the Sonoran Desert, our study shows that there are at least 11 species of *Chyphotidae* (Chyphotidae), based on the collection of 1,513 specimens, there are at least 22 species of brachycistidine Tiphidae species in five genera, based on the collection of 13,960 specimens, and at least 35 species of nocturnal mutillids in six genera, based on 8,477 specimens. Brachycistidine Tiphidae populations peak earlier in the season compared with the other two groups. Also we found an increase in Chyphotidae, Brachycistidinae, and Mutillidae diversity and abundance with decreasing latitude. Several species appear to be spatially restricted to one desert region; others exhibit temporal isolation, only being collected during specific months. Our study suggests that JTNP houses a diverse community of nocturnal aculeate wasps with the Sonoran Desert being more diverse than the Mojave Desert.

Key words: Sonoran Desert, Mojave Desert, transition zone, United States, biodiversity

National Parks and other protected areas can play an important role in the maintenance of biodiversity (Bruner *et al.* 2001). In North America, much of the conservation efforts in national parks have focused on vertebrates (Clevenger and Waltho 2000, Mortiz *et al.* 2008) or on rare plants (Miller and White 1986, Frank and McNaughton 1992). Despite the conservation focus of National Parks in the United States, little has been published about the diverse insect communities housed in these protected areas.

Joshua Tree National Park (JTNP) is unique in that it contains portions of two distinct desert ecoregions. This park gained U.S. National Park status in 1994 and is large covering ~3,200 ha in southeastern California (National Parks Service). The northern regions of JTNP are part of the Mojave Desert and the southern regions are part of the Sonoran Desert. These two deserts that exist within JTNP, and the transition zone connecting them, provide a unique opportunity to study patterns of insect biodiversity in a potentially diverse ecotone.

Nocturnal aculeate wasps (Hymenoptera: Chyphotidae, Brachycistidinae [Tiphidae], and Mutillidae) are ubiquitous in North America's deserts, and, although it is expected that they would play an important role in the ecology of these areas, their patterns of diversity, however, are not well studied. *Chyphotidae* Blake (Hymenoptera:

Chyphotidae) is a genus of wasp that includes many species endemic to the deserts of North America, though some species can be found as far south as Mexico. *Chyphotidae* females, as well as the related genera in Typhoctinae, presumably parasitize the larval or pupal stages of Coleoptera, based on phylogenetic relationships, but Brothers and Finnamore (1993) suggested camel spiders (Arachnida: Solifugae) based on a single record. This is the only sparse natural history information that exists for this group. Although the genus has been revised twice previously by Buzicky (1941) and Mickel (1967), the taxonomy remains unsettled, making species identification challenging.

In the southwestern deserts of the United States, nocturnal wasps in the family Tiphidae (Hymenoptera: Tiphidae: Brachycistidinae) likely play an important ecological role as parasitoids based on their high abundance. However, little has been published on this group besides taxonomy. Many Brachycistidinae are endemic to specific arid regions of North America (Kimsey and Wasbauer 2006), though the subfamily can be found as far south as Costa Rica. Little is known about the natural history of this group, but it is thought that Brachycistidinae females parasitize the larval or pupal stages of Coleoptera, based on a single recent record (Borowiec and Kimsey 2015).

Mutillidae (Hymenoptera), also known as velvet ants, is a family of wasp that also has species, both diurnal and nocturnal, endemic to the deserts of North America. However, the nocturnal velvet ant fauna of JTNP is poorly known. Velvet ant females parasitize the larval or pupal stages of holometabolous insects, such as Diptera, Coleoptera, and Hymenoptera, with most known hosts being aculeate Hymenoptera (Brothers *et al.* 2000). As with *Chyphotes*, only sparse natural history information exists for most species of velvet ants.

For all three of these groups, the females presumably spend most of their time underground searching for hosts, and, therefore, are encountered less frequently than males. Males of these groups, however, are easily collected as they are attracted to light traps.

The objectives of this study are to determine species diversity of nocturnal aculeate wasps at JTNP, to determine faunal differences between the different deserts of the park, and to determine relative species abundances in the distinct desert regions. Specimens were collected in a transect spanning both deserts and the transition zone. Understanding patterns of diversity in diverse, desert-adapted insects can inform future conservation efforts and will lead to a better understanding of biodiversity in JTNP.

Materials and Methods

JTNP includes the Mojave Desert, Sonoran Desert, and transition zone between the two. These areas can be identified based on their characteristic vegetation. JTNP is named after the Joshua tree (*Yucca brevifolia*), which is endemic to the Mojave Desert and is restricted to the northern portion of the park. This area also houses piñon pine (*Pinus monophylla*), California juniper (*Juniperus californica*), desert scrub oak (*Quercus turbinella*), Tucker's oak (*Quercus john-tuckeri*), and Muller oak (*Quercus cornelius-mulleri*) (Ricketts *et al.* 1999). The southern part of the park, below 910 m, in the Sonoran Desert has flora that includes creosote bush (*Larrea tridentata*), scrub ocotillo (*Fouquieria splendens*), desert saltbush (*Atriplex* spp.), *Yucca* and cholla cactus (*Cylindropuntia bigelovii*) (Ricketts *et al.* 1999).

Within JTNP, Pinto Basin Road served as the perfect transect between the Mojave and Sonoran deserts. Beginning at the park boundary at the North Entrance and continuing along Pinto Basin Road to the Cottonwood Visitor Center, light traps were deployed approximately every 5 km (Table 1). Trapping along Pinto Basin Road provided a 43-km transect with a 727 m change in elevation. This allowed five light traps to be placed in the Mojave Desert; the sites of these traps are designated N9, N7, N5, N3, and N1, where N stands for north of the transition zone and the number represents the distance from the transition zone in miles. This also allowed for one trap in the transition zone (T) and eight traps south of the transition zone

Table 1. Joshua Tree National Park Transect Site Information

Site name	Site location	Distance from road edge (m)	Elevation (m)	Dominant vegetation type
N9	N34.00482 W116.04924	66	1,268	Joshua Tree
N7	N34.02017 W116.01778	88	1,111	Yucca & Joshua Trees
N5	N33.99412 W116.02134	90	1,193	Yucca and Joshua Trees
N3	N33.97477 W115.99798	60	1,050	Yucca and Creosote
N1	N33.95148 W115.98084	76	900	Creosote and Cheesebush
T	N33.94111 W115.96973	59	842	Creosote, Mesquite, and Smoke tree
S1	N33.93315 W115.95633	56	774	Smoke tree
S3	N33.92409 W115.92458	32	631	Jumping Cholla
S5	N33.92305 W115.89362	56	559	Small Creosote
S7	N33.91169 W115.86460	71	541	Small Creosote and Cheesebush
S9	N33.90141 W115.83225	64	544	Small Creosote
S11	N33.87896 W115.81215	77	608	Creosote and Mormon tea
S13	N33.85631 W115.79056	55	680	Creosote
S18	N33.80103 W115.78088	62	851	Creosote

Site names indicate location in reference to the transition zone between the Mojave and Sonoran deserts and distance in miles from the transition zone. Site names labeled as N indicate it was located north of the transition zone (Mojave Desert), T indicates it is directly in the transition zone, and S indicates it was south of the transition zone (Sonoran Desert).

in the Sonoran Desert (S1, S3, S5, S7, S9, S11, S13, and S18). Once again, where S stands for south of the transition zone and the number represents the distance from the transition zone in miles (Fig. 1).

Specimens were collected from each site using light traps. The light traps consisted of a fluorescent battery-powered camping lantern and small, clear bowls filled with slightly soapy water. Lights were turned on at dusk and off at dawn. Sites were sampled four times, once each month from July to October 2012 (18–21 July,

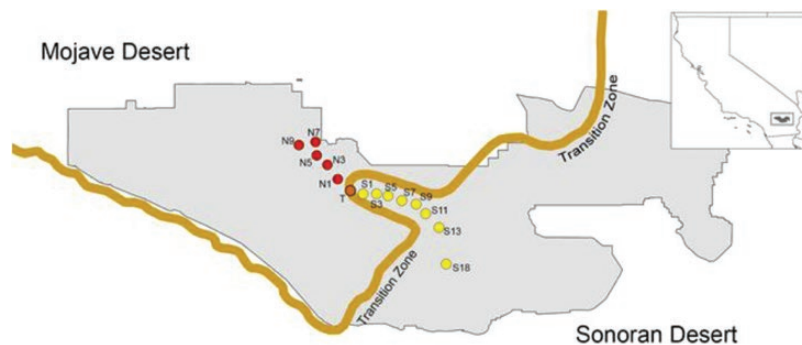


Fig. 1. Joshua Tree National Park map (gray) with park boundary. Location of the Sonoran Desert, transition zone, and Mojave Desert are labeled. Transect collection sites are indicated on the map by circles and are labeled with site names corresponding to Table 1.

Table 2. Number of individuals of each *Chyphotes* species collected at each site from north to south

Species	Collecting site														Total no. per spp.
	N9	N7	N5	N3	N1	T	S1	S3	S5	S7	S9	S11	S13	S18	
<i>Chyphotes aenigmus</i>	3	1	1	7	19	25	36	93	47	28	31	27	67	75	460
<i>Chyphotes atriceps</i>	13	43	17	42	15	2	17	5	4	16	15	24	19	69	301
<i>Chyphotes bobarti</i>	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1
<i>Chyphotes calexicensis</i>	–	–	–	–	–	–	–	–	7	14	14	6	3	2	46
<i>Chyphotes californicus</i>	2	2	1	–	37	48	31	2	1	–	–	3	2	10	139
<i>Chyphotes incredulus</i>	–	–	–	–	–	–	–	–	18	31	22	13	3	–	87
<i>Chyphotes melaniceps</i>	–	–	1	1	21	11	59	62	5	7	11	16	41	85	320
<i>Chyphotes attenuatus</i>	4	–	5	10	2	–	–	–	1	–	–	–	7	23	52
<i>Chyphotes minisculus</i>	–	–	–	–	7	16	–	–	2	1	1	2	5	1	35
<i>Chyphotes pallidus</i>	–	–	–	–	–	–	–	3	21	33	5	4	–	1	67
<i>Chyphotes</i> sp. nov.	–	–	–	–	–	–	–	–	–	1	1	2	–	1	5
Total no. per site	22	46	25	60	101	102	143	165	107	131	100	97	147	267	= 1,513

Sites beginning with ‘N’ were Mojave Desert sites, those beginning with ‘S’ were Sonoran Desert sites, and ‘T’ indicates a site in the transition zone.

26–28 August, 22–24 September, and 26–28 October). During each sampling event, traps were deployed each evening for a total of two to three nights. Sampling was restricted to July to October due to permitting. All collected specimens were stored in 95% ethanol initially, and pinned, labeled, and identified at the Entomological Collection at Utah State University (EMUS). GPS locations were determined for each collection site (Table 1).

The species of *Chyphotes* were identified using Buzicky (1941) and Mickel (1967), as well as through the study of type material. The brachycistidine genera of Tiphidae were identified using Kimsey and Wasbauer (2006) and the reference collection at EMUS identified by

Wasbauer. The species of *Acanthetropis* Wasbauer, *Brachycistis* Fox, *Colocistis* Krombein, and *Stilbopogon* Mickel and Krombein were identified using Wasbauer (1966) and Kimsey and Wasbauer (1998, 2013, 2015). The mutillid genera were identified based on Schuster (1958) and the reference collection housed at EMUS.

The Sørensen’s similarity index (Sørensen, 1948), which is based on presences/absences, was used to determine the similarity between two sites. A pair-wise comparison of all sites using the Sørensen’s similarity index can be found in Table 5. The Bray–Curtis dissimilarity index (Bray and Curtis 1957), which is additionally based on abundances, was used to determine dissimilarity between two sites.

Table 3. Number of individuals of each Brachycistidinae species collected at each site from north to south

Species	Collecting site														Total no. per spp.
	N9	N7	N5	N3	N1	T	S1	S3	S5	S7	S9	S11	S13	S18	
<i>Acanthetropis noctivaga</i>	1	3	4	26	4	7	31	44	90	119	160	110	314	324	1,237
<i>Brachycistis agama</i>	–	–	–	–	–	–	–	–	4	31	5	17	14	–	71
<i>Brachycistis curvata</i>	19	21	254	23	1	1	–	17	34	33	29	18	7	4	461
<i>Brachycistis elegantula</i>	–	–	–	–	–	–	–	–	–	–	1	–	1	–	2
<i>Brachycistis imitans</i>	1	1	4	–	–	–	–	–	–	1	1	1	11	4	24
<i>Brachycistis inaequalis</i>	9	13	1	1	1	–	–	–	45	296	66	3	2	–	437
<i>Brachycistis linsleyi</i>	26	30	50	35	4	5	9	19	52	101	144	255	235	23	988
<i>Brachycistis petiolata</i>	–	–	–	–	–	–	–	–	17	30	36	4	–	–	87
<i>Brachycistis timberlakei</i>	1	40	114	74	–	1	1	20	85	194	206	189	137	40	1,102
<i>Brachycistis triangularis</i>	7	–	4	3	18	56	61	33	182	120	111	84	77	86	842
<i>Brachycistis vigilax</i>	1	4	27	73	–	1	1	6	69	111	156	18	10	9	486
<i>Brachycistina acuta</i>	44	47	21	39	19	11	7	44	125	262	71	135	135	24	984
<i>Colocistis brevis</i>	1	8	4	7	64	89	245	314	418	537	219	180	45	110	2,241
<i>Colocistis castanea</i>	45	63	30	61	106	175	264	54	73	67	52	138	137	1577	2,842
<i>Colocistis crassa</i>	62	16	21	13	3	1	3	2	–	1	9	85	72	34	322
<i>Colocistis eremi</i>	–	1	–	1	14	2	31	132	89	99	48	271	85	113	886
<i>Colocistis themarum</i>	5	8	7	9	45	103	84	18	8	5	5	9	4	2	312
<i>Stilbopogon inermis</i>	–	–	–	–	29	43	29	4	17	9	46	11	2	2	192
<i>Stilbopogon marcida</i>	–	–	–	–	5	9	9	1	68	52	75	28	21	7	275
<i>Stilbopogon megalops</i>	–	1	–	–	13	49	20	–	4	2	8	1	1	–	99
<i>Stilbopogon paupercula</i>	–	–	–	–	1	–	5	–	6	1	4	–	–	–	17
<i>Stilbopogon perpunctata</i>	–	–	–	–	1	4	1	1	8	24	9	4	–	1	53
Total no. per site	222	256	541	365	328	557	801	709	1394	2095	1461	1561	1310	2360	= 13,960

Sites beginning with ‘N’ were Mojave Desert sites, those beginning with ‘S’ were Sonoran Desert sites, and ‘T’ indicates a site in the transition zone.

A pair-wise comparison of all sites using the Bray–Curtis dissimilarity index can be found in Table 6.

Results and Discussion

Chyphotes (*Chyphotidae*)

Our trapping efforts resulted in the collection of 1,513 male specimens representing 11 species (Table 2). *Chyphotes aenigmus* Mickel ($n = 460$), *Chyphotes melaniceps* (Blake) ($n = 320$), and *Chyphotes atriceps* Mickel ($n = 301$) are the most abundant of all the species found at the park. The rarest species, those with less than 10 individuals found throughout the course of the study, include only *Chyphotes boharti* Mickel (one specimen) and *C. sp. nov.* (five specimens), which will be described in a different publication.

Tiphiidae (*Brachycistidinae*)

Our trapping efforts resulted in the collection of 13,960 male specimens representing 22 species (Table 3). The most abundant species collected at JTNP were *Colocistis castanea* (Cresson) ($n = 2,842$),

Colocistis brevis (Fox) ($n = 2,241$), and *Acanthetropis noctivaga* ($n = 1,237$). The rarest species was *Brachycistis elegantula* Cockerell and Casad (two specimens) (Table 3).

Mutillidae

Our trapping efforts resulted in 35 species in six genera totaling 8,477 male specimens (Table 4). *Odontophotopsis microdonta* Ferguson ($n = 1,803$), *O. clypeata* Schuster ($n = 1,036$), and *Sphaerophthalma yumaella* Schuster ($n = 825$) are the most abundant of all the species found at the park. The rarest species, those with less than 10 individuals found throughout the course of the study, include *Odontophotopsis dalyi* Sadler and Pitts (4 specimens), *Odontophotopsis obscura* (Cockerell) (3), *Odontophotopsis odontoloxia* Sadler and Pitts (1), *Odontophotopsis parva* Schuster (2), *Odontophotopsis setifera* Schuster (8), *Photomorphus schoenwerthi* Sadler and Pitts (1), *Sphaerophthalma nana* (Ashmead) (1), and *Sphaerophthalma triangularis* (Blake) (2) (Table 4). *O. setifera* Schuster and also *S. nana* were considered rare according to surveys of the Ash Meadows National Wildlife Refuge (Boehme *et al.* 2012).

Table 4. Number of individuals of each Mutillidae species collected at each site from north to south

Species	Collecting site															Total no. per spp.
	N9	N7	N5	N3	N1	T	S1	S3	S5	S7	S9	S11	S13	S18		
<i>Acanthophotopsis falciformis</i>	–	–	–	–	–	2	3	–	5	2	14	3	3	2	34	
<i>Acrophotopsis dirce</i>	1	20	3	5	12	9	7	1	1	–	13	–	1	23	96	
<i>Dilophotopsis paron</i>	49	11	41	4	7	5	1	2	–	1	–	6	5	134	266	
<i>Odontophotopsis armata</i>	–	11	2	3	20	84	130	6	1	2	2	–	1	3	265	
<i>Odontophotopsis bellona</i>	4	5	8	8	2	14	41	77	40	20	45	9	15	49	337	
<i>Odontophotopsis biramosa</i>	–	–	–	–	–	–	–	2	4	5	3	6	10	1	31	
<i>Odontophotopsis clypeata</i>	1	4	–	5	3	3	49	128	144	203	71	108	107	210	1,036	
<i>Odontophotopsis dalyi</i>	–	2	–	–	–	–	–	–	–	2	–	–	–	–	4	
<i>Odontophotopsis delodonta</i>	–	2	–	1	–	1	6	7	8	52	48	18	17	1	161	
<i>Odontophotopsis inconspicua</i>	–	1	–	5	5	17	104	18	3	10	30	11	13	59	276	
<i>Odontophotopsis mamata</i>	–	–	–	–	1	29	75	19	2	6	3	4	2	12	153	
<i>Odontophotopsis melicausa</i>	10	15	–	9	–	2	4	–	–	1	–	9	13	23	86	
<i>Odontophotopsis microdonta</i>	79	53	76	125	22	19	13	195	23	11	43	724	286	134	1,803	
<i>Odontophotopsis obscura</i>	–	–	–	–	–	–	–	–	–	–	3	–	–	–	3	
<i>Odontophotopsis odontoloxia</i>	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	
<i>Odontophotopsis parva</i>	–	–	–	–	–	–	–	–	–	–	2	–	–	–	2	
<i>Odontophotopsis quadrispinosa</i>	–	–	–	3	–	2	7	26	11	20	26	24	4	5	128	
<i>Odontophotopsis serca</i>	3	6	1	8	51	256	375	19	5	2	10	17	6	17	776	
<i>Odontophotopsis setifera</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	8	8	
<i>Odontophotopsis sonora</i>	–	–	–	–	–	–	1	1	1	5	4	–	–	–	12	
<i>Photomorphus schoenwerthi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	
<i>Sphaerophthalma amphion</i>	3	2	3	1	5	16	34	14	2	3	3	2	9	9	106	
<i>Sphaerophthalma angulifera</i>	14	–	9	–	–	1	–	–	–	–	–	–	1	6	31	
<i>Sphaerophthalma arota</i>	–	1	–	–	1	5	6	3	2	1	–	–	3	8	30	
<i>Sphaerophthalma becki</i>	–	2	7	13	11	34	13	48	32	23	9	50	44	57	343	
<i>Sphaerophthalma blakeii</i>	11	10	37	66	8	2	15	19	15	18	31	18	58	93	401	
<i>Sphaerophthalma difficilis</i>	20	37	43	40	17	39	62	70	57	111	89	63	67	106	821	
<i>Sphaerophthalma fergusonii</i>	1	1	–	2	1	52	70	7	1	5	2	3	5	9	159	
<i>Sphaerophthalma macsuwaini</i>	–	–	–	–	3	32	10	–	–	–	–	–	–	–	45	
<i>Sphaerophthalma megagnathos</i>	–	–	–	–	–	–	1	–	–	–	–	–	–	11	12	
<i>Sphaerophthalma mendica</i>	–	1	1	3	2	4	16	2	–	–	5	–	7	154	195	
<i>Sphaerophthalma nana</i>	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	
<i>Sphaerophthalma pallidipes</i>	–	–	–	–	–	–	–	–	7	12	7	–	1	–	27	
<i>Sphaerophthalma triangularis</i>	–	–	1	–	–	–	–	–	–	1	–	–	–	–	2	
<i>Sphaerophthalma yumaella</i>	2	2	21	55	26	16	49	81	74	64	91	52	132	160	825	
Total no. per site	198	187	253	356	197	644	1092	745	439	580	554	1127	810	1295	= 8,477	

Sites beginning with “N” were Mojave Desert sites, those beginning with “S” were Sonoran Desert sites, and “T” indicates a site in the transition zone.

Table 5. Sørensen's similarity coefficient based on the combined presence/absence data for all three groups of nocturnal wasps (Hymenoptera: Chyphotidae, Brachycistidinae [Tiphidae], and Mutillidae)

	N9	N7	N5	N3	N1	T	S1	S3	S5	S7	S9	S11	S13	S18
N9														
N7	0.83													
N5	0.87	0.80												
N3	0.84	0.90	0.85											
N1	0.72	0.81	0.76	0.80										
T	0.75	0.86	0.76	0.85	0.87									
S1	0.68	0.82	0.69	0.81	0.86	0.92								
S3	0.71	0.83	0.75	0.84	0.84	0.88	0.89							
S5	0.63	0.71	0.64	0.73	0.80	0.80	0.81	0.84						
S7	0.63	0.73	0.63	0.74	0.77	0.81	0.82	0.83	0.91					
S9	0.59	0.70	0.63	0.74	0.76	0.78	0.79	0.82	0.90	0.91				
S11	0.69	0.75	0.65	0.77	0.77	0.83	0.80	0.83	0.88	0.93	0.88			
S13	0.73	0.81	0.74	0.82	0.82	0.90	0.83	0.84	0.88	0.87	0.86	0.88		
S18	0.72	0.77	0.73	0.81	0.81	0.89	0.86	0.89	0.83	0.84	0.81	0.86	0.89	

A value of 1 indicates the two localities share all of the same species, and a value of 0 indicates they do not share any of the same species. Indices at, or above, 0.90 are bolded.

Biogeographical and Ecological Trends

There was a trend showing an increase in the abundance and diversity of all three groups with decreasing latitude (i.e., more specimens representing more species were collected at the south end of the park than the north end) with an average of 631 specimens per site caught in the Mojave Desert, 1,303 in the transition zone and 2,436 in the Sonoran Desert. Furthermore, the similarity of the sites decreased and the dissimilarity increased as sites are compared from north (Mojave Desert) to south (Sonoran Desert) (Tables 5 and 6), although some adjacent sites, such as S5, S7, and S11, were quite similar. For nocturnal aculeate wasps, the Sonoran Desert is more diverse than the Mojave Desert, which is the case for other flora and fauna (Phillips *et al.* 2015). Given the number of specimens collected and the parasitic nature of all three of these groups, aculeate nocturnal wasps must be ecologically significant in these deserts reducing the overall numbers of both potential pollinators, predatory hymenopterans, and phytophagous insects.

Interestingly, there were several species that appeared to be restricted to the Sonoran Desert portions of the park. For example,

Chyphotes boharti, *Chyphotes calexicensis* Bradley, *Chyphotes pallidus* Buzicky, *Chyphotes incredulus* Mickel, and *C. sp. nov.* (Table 2), *Brachycistis agama* (Dalla Torre), *B. elegantula*, and *B. petiolata* Fox (Table 3), and *Acanthophotopsis falciformis* Schuster, *Odontophotopsis biramosa* Schuster, *O. obscura*, *O. odontologia*, *O. parva*, *O. setifera*, *O. sonora* (Schuster), *Photomorphus schoenwerthi*, *Sphaerophthalma megagnathos* Schuster, and *Sphaerophthalma pallidipes* Schuster (Table 4) were only collected from Sonoran Desert sites. Several other species were much more common in the Sonoran Desert, although limited individuals were also collected north of the transition zone. For example, all five of the *Stilbopogon* species were primarily collected in the Sonoran Desert, with only a few individuals collected more than 1.6 km north of the transition zone. *C. aenigmus* was collected from every site, but only 31 individuals were collected from the Mojave region, while 404 individuals were collected from the Sonoran. Some species of mutillids, such as *Odontophotopsis clypeata*, *Odontophotopsis delodonta* Viereck, and *Odontophotopsis inconspicua* (Blake) showed a similar trend. Other species seemed to be most abundant in the transition between

Table 6. Bray–Curtis dissimilarity coefficient based on the combined data for all three groups of nocturnal wasps (Hymenoptera: Chyphotidae, Brachycistidinae [Tiphidae], and Mutillidae)

	N9	N7	N5	N3	N1	T	S1	S3	S5	S7	S9	S11	S13	S18
N9														
N7	0.35													
N5	0.49	0.50												
N3	0.49	0.34	0.41											
N1	0.67	0.59	0.73	0.64										
T	0.83	0.75	0.83	0.75	0.42									
S1	0.87	0.81	0.85	0.76	0.57	0.32								
S3	0.73	0.69	0.73	0.58	0.66	0.66	0.51							
S5	0.80	0.72	0.71	0.61	0.71	0.71	0.59	0.37						
S7	0.86	0.79	0.76	0.70	0.79	0.78	0.67	0.50	0.26					
S9	0.79	0.71	0.67	0.59	0.71	0.71	0.60	0.47	0.31	0.30				
S11	0.77	0.75	0.73	0.65	0.74	0.73	0.66	0.46	0.46	0.46	0.43			
S13	0.73	0.71	0.67	0.57	0.72	0.71	0.66	0.45	0.47	0.51	0.43	0.28		
S18	0.84	0.81	0.82	0.73	0.80	0.76	0.65	0.57	0.65	0.66	0.64	0.62	0.49	

Values close to 1 indicate the communities at these locations are completely different, and values close to 0 indicate they are more similar.

Mojave and Sonoran regions. For example, *Stilbopogon megalops* Kimsey and Wasbauer and *Colocistis themarum* (Bradley), while collected from both deserts, were more abundant in the transition zone site and sites adjacent to it. *Chyphotes californicus* Baker, while collected from both deserts, was found in higher abundance in the transition zone or in the sites adjacent to it. Surprisingly, none of the species collected were restricted to the Mojave Desert portions of the park, though one, *Brachycistis curvata* Malloch, was more abundant in the Mojave sites than in the Sonoran sites.

The diversity of wasps was not even across the collecting dates. Unsurprisingly, the number of individuals collected decreased as the season progressed. For example, 8,287 brachycistidines were collected in July, 2,563 in August, 2,727 in September, and 383 in October. Although the beginning of the flight season could not be determined due to permitting, overall there was a decrease in abundance as the summer progressed. This pattern, however, was not consistent across all species. Some species, such as *Co. brevis* and *Co. castanea*, were more commonly collected in July. Other species, such as *B. agama* and *B. curvata*, were more often collected in September or October, and *C. pallidus* and *A. falciformis* were more commonly collected in the later summer months (August and September) than in July. In addition, brachycistidine tiphiids peaked earlier in the season compared with that of the other two groups. This suggests that in addition to the observation that some species are spatially isolated, some species also appear to be temporally isolated.

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