

**NOVITATES 3856 Supplementary file: Portion of unpublished, undated ms. by Gerald I. Stage (numbered pp. 14–96 and pp. 406–410), on the biology of the bee genus *Hesperapis***

Introductory note by Jerome G. Rozen, Jr., author of NOVITATES 3856:

“More than quarter century ago, Gerry I. Stage sent me a part of a preliminary manuscript treating 11 species of the bee genus *Hesperapis* that he had drafted and intended to publish under his name and that of Roy Snelling as part of a major work entitled “A revision of Nearctic Melittidae: the subfamily Dasypodinae (Hymenoptera: Apoidea).” The part sent, pages 14–96, pertains to various aspect of the nests, nesting biology, and immature stages of these species about which little had been known. In addition, he included pages 406–410, which are tables providing additional data about the biology of the species. This work was never published, and both Stage and Snelling have died. Because most the information is rich, detailed, and valuable but still unknown, it is offered below.

**“WARNING: Users of this information should be aware that the fallowing species names are invalid: “*hermosa*,” “*kayella*,” and “*peninsularis*.” Descriptions of the taxa were never published.”**

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file under  
Stage

territorial behavior at sites in San Francisco. All the other published biological data concerning species of Hesperapis consists of scattered flower association and distribution records usually in conjunction with original descriptions of the species.

#### BIOLOGY

This section contains a review of what is now known about the various phases of the biology of the species of Hesperapis. For this purpose biology is considered in its broadest sense.

One of the prime objectives of the biological investigations undertaken in this study was to obtain additional characters which should be used to check and further refine the classification of the genus. Thus, emphasis was placed on certain aspects of the biology of these bees that most likely would afford the best interpretation either in terms of species isolating mechanisms or as biological characters which could be evaluated along with the morphological characters. Comparative studies of behavior during nest construction, foraging, and sleeping were found to be the most rewarding sources of biological characters while data on distribution, mating behavior, and nest site selection proved to be the most useful in recognizing possible isolating mechanisms.



The ease of obtaining various types of biological information varied enormously with the result that treatment of the subjects concerned is unequal. Distributional data, both seasonal and geographic, is the most complete with at least some information available for all species thanks to records associated with museum specimens. Likewise, information on foraging behavior is relatively complete due to museum records and the ease of observing these bees at the flowers. However, information on most other aspects of the biology of the species of Hesperapis is available for only a few species since it was difficult to locate active nest sites. Even in local areas where species of Hesperapis were abundant on flowers it was not unusual to search for hours and never discover their nests. Nineteen nest sites representing seven species, H. <sup>hermosa</sup> ~~kayella~~ Stage, <sup>and Snelling</sup> H. rufipes (Ashmead), H. ilicifoliae (Cockerell), H. regularis (Cresson), H. pellucida Cockerell, H. nitidula Cockerell and H. peninsularis Stage, <sup>and Snelling</sup> are known and have been studied.

Publications by Linsley, MacSwain, and Smith (1952) and Michener et al. (1955) were relied upon heavily for guidance during this phase of the work.



## Life history

This account is intended to serve as a general background for the following sections which treat selected subjects in much greater detail. Only those subjects not treated later are amplified to any appreciable extent here.

Adults of one species or another of Hesperapis can be found flying during any month of the year except December although individual species in local areas tend to have relatively short flight seasons which can usually be classified more or less as either vernal or autumnal. Records from museum specimens supported by field observations indicate that at least two species, H. regularis and H. pellucida, are protandrous with males emerging as long as five days before the females.

Mating occurs early in the flight season and soon thereafter females begin nesting. Nests are generally loose assemblages of cells connected by lateral tunnels to a main burrow which descends from the surface of the ground. Each lateral tunnel is filled after its single cell has been supplied with a pollen ball and an egg. Soil for this purpose is apparently excavated from the new lateral which will eventually terminate in the next cell. A few nests have been found showing a partly filled lateral to a complete cell and a partly excavated new lateral. However, nests have never been found to have more than one open



cell. The laterals are generally sufficiently long that cells rarely are found in close proximity to each other. Cells of most of the species are no more than crudely finished, suboval chambers in the substrate (figs. 18-21, 23). The only known exceptions are the cells made by H. lilicifoliae and H. rufipes. Cells of these two species have very smooth walls which appear to have been smoothed by the tongue and impregnated with saliva or some other material which makes the surface hard. However, there is no detectable lining deposited on these walls. These cells are not impermeable to water though drops placed on them are absorbed considerably less rapidly <sup>than</sup> drops placed on the adjacent cell matrix. This would suggest that these treated cell walls might offer the enclosed bee larva some degree of control over humidity in the cell. Walls of the cells of all the species of Herperapis studied other than H. lilicifoliae and H. rufipes do not inhibit transfer of water to any detectable degree. The complete cells are supplied with provisions of nectar and pollen molded into the form of a nearly perfect sphere. In no case was a pollen ball found to be covered by a protective membrane such as that found on the pollen balls of the species of Nomadopsis studied by Rozen (1958).

It is possible to reconstruct roughly the events which occur during the preimaginal life of these bees even though none of the species has been successfully reared in the laboratory. A



study of the contents of over one hundred cells of H. peninsularis at the San Felipe, Baja California nest site form the basis of most of the following generalizations although supporting observations have been made at excavations of the nests of several other species, particularly H. ~~kayella~~ <sup>hermosa</sup>, H. lilicifoliae, H. regularis and H. pellucida.

The strongly curved, cylindrical egg is placed on top of the pollen ball in such a way that only its ends are in contact with it (figs. 18 and 19). The duration of the egg stage is not known but presumably is short as in most other bees.

Upon eclosion the small larva starts feeding near the top of the pollen ball (fig. 20). While still small it gradually works its way down and around the pollen ball until it achieves a characteristic position curled around and under the pollen ball (fig. 21). At this time the larva is in a C-shape with one of its sides, not its dorsum, against the floor of the cell and its venter against the pollen ball. In this position the larva continues to feed but at the same time it slowly rotates the pollen ball by a constant twitching motion of the terminal segments of the abdomen. As the larva becomes larger this action tends to lift the pollen ball so that it becomes entirely supported by the larva. The effect of this unusual feeding behavior is that the pollen ball is evenly grazed and remains nearly spherical until it has been almost completely consumed.



One possible adaptive advantage of this behavior seems obvious. In most wild bees, contamination of cell and its provisions by such agents as mold causes a problem since the ensuing growth often destroys or otherwise makes the provisions unsuitable for the larva. Most of the species of Hesperapis ought to be particularly susceptible to such damage because they neither line their cells with protective substances nor do they cover their pollen balls as do most types of ground nesting bees. However, examination of hundreds of cells of various species of Hesperapis has shown that this is not the case. Moldy or otherwise spoiled provisions were encountered infrequently at most sites of most species. It seems likely that this apparent enigma is at least partly explained by the peculiar feeding behavior described above. As with the proverbial "rolling stone that gathers no moss" a pollen ball whose entire surface is continually being grazed would present little opportunity for developing cultures of mold. (For additional discussion see the section on natural enemies.)

The exact number of larval instars has not been established with certainty although a study of the measurements of the width of the head capsule of forty-five specimens of larvae of H. peninsularis indicate these are few. The distribution of these measurements clearly cluster around three separate peaks which presumably would reflect the presence of only three instars in



the sample (table 1). Since the first group contained measurements from two larvae dissected from eggs, this is most likely the first instar of this species. Similarly the last group contained the only sample of a post-defecation, overwintering larva as well as many samples of very large, apparently fully fed larvae. This seems to indicate that the number of instars is only three.

Larval feeding and development progress rapidly. It was generally possible to find a high percentage of greatly distended, fully fed larvae (fig. 22) as well as some post-defecation, overwintering larvae (figs. 23 and 24) when excavations are made in a given nest site during the latter part of the flight season of the population. Contrary to the statement of Burdick and Torchio (1959) the digestive tracts of the larvae of H. regularis as well as those of all the other species studied, i.e., H. <sup>hermosa</sup> ~~kayella~~, H. ilicifoliae, H. pellucida and H. peninsularis, are not open throughout all the larval instars. Observations in the laboratory of living field collected larvae clearly show that no defecation occurs until feeding is completed or at least very nearly completed. Prior to that time all the ingested pollen is accumulated in the greatly distended mid-gut which is not connected with the developing hind gut. At some time near the end of the larval feeding period the digestive tract completes development and



defecation begins. Defecation continues over a period of a couple of days during which time the larvae are relatively active. Their slow writhing movements account for the uniform deposition of the feces over the bottom of the cell (fig. 23). The fecal material is composed primarily of the empty exines of the pollen grains.

Post-defecation larvae have a characteristic shrunken appearance and their integument is conspicuously tough and thick making the body relatively rigid. It is while in this condition that the larvae enter diapause and spend most of their life, i.e., summer, fall and winter for the vernal species; winter, spring and summer for the autumnal species; and fall, winter and spring for the summer species. In no case have <sup>e</sup>cocoons been observed. Overwintering larvae of H. rufipes and H. regularis have been described and illustrated by Michener (1953) and Burdick and Torchio (1959), respectively. <sup>e</sup>

The tough, apparently resistant form of the overwintering larvae of the species of Hesperapis is very likely related to their need for protection from their cell environment during adverse seasons. Michener (1964), with no pertinent data on Hesperapis available to him, reported that nearly all bees employ one of two protective devices during adverse seasons, i.e., either cocoons or coated cell walls. Since most of the species of Hesperapis utilize neither of these protective



devices, it seems reasonable to assume that the unusually tough integument of their larvae might be a substitute adaptation serving the same function. Evidence of refinement of this adaptation can be seen among the species of Hesperapis. Overwintering larvae of the few species which have been observed fall into two distinct classes based on the degree of toughness of their integument and the rigidity of their bodies. The integument of the larvae of H. <sup>hermosa</sup> ~~kayella~~, H. regularis (fig. 23), H. pellucida, H. nitidula, and H. peninsularis is extremely tough and rigid while that of the larvae of H. rufipes and H. ilicifoliae is notably less so. This is significant because these latter two species are the ones which construct the most protective cells among the species of Hesperapis.

The factors which control the breaking of diapause of the overwintering larvae are not known although evidence was presented by Hurd (1957) that indicates moisture may be an important triggering stimulus for at least one species, H. fulvipes. Dr. Hurd's observations are elaborated more fully in the section on distribution. In the laboratory several diapausing larvae of H. regularis have been kept alive under room conditions for more than one year and one broke diapause, pupated and emerged after a time lapse of three years. Both these observations might be explained by the existence of a diapause-breaking mechanism which requires one or several



stimuli with an intensity above a certain threshold in order to be activated. As time passes, the threshold must become gradually lower until eventually the diapause-breaking mechanism would activate spontaneously as it apparently did in the second case cited above. For desert bees such as most Hesperapis, such a mechanism would have an obvious survival value if it is assumed that the presence and intensity of the requisite stimuli are correlated with the blooming of the host plants. In good years with an abundance of flowers there would be an almost total emergence while in a very poor year none of the population would probably emerge. However, the greatest value of this mechanism would be when a series of poor years occurs. If no lowering of the threshold existed all the larvae would probably eventually die. The presence of a gradually lowering threshold permits a limited emergence after a couple of years so that the population is able to take advantage of the sparse food available while at the same time maintaining a relatively large, vigorous reservoir of diapausing larvae which could take advantage of the first good year.

Details of the external morphology of the pupae of two species of Hesperapis, H. regularis and H. peninsularis, have been studied, compared with both species of Hesperapis and other bees described by Michener (1954). Since in most respects the shape and form of bee pupae closely resemble those of the adult only those features ~~which are~~ not present in the adults will be



considered in this discussion. As Michener has pointed out, these peculiar features consist primarily of spines and projections arising from various parts of the body. Some apparently provide space for the hair on the corresponding parts of the developing adult such as those found on the basal segments of the legs. Some serve no evident function. Since there are a number of pupal differences between these two species of Hesperapis, H. peninsularis will be described first and used as a basis for comparison of H. regularis and the non-melittid bees described by Michener.

On the head the most conspicuous peculiarity is a triangle of long acute tubercles situated over the developing ocelli. The two lateral tubercles are directed posterolaterally while the front tubercle is directed anteriorly. There is no sign of developing hairs within them. A hair-filled, apically blunt, ventrally directed tubercle is situated on the ventral angle of the gena immediately behind the base of the mandible. Each mandible possesses a single, subapical, hair filled lobe. On the thorax the posterior lobes of the pronotum are produced and the median area of the metanotum is weakly produced and the median area of the metanotum is weakly produced into a broad, convex node. All these contain developing hairs. On all three pairs of legs hair-filled tubercles are present on the coxae, trochanters and on the bases of the femora though these are relatively poorly developed on the posterior pair of legs. In



addition the hind tibia possesses a hair filled, slender tubercle on the outer apex on the opposite side from the tibial spurs. On the metasoma, entire, subapical rows of short, acute, spine-like tubercles occur on terga 2 through 6 and similar tubercles appear on tergum 1 laterally. Finally a large, apically acute, posterodorsally directed lobe is situated above the anal region. None of the metasomal protuberances appear to contain developing hairs.

The head of the pupa of H. regularis is virtually the same as that of the preceding species for the characters mentioned except for the conspicuous lack of the long ocellar tubercles. Instead, in their place are three tiny, low, ocelloid convexities. The thorax is nearly identical to that of the preceding species although the lateral lobes of the pronotum are much less produced. The lobes on the legs of the pupa of H. regularis correspond with those of the preceding species except the outer, apical tibial tubercle is much longer. The metasoma is the same in the two species except the tubercles in the subapical rows are much smaller in H. regularis. As can be seen from the evident differences between these two species a thorough comparative morphological study of the pupae of all the species of Hesperapis might yield many useful characters which might help refine the systematics of the group.



The pupae of the species of Hesperapis described above possess at least four structures not found on the non-melittid bees studied by Michener (1954). Conceivably these features, i.e., a median ocellar tubercle, the genal tubercles, the mandibular lobes, and the caudal lobe on the apex of the metasoma, might prove to be useful generic or perhaps even familial characters.

In all the species studied, pupation occurred shortly before emergence. Information on the length of the pupal stage is supplied by Burdick and Torchio (1959). In the laboratory the pupal stage of the specimens of H. regularis they observed lasted from five to thirteen days and the adults were able to fly within twenty-six hours after preimaginal ecdysis.

#### Nest notes

The terminology and concepts of plant communities used below for descriptive purposes are those employed by Munz and Keck (1959).



Hesperapis <sup>hermosa</sup> ~~kayella~~ Stage and Snelling

Hesperapis <sup>hermosa</sup> ~~kayella~~ Stage was observed nesting in two successive years 2.8 miles west of Wadsworth, Washoe County, Nevada in the west-central portion of the Great Basin Desert. The predominant vegetation in the area was sagebrush scrub in which Tetradymia comosa and Dalea polyadenia were particularly abundant. The nesting site was along the north side of U.S. Highway 40 in a small valley approximately 1.5 miles in length. The exact limits of the site were not determined although nests were encountered intermittently throughout an area thirty to fifty meters wide extending for nearly eighty meters along the highway. Nests were situated individually or in small diffuse aggregations in the open sand between the sagebrush where they recieved full sunlight most of the day. Though usually smaller, individual aggregations contained as many as fifty active nests which generally were from eight or ten to thirty or more centimeters removed from each other. The density of nests in the aggregations sometimes approached fifty per square meter although usually the number was more nearly half that figure. Generally they were constructed on level or slightly sloping ground while the steep sides of a gully were avoided. The soil, damp below about nine centimeters, was composed of nearly pure sand to a depth of at least a meter, well beyond the depth of



the cells. The pollen source of the bee, Coldenia nuttallii, a small, prostrate, boraginaceous plant, was only sparsely scattered through the site in 1962 although in 1963 it was abundant. Two other species of Hesperapis, H. <sup>ruida</sup> ~~nuda~~ and H. wilmatte, foraged in the area but their nests were not found.

Hesperapis rufipes (Ashmead)

Information on the nests of Hesperapis rufipes (Ashmead) is available primarily as a result of observations made by Professor J.W. MacSwain in 1952 at the Tanbark Flat, Los Angeles County, California. In 1963 I briefly visited the site and made some observations on the behavior of the adults but was unable to locate any nests. This locality was in the San Dimas Experimental Forest in the San Gabriel Mountains where the predominant vegetation at the elevation of this site was chaparral. However, in the immediate vicinity of Tanbark Flat the introduction of trees and other plants foreign to the area had greatly altered the original vegetation. The nest site was located in a small level clearing among pine trees near one of the cabins in the middle of the installation. Most of the area was densely covered with short, dry grass which presumably



concealed the nests. The soil was heavy and hard-packed though moist a few centimeters below the surface. Navarretia hamata, the pollen source of the bees at this site, was common throughout the clearing.

Hesperapis ilicifoliae (Cockerell)

The nesting activity of ~~Hesperapis~~ Hesperapis ilicifoliae (Cockerell) was studied in 1962 at a locality five miles northeast of Santa Margarita, San Luis Obispo County, and in 1963 at a site in the Diablo Range four miles east of Walnut Creek, Contra Costa County. Both localities were in the inner Coast Ranges of California and had a vegetation cover that was locally chaparral though at both sites elements of foothill woodland were present or nearby.

The Diablo Range nest site of H. ilicifoliae was discovered by Mr. Vincent B. Whitehead and Dr. Daniel H. Janzen who subsequently led me to it. The site extended about ten meters along a well worn deer trail through the middle of a dense stand of Adenostoma fasciculatum covering the western slope of a steep ridge. In spite of the steep slope and the adjacent Adenostoma the sun was on the site most of the day. Most of the nests were situated in the open on the deer trail though some were in the adjacent dense, dry grass. In local areas the nests were as



close together as two centimeters though in most of the site they were much farther apart. The slope of the ground at the site was about twenty degrees from the horizontal. The light colored soil was very hard-packed and dry to a level well below the bee cells. The adjacent Adenostoma was the pollen source of the bees. Hesperapis regularis also nested in the grass along the deer trails but their sites were separate from those of H. ilicifoliae.

The nests of H. ilicifoliae at the Santa Margarita site were loosely aggregated in an open area between a dense stand of Adenostoma fasciculatum and a stand of pines and consequently received direct sunlight most of the day. The surface of the ground, which gently sloped to the south, was covered with short, sparse, dry grass with occasional plants of blooming Clarkia speciosa and several other small annuals intermixed. The nests of these small bees <sup>were</sup> ~~was~~ very difficult to see since the surface of the ground were coarse and the nests had no tumulus to attract attention. However, judging from the number of females with pollen loads seen in the site, which encompassed about three square meters, at least fifteen or twenty nests must have been present. The soil, which was dry below the level of the cells, was a heavy, coarse, loam containing many small rocks and much fine gravel. As at the Diablo Range site the Adenostoma was the pollen source. Hesperapis regularis also



nests in this area but not in the vicinity of H. ilicifoliae. This site was burned by a forest fire several weeks after observations were made in 1962.

Hesperapis regularis (Cresson)

Observations on the nesting habits of Hesperapis regularis ~~(Cresson)~~ were made in detail at three locations on the margin of or in the Central Coast Ranges of California: the first near Antioch, Contra Costa County, the second along Isabell Creek east of Mount Hamilton, Santa Clara County, and the third near Arroyo Seco Campground, Monterey County. All three sites are referable to Foothill Woodland although the first two have been altered considerably by agricultural practices.

The Antioch site, originally shown to <sup>615</sup>me by the late Dr. Paul D. Hurd, Jr., is on top of a low bluff on the edge of the Sacramento River a short distance east of Antioch. The predominant ground cover in the area of the nests at the time they were active was short, dry grass and other annuals though larger plants, particularly Oenothera deltoides var. howellii, were present and even abundant nearby. The nests (fig. 12) were located on flat ground among the dry weeds but away from the larger plants and consequently received direct sunlight all



day. Nests were loosely aggregated in an irregular area of about two hundred square meters with individuals rarely closer than twenty-five centimeters from each other. The soil primarily consisted of fine sand though much fine gravel was present in the upper ten or twenty centimeters. In 1963 at the time the bees were actively nesting it was very moist below about fifteen centimeters although it became increasingly dry as the season progressed. The pollen source of H. regularis at this site, Clarkia unguiculata, grew abundantly over the steep face of the bluff adjacent to the site.

The Isabell Creek site is in a field on the west side of San Antonio Valley Road near the bridge over Isabell Creek behind Mount Hamilton. At the time the bees were nesting most of the ground cover of sparse grass and annual weeds was dry and brown though many plants of Clarkia purpurea subsp. quadrivulnera were still blooming in the immediate vicinity. There were no large shrubs or trees shading the nests which were loosely aggregated in an area about four by six meters near the center of the field. Nests were often as close as ten centimeters from each other although the average density was considerably less than thirty per square meter. The soil was a heavy, hard-packed loam which was dry at least as deep as the deepest cells. The pollen source of these bees was not found although subsequent examination of the pollen loads of foragers returning to the



nests indicated it was a species of Clarkia but not the C. purpurea subsp. quadrivulnera which grew in the site.

The site near Arroyo Seco Campground, which I once visited briefly, is where the biology of H. regularis was investigated by Burdick and Torcnio (1959). The site was on the east side of the relatively flat floor of a small steep-sided canyon. The canyon floor was covered with Foothill Woodland and its walls with chaparral. The nests were situated in an area sparsely covered with grasses and a few bushes of Eriodictyon californicum. Due to the orientation of the canyon and the steepness of its east wall the sun did not reach the site until nearly eight o'clock in the morning though the site was sunny the rest of the day. The soil was composed primarily of hard-packed sand. The major nectar source, Chorizanthe douglasi, and the pollen source, Clarkia unguiculata, were growing abundantly over the surface of the adjacent wall. Hesperapis ilicifoliae also occurred in this area but not in association with H. regularis.

Hesperapis regularis has been observed at least briefly at three other sites in the California Coast Ranges. As mentioned earlier it was nesting at the two localities, one in the Diablo Range and the other near Santa Margarita, where H. ilicifoliae



was studied. At the former the nests were widely scattered in dense, dry grass that was adjacent to the deer trail below the H. ilicifoliae site. Clarkia unguiculata, the bee's pollen source there, was widely scattered over the slope but most abundant at a level nearly three-hundred meters below the site. At the Santa Margarita locality a few H. ~~regularis~~ nests were /e found in sandy loam in the flat bottom of the small valley at the foot of the slope where H. ilicifoliae nested. The immediate vegetation cover was Foothill Woodland though the adjacent slopes had extensive patches of chaparral. Four species of Clarkia, C. unguiculata, C. speciosa, C. cylindrica and C. purpurea subsp. quadrivulnera, grew abundantly throughout the area though only the first three were utilized by H. regularis for pollen. The third site where this species was seen nesting was along the Cuyuma River in an area of Foothill Woodland twenty-eight miles northwest of New Cuyuma, Santa Barbara County, California. Here the nests were loosely aggregated in an open field near the river bed where numerous small shrubs were present though the main ground cover was short, dry grass mixed with other annuals. As at the other sites the nests were loosely aggregated among the grass. The soil was a deep, sandy loam. The nearest pollen source for these bees, a large patch of Clarkia unguiculata and C. cylindrica, was over a hundred meters from the nests.



Hesperapis pellucida Cockerell

Nest sites of Hesperapis pellucida ~~Cockerell~~<sup>9</sup> were observed at two sites along the coast on the Monterey Peninsula, Monterey County, California and at five isolated sites in or near San Francisco. The former sites are both in the sand dunes of the Coastal Strand and most of the latter were probably in a similar habitat originally though it is difficult to determine since the city has changed some of them so profoundly.

The two Monterey Peninsula sites, one at Asilomar Beach State Park and the other a mile northeast of Point Joe, were very similar to the beach where vegetation was very sparse. At both, females aggregated their nests in local, nearly level areas <sup>with a sparse cover of</sup> ~~where Carex pansa grew sparsely~~<sup>3</sup>. At the Point Joe site, nest density was fairly high in local areas with nests often not much more than eight or ten centimeters from each other. At the other site they were much less dense. The pollen source of H. pellucida at least sites, Eschscholtzia californica, grew abundantly in the dunes adjacent to the aggregations with a few other conspicuous plants including Polygonus paronychia which was utilized as a nectar source.

The five San Francisco nest sites of H. pellucida were in more varied situations than those along the Monterey Peninsula. These were visited at least briefly on numerous occasions during



the spring and summer in 1960, 1961, 1962, and 1963. The two most thoroughly studied, one on the edge of Laguna Puerca in the Sunset District and the other near the mouth of Lobos Creek in the Presidio of San Francisco, were similar, flat, empty lots bearing little natural vegetation. Both were predominantly covered with grass and weeds though scattered bushes of lupine and dense patches of Mesembryanthemum were also conspicuous. At each site the nests aggregated in areas where the grass was sparse, resulting in numerous little open spots of sand. The density of the aggregations varied considerably though at both sites nest were often as close to each other as five centimeters. The actual area of the aggregation at Laguna Puerca was about four square meters but considerably more area was involved at Lobos Creek. At the latter site three separate aggregations occurred with a combined area perhaps as great as twelve square meters. At both sites the soil, moist below the first four or five centimeters, was primarily composed of sand though at the Lobos Creek site much gravel had been mixed with it. Eschscholtzia californica was abundant at both sites where it normally served as the pollen source. Several other flowers were also present including the following nectar sources: Polygonum paronychia, Gilia capitata ssp. chamissonii, Oenothera cheiranthifolia, Oenothera contorta, Hedysotis cretica, Chorizanthe cuspidata and Brassica sp. In the spring of 1963 the Laguna Puerca nesting site was destroyed when it was landscaped and extensive lawns were planted.



The third San Francisco nest site is in the sand dunes of the Presidio about a mile from the Lobos Creek site and the fourth is at the top of a bluff in Sunset Heights. Both of these sites are similar to the first two in that the ground cover is sparse, the soil is primarily sandy, and Eschscholtzia californica is present. Both differ from the first two in having a flora which resembles more closely the Coastal Strand Community along the Monterey Peninsula and both are exposed to more direct wind from the ocean. In addition, the Presidio site is on a twenty degree slope that faces west. <sup>We</sup> I suspect that neither of these sites were as well suited to the needs of H. pellucida as were the first two since during the three years of observations the nests at these always remained sparse and the bees scarce in spite of an abundance of flowers available to them.

The fifth San Francisco nest site of H. pellucida is located just outside the city where open sand exists at the base of the northwestern ridge of the San Bruno Mountains. In the immediate vicinity of the site the ground cover is predominantly weeds and grass though flowering plants including Eschscholtzia californica, Sonchus oleraceus and Hypochoeris radicata were abundant. Of those named, the former was used as a source of pollen while the latter two were visited for nectar by the bees. At this site the nests were sparsely aggregated on a gentle slope where the grass was very sparse. This site was



like the other Presidio site and the Sunset Heights site in that it was also directly exposed to the ocean winds. However, unlike them the frequency of heavy, wet fogs during the flight season of the bees was much greater than at any of the other San Francisco sites during the period of observations. Perhaps the scarcity of bees there was correlated with the more harsh climate.

Hesperapis nitidula Cockerell

A small nest site of Hesperapis nitidula ~~Cockerell~~ was found by <sup>RRS</sup> ~~the junior author~~ in Eaton Wash about a mile below the mouth of Eaton Canyon on the edge of Altadena, Los Angeles County, California. Here the nests were in a wide, level space in a trail where the soil was sandy but with much coarse gravel intermixed. About thirty nests were present in the aggregation extending over an area of about two square meters. Oenothera bistorta blooming in the immediate vicinity of the site was utilized by those bees for pollen.



Hesperapis peninsularis Stage and Snelling

An extensive nest site of Hesperapis peninsularis ~~Stage~~ was studied in the Colorado Desert at San Felipe, Baja California del Norte, Mexico in March 1963. This site was the fortunate discovery of Dr. Paul Arnaud, Jr., whose subsequent directions and maps permitted GIS to relocate it. The prominent vegetation in this area was creosote bush scrub which extended for many miles inland from Bahia de San Felipe. The site was situated along the old, 175 meter wide, high level, sparsely overgrown beach which ran between the present beach and the still higher desert inland. The full extend of the nesting site was not determined but the area where nests were most dense apparently extended for at least two hundred meters in a strip that varied from thirty to fifty hundred meters in a strip that varied from thirty to fifty meters wide along the base of the abrupt embankment that rose five or six meters to the desert above. Most of the nests were in open flat ground but many were situated in areas covered with dry grass on the lower part of the embankment where the slope was about thirty degrees. Individual nests of this large bee were often as close as twenty centimeters from each other at which time the local density would be as high as twenty-five per square meter. Calculations based on crude but conservative estimates of average nest



density and total area of the main section of the site suggest that there were probably well over a hundred thousand active nests in the site. As shown by the profile in Table 5 the soil was composed of alternate layers of sand and sandy clay and was moist below the first fifteen centimeters. The pollen source for H. peninsularis at this site was Encelia farinosa which grew abundantly throughout the adjacent creosote bush scrub and even sparsely in the nest site. Several other species of Hesperapis, (H. macrocephala, H. leucura, H. wilmattae, and H. <sup>mentzeliae</sup> ~~laticeps~~) ~~rufiventris~~ were found foraging in the vicinity of San Felipe but not in association with H. peninsularis.

In the preceding paragraphs nineteen nest sites representing seven species of Hesperapis have been described. Though it would be premature to extend generalizations from them to the whole genus or even to any one species it is nevertheless informative to point out some of the gross similarities and differences among these sites. All were similar in being on flat or gently sloping ground where they received full sunlight most of the day. The actual placement of nests in relation to local ground cover varied considerably, e.g., those of H. <sup>hermosa</sup> ~~kayella~~ were always found in the open, those of H. regularis and H. pellucida were usually found in sparse grass but sometimes in the open, while those of H. peninsularis were usually in the open but sometimes in grass. At all the sites most of the nests



ere in aggregations. The absolute density of these appeared to be ~~crudely~~ inversely correlated with the size of the individuals of the species, i.e., smaller species regularly had more nests per unit area in aggregations than large species. The type of soil most frequently encountered was soft sand or sandy loam though H. rufipes and H. ilicifoliae were only found at sites where the soil was relatively hard-packed and some sites of H. regularis were also situated on such soil. Soil moisture also varied considerably between sites at the time the sites were studied. At some, such as that of H. regularis at Isabell Creek and those of H. ilicifoliae at both sites the ground was dry below the level of the cells while at most others it was moist at that depth. In most cases the pollen source was proximate to the site though in at least one case, H. regularis at the Cuyama River site, females had to fly at least a hundred meters to the nearest source.

#### Mating behavior

For the purpose of this discussion mating behavior is considered to include not only the act of copulation but also permating behavior. The complete sequence of events has been observed for only three species, H. regularis, H. pellucida, and



H. peninsularis, although permating behavior of the males has also been observed for H. <sup>hermosa</sup> ~~kayella~~ and H. ilicifoliae.

Hesperapis regularis ~~(Cresson)~~

The two published accounts of mating behavior of Hesperapis are both concerned with H. regularis. Linsley and MacSwain (1958) observed that males at the Antioch site actively searched for females through the nesting areas as well as at the nectar and pollen sources. Searching began nearly an hour before the first females appeared in the site in the morning. The only observed act of copulation took place in a blossom of Oenothera as the female was seeking nectar. The union lasted slightly over three minutes. Burdick and Torchio (1959) supplied further details on this species based on their observations at the Arroyo Seco site and on the behavior of laboratory reared material from there. They observed males patrolling in search of females in the nest area but not at the flowers. As at Antioch male activity commenced nearly an hour ahead of the appearance of the females. Burdick and Torchio observed actual mating on two occasions which they describe as follows:



"One mating attempt was noted near the nesting spot at 1:30 p.m. The female had been sitting motionless on the ground for two minutes, while numerous males were flying over the area. One male dropped on her from two inches above and immediately grasped her around the pro- and meso-thoracic segments with his legs. With his every attempted coition, the female would flip her abdomen up and extend her metathoracic legs away from her body. Six attempts were counted before the male flew away. A male and female were found in the mating position described above, in a rearing chamber at 8:00 a.m. This position was maintained for five minutes after their discovery, with one act of copulation noted, lasting 48 seconds. During this interval, the female bent her abdomen downward and moved it in a circular motion, while her metathoracic legs kept reaching toward the genital region of her abdomen. The male had his mandibles spread and the wings slightly uplifted until the act was terminated by the female flipping her abdomen up twice in succession. Both the female and male had emerged from their pupal skins during the previous evening, so the wings were not sufficiently hardened for either to fly."

<sup>we</sup>  
I have not been fortunate enough to observe successful copulation in this species though <sup>we</sup> I have observed the premating behavior of the males on many occasions and attempted mating, i.e., the tumbling of females by males, several times. As



described above, the males regularly appeared as much as an hour ahead of the females at which time they patrolled both the nest site and the flowers destined to be visited by the females. As might be expected, females were subject to tumbling at both of these locations. Occasionally males followed females in flight but did not attempt contact while the females were still on the wing. The most intensive premating and mating behavior activity generally occurred in the morning.

Hesperapis peninsularis ~~Stage and~~

The complete sequence of mating behavior of Hesperapis peninsularis has been observed repeatedly at the huge nest site at San Felipe. The mating flights, observed during five consecutive mornings, were spectacular events. As with regularis, males were the first to appear on the scene but in this case only fifteen to twenty minutes ahead of the first females. By the time the females were common the air was thick with hundreds of thousands of males patrolling in zig-zag patterns through the nest site within about thirty centimeters of the ground. As rapidly as the semitorpid females crawled from their nests they were pounced upon by the ubiquitous males. Some females appeared at their burrow entrances but did



not immediately venture forth. On several occasions males were observed to drag these females out and copulate with them. Competition for females was so intense that males appeared to continually interfere with each other during copulation. Indeed, mating pairs (Fig. 17) were rare while mating trios (Fig. 16) were most common. Mating clusters with a dozen or more males tumbling around one female were ~~even~~ frequently encountered. During the period of maximum activity, generally about one-half hour after the first matings, twenty to thirty mating groups were usually in view simultaneously. After this peak, the incidence of matings gradually declined until about an hour to one and one-quarter hour after onset, they had virtually ceased. Nevertheless, male patrolling activity continued undiminished for the remainder of the morning and to a much lesser degree into the afternoon. During this entire period they unrelentingly continued to tumble the females. However the females, now no longer semitorpid, appeared to escape easily in most cases. Only on four occasions during five days were flower visiting females seen to be tumbled by the males. In all four cases the males were unsuccessful in their mating attempts. The actual sequence of events leading to and during an individual act of coition was difficult to observe but was at least crudely determined. A female on the ground usually would be approached by a patrolling male which could drop on her from above and



behind. Initially the male would orient on top of her so that the venter of his thorax was close over her dorsum while he grasped the lateral part of her thorax and abdomen with all six legs. From there the male would quickly work his way posteriorly while probing ventrally and posteriorly with the recurved apex of his abdomen. When the union of their genitalia was complete the male would be situated so far posteriorly that only his head would reach the thorax of the female. After union was achieved the male commenced a rhythmic pumping motion of the abdomen in which it alternately contracted and extended longitudinally. Gradually the pumping would subside until the pair was still. Eventually the male would lose his grip on the female and for a time would be held in place only by the joined genitalia. Separation generally occurred from three to seven minutes after the union commenced. During coition the female remained relatively still unless disturbed by too many males in which case the entire cluster would tumbler around considerably. Usually males held their antennae still and back over the head when mounted, while females directed their antennae forward and at an angle of forty-five degrees to each other (figs. 16 and 17). As with H. regularis the mandibles of both were partly open at this time. During matings with a second male present the first usually became dislodged and fell backward to the positions shown in Figure 16. However,



genitalia were rarely separated prematurely in these cases and in spite of persistence the second male usually failed his objective.

<sup>t</sup><sub>^</sub> The dual sleeping habits of the males of H. peninsularis had an interesting effect on the mating flights. As described more fully in a later section, about half the male population slept exposed above the ground in the vegetation around the site while the other half slept<sup>t</sup><sub>^</sub> underground in special male sleeping burrows. By observing both situations simultaneously, two observers were able to determine that the males sleeping on the vegetation commenced activity from fifteen to twenty minutes ahead of those males sleeping in the ground, with the latter first appearing more or less concurrently with, and in the same semitorpid condition as the females. Apparently the latter group of males, like the females, were not able to benefit from the warm, direct sunlight that must have aided in mobilizing the exposed males. Regardless of the cause it was evident that because of this differential between the two groups the males which slept on the vegetation had an advantage at least initially each day in competition for the females. From the standpoint of natural selection this mating advantage might conceivably be an important factor which offsets the apparent disadvantages in the vegetation sleeping habit, i.e., no protection from the elements and exposure to predators. However, before such a relationship could be argued it would be



necessary to demonstrate that males are relatively constant in their choice of sleeping sites and that predisposition toward one or the other sleeping habit is inherited. Unfortunately nothing is known about these factors.

Hesperapis pellucida ~~Cockerell~~

A relatively complete picture of the gross mating behavior of H. pellucida has been composed as a result of intermittent visits during five consecutive years to several nest sites in San Francisco and Monterey Counties. Like H. regularis, and males of H. pellucida began activity nearly an hour before the females. However, unlike the other species the males exhibited no general patrolling behavior either at the nest site or around the flowers. Instead, H. pellucida males were most commonly observed on the ground in open spots scattered through the site in the vicinity of the nests where they watch for females. From these observation posts they frequently darted after females, males, or almost any other similar sized, flying insects which attracted their attention. If the object of the chase was another male, what appeared to be a fight often followed after which one would flee and the other would usually return to the



observation post. Other species of insects either fled or ignored the males when they were pursued. If the object of the chase was a female of H. pellucida an attempt at copulation usually followed, though contact was not usually made until she landed. On the ground they violently tumbled until either the male was successful or the female escaped. Occasionally, other males were involved in the chase and subsequently interfered with the tumbling pair, in which case the female almost invariably escaped. Females on the ground were also frequently spotted and tumbled by males during their short sorties. Such females regularly exhibited a peculiar wing maneuver when approached by these males. From the normal resting position with the wings flat over the abdomen, they were abruptly raised slightly and rotated ninety degrees about their long axis to a position where their planes were again parallel to each other but vertical to the substrate. The function of this posturing was not determined. However, since it usually preceded flight from males and since it was observed occasionally when the females were alarmed by agents other than males, it seemed likely to be more directly related to escape than to mating per se.

Successful matings have been observed only a few times. These occurred on the ground in the nest site with only one male present. Initially there were a few seconds of violent tumbling



after which the female became still and the male assumed a position similar to that described for the other species. In this position the head of the male was slightly behind that of the female and all six legs were used to grasp her thorax. Union was accomplished in the same manner described for H. peninsularis; however, the genital capsule was generally inserted somewhat off center with the abdomen of the male twisted laterally in a manner which left the pygidial plate of the female at least partially exposed. During coition the abdomen of the male rhythmically pulsed in a manner like that described for H. peninsularis while the outstretched antennae intermittently vibrated rapidly. Each series of vibrations coincided with each abdominal contraction. Duration of the union, timed on seven occasions, varied from twenty seconds to seven minutes with an average of about three minutes. The females usually terminated the union by dislodging the male.

The most significant feature of the mating behavior of H. pellucida is that males exhibit a type of territorial behavior unlike any previously described for solitary bees. Published accounts (Pagden, 1933; Wantanabe, 1958; Linsley and Michener, 1962; Cazier and Linsley, 1963; Janzen, 1964; Linsley, 1965) ; ^ \* ^  
pertain to various species of Xylocopa and Protoxaea whose males were observed to defend specific loci in the air where they hovered near vegetation. In Hesperapis pellucida the



observation posts on the sand described above are the centers of the territories of the males. This was first demonstrated in 1960 at the Laguna Puerca site (Stage, 1962) when nine males exhibiting typical premating behavior as described above were captured and distinctively marked on the mesoscutum with various colors of paint. The marks were sufficiently conspicuous that recognition of individuals after release was possible without recapture. Subsequently it was determined that individual males regularly returned to the same observation posts which they actively defended. None of the marked males were observed to grossly change the location of their territories although on one occasion a male shifted his observation post twenty-four centimeters towards a vacant area after a minimum of five days constancy to the first site. Marked males occasionally were found as far as twenty to thirty meters from their territories but only when they visited flowers for nectar or sleeping. In all cases, males which ceased frequenting their territories were never seen again in the site. In 1963 observation of marked males was made at the Lobos Creek site. Their behavior agreed with that seen at the Laguna Puerca site in all respects while a new record of twelve days was established for constancy to a single territory. Table 2 summarizes the records of duration on constancy to territories for all the individually marked males observed at both sites.



Distribution of territories through the sites at the height of the season indicated a strong tendency for males to aggregate where the female nests were most concentrated. In these aggregations the males were relatively evenly spaced, suggesting that their territories were contiguous and that the average effective area of each was relatively constant. This was demonstrated with a crude marking experiment at the Lobos Creek site in 1963. On the first day a plot was chosen within one aggregation and all the included territorial males were marked, counted, and the position of their territories mapped. On each succeeding day another count of the total was made and new males marked with distinguishing colors, in order to determined the daily variation in density of territories as well as the amount of replacement of males which might occur. Unfortunately, on the fourth day a period of cold, overcast weather began and males became scarce throughout the site. However, data from the first three days tended to support the above statement since the density remained fairly constant, i.e., 21, 20 and 16, with vacancies in the plot filled from outside, i.e., on the second day six of the previously marked males were missing but the vacant spaces were filled by five new ones. Since the size of the plot was roughly nineteen square meters the effective area of each territory averaged from about .90 to 1.2 square meters. This was more than ten times the area of the central observation posts where males regularly landed.



Unlike all the closely related, drab colored species of Hesperapis, the males of H. pellucida are clothed with dense, silvery-white pubescence which made them very conspicuous at the site. As with conspicuous colors in many territorial birds this conceivably is a morphological adaptation behavior. This interpretation could be argued more strongly if it were known that the inconspicuous, closely related species of Hesperapis were not territorial or at least less rigidly so, but unfortunately nothing is known of their premating behavior.

hermosa  
Hesperapis ~~kayella~~ Stage

Premating behavior of males of H. <sup>hermosa</sup> ~~kayella~~ has been observed on several occasions at the Wadsworth site. There, males spent most of their time on the sand in the nest aggregations and behaved in a manner very similar to the territorial males of H. pellucida. However, because of the small size and fast flight of these males it was not possible to determine if they were also territorial. Mating or tumbling of females has not been observed.



Hesperapis ilicifoliae (Cockerell)

Premating behavior has also been observed for H. ilicifoliae males. These were seen at the Diablo Range site where the males patrolled in large numbers along the deer trail where the females nested. Like most of the other species, the males began activity ahead of females which they detected on the ground or followed to the ground. When alarmed by males or other agents the females displayed the same peculiar wing maneuver previously described for H. pellucida.

Even though details of mating behavior are known for only a few species of Hesperapis it is clear that this would be a fruitful subject for further investigation. Since such dramatic interspecific variation was found to exist, it offers a potential wealth of ethological characters which might be particularly helpful in distinguishing closely related allopatric species such as those which appear to compose the semirudis group. Even more important, certain aspects of the mating behavior of some species, namely territoriality in H. pellucida and differential mating in H. peninsularis, offer unique opportunities to explore fundamental biological problems relating to intraspecific competition and natural selection.



## Nest construction, architecture and provisions



Various aspects of nest construction have been directly observed in H. <sup>hermosa</sup> ~~kayella~~, H. ilicifoliae, H. regularis, H. peninsularis and H. pellucida. Since the behavior of the last named species is perhaps the most completely known it will be described it first to serve as a basis for comparison of the available data on the other species.

Hesperapis pellucida Cockerell

Hesperapis pellucida has been observed over several years at five nesting sites within San Francisco as well as at two sites near Pacific Grove, Monterey County. At these sites the behavior of this species was remarkably consistent. Initiation of a burrow was usually preceded by a period of searching for a suitable burrow site. This searching was observed to continue for as long as twenty minutes before the bee either departed or initiated a burrow. During this period the female made numerous, relatively slow, meandering flights back and forth near the ground through various parts of the nest area while



stopping frequently at potential sites. Surface features including almost any sort of small irregularities such as pits or partially covered stones and twigs were examined but apparently ~~one of the~~ most attractive sites were little spots of shade on the open sand usually caused by a leaf or some thickness in the adjacent overhanging low, weedy vegetation. After hovering a moment or two over such a spot the female usually landed and scratched around in the sand. The preliminary scratching generally continued for only a few seconds after which the female would sometimes shift to a new position a few centimeters away, or she would resume the searching flight, or ~~she~~ might be chased away by one of the ubiquitous males attempting to mate. ~~It is interesting that the~~ spots of shade seemed to offer the female a certain amount of protection from the males since the females seemed to be disturbed far less frequently while exploring such sites. If the site was suitable and the female was not disturbed she would concentrate her efforts on one spot and continue digging. Digging was accomplished with the prothoracic legs working to loosen the sand while the mesothoracic legs pushed the sand under the venter and the metathoracic legs violently kicked it out obliquely behind. The mandibles did not appear to be used unless particularly difficult objects <sup>were</sup> ~~are~~ encountered by the bee. This method of digging was very effective in the soft sand



where the bees nested. At one San Francisco site females were observed to require ~~between~~ sixty to ninety seconds to dig out of sight after initiating a burrow while in the sand dunes south of Pacific Grove one female was observed to do <sup>so</sup> it in thirty seconds. As the burrow became deeper the necessity to transport the loosened sand to the surface forced the bee to change her digging technique. Instead of immediately expelling the loosened sand as described above, the bee accumulated it into a load for transporting. How the bee manipulated this load below the surface was not determined but when she arrived at the burrow entrance she invariably came abdomen first with a mound of sand under it, apparently being pushed a long or carried by the mesothoracic legs. Upon reaching the burrow entrance she rapidly expelled the sand with ten to fifteen violent outward and backward kicks of the metathoracic legs while the other legs and the tip of the abdomen supported her. As the burrow deepened, ~~her~~ trips to the surface became much less frequent with intervals of as much as four or five minutes between them.

//ng

During this period the female occasionally stopped work for two or three minutes and remained motionless in the burrow entrance, hidden except for her head. The function of this behavior is not known. The possibility that it may be involved with nest defense seems remote since the females immediately flee or retreat into the nest when disturbed. Perhaps it simply is a



warm place to rest which offers some degree of protection. This resting behavior as well as the digging behavior could be observed during most of the warm part of the day in the nest site at both new<sup>and</sup> long established nests. In the older nest<sup>s</sup> the expelled sand appear<sup>e</sup>d to result from general maintenance of the primary<sup>y</sup> tunnel as well as from digging new branch tunnels and cells. The necessity for maintenance activity was evident from examinations of the structure of the older burrows. Typically the upper portion of the burrow was from eight to fourteen millimeters in diameter with an irregular surface but flattened below while the burrow in the vicinity of the cells was usually nearly circular and not more than five millimeters in diameter<sup>?</sup>. The large diameter and irregular shape of the upper portion seemed to be due to incureased erosion caused by longer use of the upper parts of the burrow. The debris from this erosion would have to be constantly removed if the bee was to continue working in the nest. At the end of the daily activity period the female closed the burrow at the surface from within. This was accomplished in much the same manner as the excavation. The female appeared at the entrance abdomen first with a load of sand~~from below~~. However, instead of kicking it away she allowed the sand to remain in the entrance. After six or seven such loads the entrance became solidly blocked. At no time during this process was the female seen to turn around and use her head to compact the resultant plug.



Hesperapis <sup>hermosa</sup> ~~kayella~~ ~~Stage~~, H. peninsularis ~~Stage~~,  
and H. regularis (Cresson)

Nesting activity was observed for H. <sup>hermosa</sup> ~~kayella~~ (Fig. 14) ~~and~~  
~~H. peninsularis~~ <sup>and for H. peninsularis near</sup> at sites near Wadworth, Nevada, <sup>San</sup> and San Felipe,  
Baja California, Mexico, ~~respectively~~, and H. regularis at sites  
at Antioch and near Isabell Creek behind Mount Hamilton,  
California. The behavior of these species at all these sites  
was very similar to that described above for H. pellucida. The  
only conspicuous difference was that females of H. peninsularis  
were not attracted to shady spots when searching for burrow  
sites although those of H. <sup>hermosa</sup> ~~kayella~~ were. The only activity  
described for females of H. pellucida not observed in these three  
species is the method of nest closure. However, ~~they~~ <sup>3-2</sup> all do  
close their nests for the night and the appearance of the plug  
was very similar to those of H. pellucida. Burdick and Torchio  
(1959) have reported on nesting activity of H. regularis at  
Arroyo Seco, Monterey County, California. Females <sup>they observed</sup> ~~under their~~  
~~surveillance~~ brought sand from below and pushed it up with their  
head until it formed a plug which protruded as a small mound  
filling the inner portion of the tumulus. All other aspects of  
nest construction which they describe are as described for H.  
pellucida.



Hesperapis ilicifoliae (Cockerell)

Hesperapis ilicifoliae was the only species whose behavior during nest construction radically differed from that described for the others. Behavior of females of this species was studied on two successive days at a nest site in the Diablo Range about four miles east of Walnut Creek, California. At this site ~~females~~ <sup>females</sup> were observed removing soil from established burrows. As in H. pellucida they arrived at the burrow entrance abdomen first with the loose soil under the ~~the~~ body. However, instead of holding the soil with only the mesothoracic legs they also used the prothoracic legs for that purpose. The only locomotive force was supplied by the peculiar action of the metathoracic legs which awkwardly dragged the bee along. The legs operated in a manner similar to the rowing motion of oars in a boat (fig. 13). Furthermore, the H. ilicifoliae females did not stop at the burrow entrance and kick the soil out like the others but rather they dragged it beyond the entrance a distance equivalent to two or three times ~~their~~ <sup>2</sup> body length <sup>3</sup> where they left it. This excavating behavior is of interest not only because it radically differs from that known for the other species of Hesperapis but because it is similar to that described by Müller (1884) and others ~~subsequently~~ <sup>2</sup> for a European species, Dasypoda hirtipes Fabricius, which is morphologically quite different from Hesperapis though in the same subfamily. Initiation of



burrows and burrow closure was not observed in H. ilicifoliae.  
 Nest closure did occur but the plugs did not extend <sup>external</sup> as mounds <sup>1</sup> ~~externally~~ <sup>0</sup>

#### Nest architecture

Data <sup>are</sup> ~~is~~ available on the nest architecture of ~~Herperapis~~ <sup>0</sup>  
rufipes and H. nitidula as well as for all the species of  
~~hesperapis~~ discussed above, viz <sup>hermosa</sup> ~~H. kayella~~, H. ilicifoliae, H.  
regularis, H. peninsularis <sup>1</sup> and H. pellucida. As above, H.  
pellucida will be discussed first since it is perhaps the best  
 known and will serve as a basis for comparison for the other  
 species.

#### Herperapis pellucida ~~Cockerell~~

At all the sites where the nests of H. pellucida have been  
 observed the architecture of the nests consistently followed the  
 same pattern. The entrances to the burrows were always at a  
 very shallow angle below the horizontal and were oriented in all  
 directions. The only exceptions were in the rare situations  
 where the ground was gradually sloped <sup>1</sup> in which case the



entrances faced down<sup>h</sup>ill. The upper section of the tunnel usually made a wide, downward spiral at a gradually increasing angle. In cross-section this portion of the tunnel was <sup>tr</sup>irregu<sup>A</sup>lly semi<sup>f</sup>circular with the tunnel floor wide and flat. As the tunnel deepened it also became less curved, steeper, rounder and smaller in diameter until along the lower third it was rather uniformly rounded in cross-section, narrow in diameter (tabel<sup>A</sup> 3) and ~~perhaps~~<sup>about 45°</sup> at an angle of ~~forty-five degrees~~<sup>^</sup> from vertical. An indication of the average rate of tunnel descent can be seen by comparing the length of each tunnel with the depth of the corresponding terminal cell (table 3). For H. pellucida this seems to be a relatively constant ratio, i.e., 2:1. The tunnels made an abrupt angle about two centimeters before the cell and continued horizontally or even at a slight angle above the horizontal to it. The horizontally oriented cells were nearly spherical, <sup>with</sup> the length only slightly greater than the width, <sup>and</sup> ~~with~~ the floor sometimes slightly flattened (table 4). These cells were excavated from the substrate and were not furnished with any special lining such as wax or resin. Indeed, the surface ~~of them~~ did not seem to be <sup>tr</sup>particu<sup>A</sup>lly smoothed or compacted. Observations on the duration of use of individual nests correlated with data on the excavation activity and provisioning by the female indicate that ~~each~~<sup>each</sup> female provisioned more than one and probably several cells



per nest. Since the cells were never found in series or closely clustered ~~it seemed that~~ <sup>↑</sup> relatively long branch tunnels must be involved. Since these branch tunnels were firmly packed with sand and virtually indistinguishable from the substrate it was not possible to follow them. Only once was a dichotomy found in a tunnel (table 3) but it could not be determined if this represented a branch that led to a cell. Judging from the greater erosion evident in the upper third of most tunnels most branch tunnels were probably constructed below this section. The tumulus of the nests of H. pellucida was more or less semicircular with the highest portion opposite from the direction of the burrow. The sides of the tunnels were usually as steep as the loose sand would permit unless they had been weathered.

Hesperapis regularis (Cresson)

<sup>nest</sup>  
The architecture ~~of the nests~~ <sup>↑</sup> of H. regularis was almost identical to that described for H. pellucida <sup>differing</sup> ~~The differed~~ only <sup>in</sup> ~~by having~~ greater absolute dimensions (table 3) <sup>↑</sup> and by having the cells occasionally gently sloped. There was considerable variation in the depth of cells at various localities (table 4) <sup>apparently</sup> ~~This appeared to be~~ directly correlated with the resistance <sup>of</sup> ~~offered the bees~~ <sup>the bees</sup> by the substrate in which ~~they~~ <sup>↑</sup> nested. Cells



at Antioch ranged from 19.0 to 49.5 <sup>cm</sup> ~~centimeters~~ <sup>the</sup> below soil surface and the soil was firm but coarse, moist and easily worked <sup>while</sup> at Isabell Creek the cells ranged between 11.5 to 18.0 <sup>cm</sup> ~~centimeters~~ <sup>the</sup> below soil surface and the soil was (fine, dry) and very hard-packed. At Arroyo Seco the cells ranged from 9.0 to 16.0 <sup>cm</sup> ~~centimeters~~ in depth (Burdick and Torchio, 1959) and the substrate was hard-packed. These authors also state that their data indicated only a single cell <sup>per</sup> ~~to~~ burrow with the possibility that the female may occasionally use the same entrance but excavate a separate burrow. This did not appear to be the case at the sites <sup>above</sup> ~~under my observation~~. At Antioch cells were frequently found clustered within a few centimeters of each other and at least one nest clearly had a branch tunnel starting midway along the main tunnel <sup>while</sup> at Isabell Creek three of the four excavated nests had multiple dichotomies in the tunnel, all well below the entrance. In these cases the branches were filled with soil. The tumulus of H. regularis (fig. 12) was like that of H. pellucida <sup>but</sup> ~~only~~ larger.

Hesperapis nitidula ~~Cockerell~~

Adol 64a > [ Nests of Hesperapis <sup>hermose</sup> ~~mayella~~ were examined at the site west of Wadsworth, Nevada. In most respects their their architecture



Nests of H. nitidula were excavated at Eaton Canyon wash near Altadena, Los Angeles County, California. Except for the size of the various parts (Table 4), they were very similar to those of H. pellucida.

Hesperapis hermasa

64a - add as indicated

Jerry -  
This belongs on p. 64  
where marked.



was like that of H. pellucida except for size, the course of the terminal parts of the tunnel, and the shape of the cells. Instead of the sharp angle described above, the tunnel gradually became level as it approached the horizontally oriented cells. In addition the cells were somewhat more elongate (table 4) than in the preceding species. Nothing is known about branching of the tunnels or if it even occurs. The tumulus was also like that described for H. pellucida <sup>but</sup> ~~only~~ correspondingly smaller.

Hesperapis peninsularis ~~Stage~~

Nest architecture of Hesperapis peninsularis was studied at San Felipe, Baja California, Mexico. Like the preceding species the upper portion of the tunnel had a greater diameter and was relatively irregular compared to the lower portion. <sup>otherwise,</sup> ~~Aside from~~ <sup>the</sup> ~~nest~~ <sup>they</sup> were very different. The angle of entry was steep, usually not more than ten or fifteen degrees from vertical and the tunnel was nearly circular in cross-section up to the entrance. This rapid rate of descent continued nearly the <sup>entire</sup> ~~whole~~ length of the tunnel, as can be seen by comparing the length of the tunnels with the depth of the corresponding cells (table 3). At a point <sup>10-30 cm</sup> ~~from ten to thirty centimeters~~ before the cell the tunnel turned more or less horizontally and proceeded



~~directly to the horizontally and proceeded~~ directly to the horizontal cell. The large cells (table 4) of H. peninsularis had crude surfaces like <sup>those of</sup> the species described above. There was a wide range in depth of these cells though all were very deep (table 4). It had been suspected initially that the vertical distribution of the cells might be correlated to some extent with the conspicuous stratification of the substrate at the excavation site. Table 5 shows the vertical distribution of a sample of ~~one hundred and eleven~~ <sup>III</sup> cells compared with a soil profile showing the vertical position and extent of the clay and sand layers. Even though nearly four times as many cells were found in the sandy layers as in the clay layers, the total distribution pattern appears to approximate a normal curve suggesting that depth rather than soil composition was the important factor. However much more critical and extensive data ~~is~~ <sup>are</sup> necessary before this can be determined with any degree of reliability. Nothing is known about the presence of branch tunnels in these nests. Indirect evidence similar to that discussed for H. pellucida indicates that each female constructs several cells in each nest. Since cells were rarely found close together, fairly long lateral ~~tunnel~~ branches must be involved. The tumulus around the entrance of the nests of H. peninsularis was usually different from that seen in H. pellucida. It usually was formed in a complete circle with the entrance in the



center. Generally it was nearly radially symmetrical with the sides as steep as the dry sand would permit. The only time when the tumulus was like that of H. pelucida was in the few cases when the nests were situated on steep <sup>slopes.</sup> ~~hillsides~~.

Hesperapis ilicifoliae (Cockerell)

The nest architecture of Hesperapis ilicifoliae has been studied at two widely separated localities in California / ~~in~~ /: one in the Diablo Range east of Walnut Creek, Contra Costa County, and one northeast of Santa Margarita, San Luis Obispo County. At the latter site the ground was dry and a network of narrow cracks <sup>existed</sup> ~~was~~ below the surfaces. The bees took advantage of these cracks by partially excavating and partially filling along them to create their twisted tunnels. In one case several short branch tunnels were found about a third of the way down (table 3) but it was not determined if they were merely artifacts of the irregular substrate or functional tunnels. The entire upper two-thirds to three-fourths of the length of the tunnels was relatively wide and very irregular. The last fourth of the distance to the cell rapidly became less twisted, more nearly horizontal, very smooth, smaller in diameter, and almost circular in cross-section. The fine, smooth texture of the



surface of the distal part of the tunnel and the cell compared to the coarse heterogeneous texture of the surrounding substrate seems to be clear evidence that these parts of the nest had been lined with fine soil. Indeed, the wall of the cell ~~even~~ appeared to have been smoothed with the tongue and to have been impregnated with saliva which made it harder than the adjacent matrix. However, like <sup>those of</sup> ~~the~~ other species, ~~this~~ cell wall was not treated with resin or wax and ~~like them~~ it readily absorbed drops of water though not as <sup>quickly</sup> ~~fast~~ as the adjacent matrix. The cells were all oriented horizontally. //e

The soil at the Diablo site was finer and very hard-packed compared to that described above and contained no evident cracks for the bees to utilize. Here the nests of H. ilicifoliae were entirely excavated although the lower portion and the cells were lined as at the <sup>other</sup> ~~tochy~~ site (fig. 15). In fact, the cell walls were so strong that it was possible ~~and the cell walls were so strong that it was possible~~ to remove some of them intact (fig. 24). The average depth of cells below soil surface varied considerably between the two sites (table 4). As with H. regularis this probably is a function of the hardness of the substrate. The tumulus of the nests of H. ilicifoliae at the Diablo site was completely different from the others described above <sup>as</sup> might be expected from the unique excavating behavior of this species. They were low, very poorly defined and spread tr



over a relatively wide area (fig. 13). At the Santa Margarita site no signs of a tumulus were found at the many nest entrances observed.

Hesperapis rufipes ~~(Ashmead)~~

Data is available for one nest of Hesperapis rufipes that was excavated by ~~Professor~~ J. W. MacSwain at Tanbark Flat, San Gabriel Mountains, California. He kindly permitted <sup>GIS</sup> me to study the plaster cast of the tunnel and several intact cells, as well as a sketch showing additional details of the orientation and depth of cells. As can be seen from Table 3, only the rate of descent of the main tunnels was similar to that of H. pellucida. In most other respects it was very different. The course of the tunnel was gently <sup>and</sup> irregular <sup>twisting</sup> but not in a spiral. The diameter of the tunnel was nearly uniform the entire length (table 3) and there were several dichotomies along the lower two-thirds. All but the tunnel that had been in current use were plugged with fine pebbles. The most radical differences between this nest and those of the other species, concerned the orientation of the cells. <sup>They were all</sup> oriented with their long axis vertical and apparently some were found in vertical linear series with as many as three together.



Otherwise the structure of the radically symmetrical cells was essentially like those of H. ilicifoliae with a hard, smooth wall that was constructed on the crude surface of the coarse, heterogeneous substrate and that was apparently smoothed with the tongue and hardened with saliva. For the various dimensions in the nest see Table 3 and 4. Nothing is known of the nature of the tumulus of this species or if one is even present.

#### Provisions

Little is known of the provisioning behavior of the species of Hesperapis although the provisions themselves have been examined for several species, namely H. rufipes, H. ilicifoliae, H. regularis, and H. peninsularis. In all these species the provisions in each cell usually consisted of a homogeneous mass of damp pollen that was firmly packed into ~~the form of~~ a nearly perfect sphere (figs. 18 and 19). These pollen balls ~~which~~ <sup>and</sup> rested directly on the bottom of the cell did not have any sort of detectable coating on the surface. The only manner in which they differed between the various species was in size and in the type of pollen and possibly nectar used. The former interspecific variable is apparently correlated with the size of the bee while the latter is a function of the foraging behavior



of the species. The latter topic is discussed in the section on floral behavior. Table 6 summarizes the available data on the size of the pollen balls of the species studied. The average listed may be too low since measurements have probably been included from some pollen balls that are small because of larval feeding since it was not always possible to recognize these if the associated larva was not found.

Even though data on the nest construction, architecture<sup>↑</sup> and provisions are available for only a few species of Hesperapis, they are sufficient to show that interspecifically variably<sup>1e</sup> behavior exists. The most conspicuous aspect of the directly observable behavior that differs between species is the method of removing soil from the nest. Nest architecture varies considerably between some of the species. Important in this respect is the nature of the tumulus, the diameter of the tunnels throughout their length, their angle of entry and subsequent rate of descent, the number and arrangement of branch tunnels, the condition of the surface of the tunnels and shape, structure, orientation and depth of the cells. The nature of the provisions except for size and composition is virtually identical in all species studied.



## Foraging behavior

Like most bees, the species of Hesperapis are entirely dependent upon flowers for their food. Pollen/ collected, moistened and stored in the cells as pollen balls by nesting females, is the primary food of the larvae although nectar and glandular secretions from the female may also be important. Adult food appears primarily to be nectar although judging from examinations of gut contents (table 7) pollen is eaten in large amounts at least occasionally by both sexes of many species.

Perhaps the most interesting aspects/ of the foraging behavior of these bees is the apparent widespread occurrence of oligolecty in the genus. The concept of oligolecty embraced here is that offered by Linsley and MacSwain (1957). These authors define as oligolectic those species in which the individual members, throughout the range of the population, and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local absence of pollen. Their definition is in terms of species but as they pointed out higher taxa may also be oligolectic, e.g., the well known cases of the genus Macropis on Lysimachia (Popov, 1958), or the genus Proteriades (sensu Hurd and Michener, 1955) on Cryptantha (Hurd and



Michener, 1955). In Hesperapis all available evidence indicates that oligolecty occurs on the subgeneric, species group and species levels, ~~with it~~ possibly being nearly universal on the latter two levels. On the subgeneric level Disparapis appears to be oligolectic on a few genera in one subfamily of the ~~Compositae~~ <sup>Asteraceae</sup> (table 9) and Xeralictoides appears to be oligolectic on two closely related genera in the Loasaceae (table 8). At the species group level all but the H. semirudis group appear to exhibit some degree of oligolecty (tables 8, 9, and 10).

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/a  
Likewise, ~~at the~~ <sup>all</sup> species ~~level~~ all for which there are ~~available~~ data appear to be oligolectic (~~some~~ tables). At the species level the relationship is often much more narrow than ~~in the~~ <sup>at the species</sup> ~~group level.~~ <sup>preceding</sup> Indeed, in four species the relationship is extremely specific with only one species of flower being utilized by each bee species, i.e., H. ilicifoliae on Adenostoma fasciculatum, H. larreae and H. arida both on Larrea divaricata and H. pellucida on Escnscholtzia californica. The rest of the species of Hesperapis apparently visit several species in one plant genus or ~~even~~ <sup>several</sup> in ~~more than one~~ <sup>genera within</sup> closely related ~~plant genus~~ <sup>in</sup> one family.

The specific evidence, supporting the associations indicated in the tables and the above generalizations, is presented with the data and discussions under each species in the systematic section. Admittedly in many cases this evidence is weak when



considered for single species without reference to the others in its group or subgenus. However, these fragmentary data can be significant when they clearly fit a pattern. A good example occurs in the rhodocerata group in the subgenus Carinapis. For two of the three species, H. rhodocerata and H. fulvipes, there is sufficient floral data available that one can suggest with a high probability of being correct that these species are oligolectic on a few genera in the composite subfamily Tubiliflorae. The third species, H. occidentalis, has very few floral records associated with it. Since oligolecty at the species group level seems to be a rule for the genus and since the few records for H. occidentalis fit the pattern set by the others in the same species group one can feel fairly confident that <sup>H. occidentalis</sup> ~~it~~ will likewise prove to be more or less similarly oligolectic.

Seasonal distribution data <sup>supply</sup> ~~supplies~~ further evidence supporting the contention of widespread oligolecty in Hesperapis. It is generally acknowledged (Linsley, 1958) that oligolectic ~~species of~~ bees have a relatively short flight season ~~which is~~ usually synchronized with the blooming period of their host plant, while polylectic species often have a long flight season <sup>overlapping</sup> ~~which overlaps~~ the blooming period of many species of flowers. That the species of Hesperapis have a relatively short flight season is suggested by the summary of collection



/x. data in Table 12. In cases where the data are analyzed by specific local sites, viz, Altadena, Tanbark Flat, Surprise Canyon, Antioch, and so forth, the flight seasons are clearly short. In those cases where the flight season is apparently very long, H. parva, H. laticeps, H. infuscata, etc., it can be explained as an artifact of the geographic and perennial variation in seasons since data <sup>were</sup> ~~was~~ combined ~~that was collected~~ from all parts of the range of these species over many years.

The facultative nature of oligolectic behavior is acknowledged in the last portion of the above definition by Linsley and MacSwain, i.e., "...turning to other sources, if at all, only in the face of a local absence of pollen." This has been expressed frequently, but rarely has it been documented by close scrutiny of the foraging behavior of specific populations in the field. Such an occurrence was closely followed in the population of H. pellucida at the Lobos Creek site in San Francisco. During the last of April and the first third of May in 1960 the site was relatively undisturbed and bee activity was normal with females exclusively collecting pollen from the usual host flower, Eschscholtzia californica / ~~of that species~~. On May 11 a weed control crew went through the site hoeing down most of the annual vegetation in the open areas. The nest aggregations were only mildly disturbed but the foliage and blossoms of the

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poppies were almost completely destroyed along with large numbers of plants of Lupinus, Polygonum, Brassica, Oenothera, Hedyponis, Chorizanthe, and Gilia.

During the ensuing weeks females could be found regularly collecting pollen from Gilia capitata ssp. chamissonii although other species of flowers were also utilized and females with mixed pollen loads were occasionally encountered. By the middle of June new foliage and blossoms had been produced by the roots of the original poppy plants and the bees had almost completely transferred back to them for pollen. The foraging behavior of this population has subsequently been followed for four seasons during which time they have remained <sup>constant</sup> ~~faithful~~ to the poppies as a pollen source.

Oligolectic species often exhibit specific morphological or behavioral adaptations permitting them to exploit ~~their~~ pollen or sometimes nectar sources more effectively. At least two excellent examples of such adaptations related to peculiar features of certain flowers were found among the species of Hesperapis. Females of tiny H. <sup>hermosa</sup> ~~kayella~~, in the elegantula group of the typical subgenus, are known to regularly visit flowers of the boraginaceous genus Coldenia for pollen. The tiny flowers of this genus present special problems to most bees because the anthers are located deep within the narrow corolla tube, thereby making the pollen relatively inaccessible. Indeed, at the



Wadsworth, Nevada site where H. <sup>hermosa</sup> ~~kayella~~ was studied the only other bee species observed frequenting the flowers of Coldenia nuttallii was Perdita arenaria Timberlake, an even smaller bee on which has been found an adaptation analogous to that of H. <sup>hermosa</sup> ~~kayella~~. Females of H. <sup>hermosa</sup> ~~kayella~~ possess peculiar hairs on the mandibles basally, the stipes laterally, and the area of the gena adjacent to the proboscoidal fossa. These simple, stiff, unusually long, apically wavy hairs collectively form a brush (fig. 4) which possibly aids in the extraction of pollen from the Coldenia ~~nuttallii~~ blossoms. This conclusion satisfactorily explains the previous perplexing field observation that pollen laden females on the blossoms always were oriented with their heads down in the corolla tube as if taking nectar and were never observed collecting pollen in the conventional manner. The actual use of this brush has never been observed. That this specialized brush is presented only on females (see male, fig. 3) seems to be further evidence that it is associated with an exclusively female function such as pollen collection. Since females of Perdita arenaria ~~Timberlake~~ behaved in the same manner in the field as H. <sup>hermosa</sup> ~~kayella~~ it is not surprising to find <sup>that</sup> they possess an apparently analogous adaptation to aid in the extraction of pollen from Coldenia blossoms. However in P. arenaria the brush is more posteriorly directed, the hairs are hooked apically instead of wavy, and the hairs are restricted to



the area of the gena next to the proboscidal fossa. As in H. hermosa ~~Kayella~~ the males are unspecialized in this respect. Both ~~these cases~~ are seemingly analogous to that previously reported for the megachilid bees of the genus Proteriades whose females reach recessed anthers in the flowers of another boraginaceous genus, Cryptantha, by using a brush of stiff, curled hairs on their galeae and labial palpi (Hurd and Michener, 1955). All three of these examples are similar in that the modified oral vestiture is present in all the <sup>species</sup> ~~special~~ in their respective groups. Hurd and Michener indicate this is so for all Proteriades while Timberlake (1954) included an account of this peculiar vestiture in his original description of Heteroperdita, the subgenus of Perdita <sup>that includes</sup> ~~which contains~~ P. arenaria and six other species that visit Coldenia and the closely related, floristically similar genus <sup>CAP</sup> Heliotropium. As in the above groups, the females of all three species in the elegantula group of Hesperapis (senus stricto) possess similarly modified oral vestiture although only two, H. hermosa ~~Kayella~~ and H. pulchra, have thus far been associated with species of Coldenia.

The other example of a morphological adaptation in a species of Hesperapis associated with a peculiar feature of its host flower can be seen in H. palpalis. This species is unique in the genus in that its labium and particularly its labial palpi are extraordinarily long and large in both sexes. This unusual development could well function to aid in the extraction of



nectar from its host plants, i.e., various species of the polemoniaceous genera, Gilia, Eriastrum and Langloisia, whose nectaries are at the bottom of a very long, narrow corolla tube. The only other species in the same species group, H. rufipes, also has unusually large labial palpi but they are not nearly as extreme as those of H. palpalis. It is significant in this respect that H. rufipes also visits flowers in the Polemoniaceae for pollen and nectar but collects from species that have shorter corolla tubes such as Navarretia hamata and certain other species of Eriastrum.

One additional case of unusual morphological features associated with pollen collection has been found among the species of Xeralictoides. In this instance the modifications can not be explained readily in terms of adaptation to some peculiar feature of the host flower. Both these unusual features are found in X. laticeps, the polytypic species in the monotypic subgenus Xeralictoides. As with H. <sup>hermosa</sup> kayella the females of X. laticeps have the vestiture on the mandibles basally, the stipes laterally and the inner margins of the genal area next to the proboscoidal fossa modified into a brush (fig. 6) while the corresponding vestiture in the males is unmodified (fig. 5). Unlike those of H. <sup>hermosa</sup> kayella the hairs which compose the brush have fine barbs over their entire length. It is an inescapable conclusion that this brush functions during pollen collection



and perhaps also plays a part in pollen transportation since many females have been captured with their brush heavily laden with pollen (fig. 7). However, the need or advantage of such a brush to the bee is obscure since ~~H. laticeps~~ <sup>Xeralictoides</sup> is oligolectic on a few florally similar loasaceous flowers, ~~namely~~ <sup>(Eucnide urens</sup> and various species of Mentzelia) whose anthers are readily accessible to bees. The other features <sup>Xeralictoides</sup> of ~~the~~ females of ~~H. laticeps~~ noteworthy in this respect is the presence of many apically curled bristles on their foretarsi similar to those found on ~~the~~ <sup>of</sup> species ~~in the~~ <sup>of</sup> Calliopsis, subgenus Verbenapis. <sup>(Andrenidae)</sup> Species of Verbenapis use their specially equipped forelegs to extract pollen from the flowers of Verbena whose anthers are included within the slender corolla tube and guarded by a circle of hairs above (Linsley, 1958). However, <sup>Xeralictoides</sup> in ~~H. laticeps~~ as with the previously discussed oral vestiture, there seems to be no need for such tarsal modifications because the anthers of their ~~loasaceous~~ host plants are ~~so~~ readily accessible.

An obvious widespread morphological adaptation among oligolectic bees is the matching of the structure of the scopa with the type of pollen being carried (Linsley, 1958). ~~Thus~~ <sup>in</sup> general, oligoleges of flowers producing large pollen grains regularly have a loose scopa composed of simple or loosely plumose hairs while oligoleges of flowers producing very small pollen grains regularly have a dense scopa composed of densely



plumose hairs. However, on the basis of the structure of the scopa, nearly all the species of Hesperapis should fall into the first category yet the great majority of species are oligoleges of plants producing small pollen grains. The most conspicuous exception ~~of this~~ is H. regularis which collects the large trilobed pollen of various species of Clarkia. In most of the other species the pollen loads are carried in a moist condition which effectively serves to hold them in the loose scopa. It has not been determined if the females wet the pollen ~~themselves~~, or if the moisture is acquired from the atmosphere by ~~the~~ hygroscopic <sup>nature</sup> ~~behavior~~ of the pollen itself, or if the pollen is naturally moist from exudates from the anther.

An unusual "dance" is performed by females of H. regularis while collecting pollen from the various species of Clarkia. This dance consists of rapid lateral oscillations of the abdomen while the bee is on the anthers of the flower. ~~This dance~~ <sup>It</sup> is most pronounced when the females are collecting pollen from Clarkia species other than C. unguiculata. The function of this behavior is not known but conceivably the resultant rapid vibration of the anthers might aid in dislodging the pollen.

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"buzz pollin." →

Several other species of Hesperapis display peculiar habits or postures while visiting flowers for nectar or pollen. However, the significance of these is not evident and they are not necessarily directly related to food gathering. The females



of H. (Carinapis) rhodocerata studied in the vicinity of Rodeo, New Mexico, primarily visited flowers of two composites, Baileya pleniradiata and Heterotheca subaxillaris, for pollen. While crawling over the face of the blossoms they consistently held their posterior legs vertically over their body in such a manner that they were nearly parallel to each other and perpendicular to the long axis of their body. Such a posture was particularly conspicuous when the bees had full pollen loads thus making them appear to be carrying small orange flags. These legs appeared to be in the normal position below the abdomen while the bees were in flight and were not raised until a few moments after landing on the blossoms. Females of a superficially similar species of Hesperapis, H. (Disparapis) cockerelli, regularly collected pollen along with females of H. rhodocerata on the same flowers but were never seen to display such a posture. However, pollen-laden females of a very different bee, Psaenythia verbesinae Timberlake, consistently displayed identical posture while frequenting the same flowers. The significance of these displays is not known. The only other species of Hesperapis known to display a posture perhaps analogous to the preceding is H. (Carinapis) sphaeralceae. Females were observed near Sanders, Arizona, where they collected pollen from Sphaeralcea angustifolia subsp. lobata while partly clinging and partly hovering over the protruding cluster of

ref. re  
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stamens. At this time the posterior legs were held at an angle of about forty-five degrees above the plane of the abdomen. The significance of this leg position is not readily evident.

Another interesting example of a peculiar posture displayed by flower visiting females was reported for H. (Carinapis) alexi. According to Professor A.H. Alex who made numerous observations at the two known localities of this species, they crawl across the face of composite host flowers with their wings held vertically above their body in such a way that the planes of their wings are parallel and their long axes are perpendicular to the long axis of the body of the bee. He also noted that another bee species, Andrena fulvipes Smith, concurrently <sup>the same plants and exhibited</sup> visited the same wing posture. Since both these species are somewhat unusual in having conspicuous, heavily infuscated, nearly black wings, one might wonder if the wing displays perhaps serve some sort of infra- or interspecific communication function. There does not seem to be any obvious direct connection between it and pollen collecting. Indeed, in the same way it is conceivable that the conspicuous leg postures described above for H. rhodocerata and Psaenythia verbesinae might also serve the same function. Whatever their function, it seems certain that further investigation of this behavior would prove interesting.



Knowledge of the foraging behavior of the species of Hesperapis, though still fragmentary, has proven ~~extremely~~ valuable as evidence to support the systematic classification based on morphological characters ~~of the image~~. This is particularly true of the patterns of oligolecty which appear in most cases to closely conform to the various species groups and subgenera recognized in the classification. Of course, it might be argued that this is an invalid check on the classification because morphological characters functionally associated with oligolecty were used during the formulation of these groups. This is partially true but these correlated characters were so few compared to the total under consideration that I think the complaint is not serious. /we

#### Sleeping behavior

The sleeping behavior of the species of <sup>#</sup>Hesperapis is of interest because a relatively wide range of habits occur. Data from at least single observations are available for H. rufipes, <sup>hermosa</sup>H. kayella, H. ilicifoliae, H. larreae, H. arenicola, H. laticipes, H. nitidula, and H. rhodocerata while H. regularis, H. pellucida, and H. peninsularis have been observed repeatedly and in some detail. \x



Hesperapis regularis ~~(Cresson)~~

Sleeping habits of the males of Hesperapis were first reported by Linsely and MacSwain (1958) when they presented data ~~for~~ <sup>from</sup> four ~~local~~ <sup>populations</sup> of H. regularis <sup>at</sup> ~~in~~ Antioch, Arroyo Seco, Pinnacles, and six miles north of Santa Margarita, which they referred to as "an undescribed species of Hesperapis (Panurgomia)", H. (P.) regularis, H. (P.) regularis and "a third species, with very similar habits", respectively. At Antioch they observed hundreds of males in the early morning sleeping in large, white, day old flowers of Oenothera deltoides var. nowellii. Many were sleeping singly but most were in groups of from two to five, often ~~crowded~~ <sup>deep</sup> in the corolla or on the pistil. They also noted that more males seemed to be flying during the day than could be accounted for sleeping in the flowers which suggested that alternate sleeping habits might be involved. At Arroyo Seco and Pinnacles the males were observed to sleep on plant stems and in partially closed flowers of Clarkia speciosa. On the stems the males were oriented <sup>tr</sup> ~~up~~ <sup>up</sup>sswise, hanging on with all six legs while in the flowers they oriented with their head at the opening. Near Santa Margarita they were also associated with Clarkia speciosa. Burdick and Torchi<sup>o</sup> (1959) were able to supply additional data about the sleeping habits of this species at Arroyo Seco. The



<sup>they observed</sup>  
 males under ~~their scrutiny~~ spent the night in the ground in  
 unused burrows or short (less than 3 cm) burrows which they had  
 constructed. The entrances to these were plugged from within by  
 sand the bees pushed up with their head<sup>s</sup> and <sup>was</sup> weakly compacted  
 into irregular masses. Burdick and Torchio cited the ~~article of~~ <sup>observations of</sup>  
 Linsley and MacSwain and speculated that the ground sleeping  
 habit probably explained the extra males which could not be  
 accounted for at Antioch. ~~My own~~ <sup>by GIS</sup> subsequent observations of  
 this species <sup>at</sup> all these sites as well as several others in  
 California / (the San Bruno Mountains, San Mateo County / Isabel /;  
 Creek behind Mount Hamilton, Santa Clara County / 2.5 miles south /;  
 of Arroyo Grande, San Luis Obispo County / 25 miles west of New /;  
 Cuyama, Santa Barbara County / 7.8 miles east of Groveland, /;  
 /; Tuolumne County / 2 miles north of Nipinnawasee, Madera County /;  
 and 3 miles northeast of Jose Basin, Fresno County / have / )  
 confirmed the above data as well as supplied enough additional  
 information ~~or data~~ that a few generalizations can be safely  
 made. By far the most frequent sleeping site for males of this  
 species is in the blossoms of certain flowers, <sup>especially</sup> ~~namely~~ Oenothera  
deltoides var. howellii (fig. 10), several species of Clarkia  
 (all Godetia-like), and Eschscholtzia californica. The common  
 feature of these flowers is that the blossoms close at night  
 around the sleeping bees. Both the burrow sleeping and plant  
 stem sleeping habits were far less common and apparently ~~is~~ not



practiced when sufficient suitable blossoms are available. There also seems to be a definite tendency toward gregarious sleeping with as many as five males in a single blossom. This only occurred when large blossomed flowers such as Oenothera deltoides were available, while small ones such as Clarkia purpurea subsp. quadrivulnera were not found to contain more than one male. On one occasion at Antioch eight males were observed sleeping in relatively close proximity to each other and were exposed on the blossoms and stems of a single plant of Clarkia unguiculata. This suggests that the gregarious tendency also may carry over to the stem sleeping habit.

Hesperapis wilmattae ~~Cockerell~~ and H. nitidula ~~Cockerell~~

Linsley, MacSwain and Raven (1963) reported males of H. wilmattae sleeping in blossoms of Oenothera at many sites in the Colorado and Mojave Deserts. When sleeping the males were oriented parallel to the axis of the flower and they faced outward.

On one occasion <sup>615</sup> ~~f~~ observed a male of H. nitidula sleeping similarly oriented in a blossom of Oenothera bistorta in Eaton Wash at Altadena, Los Angeles County, California.



Hesperapis pellucida ~~Cockerell~~

The senior author has

~~I have~~ observed the sleeping habits of males of H. pellucida on numerous occasions over several years in five separate sites in San Francisco as well as at two sites near Pacific Grove, Monterey County. At all these sites the males usually slept in the blossoms of the common coastal variety of the California poppy, Eschscholtzia californica va. maritima although other flowers <sup>(namely</sup> Clarkia and Oenothera <sup>)</sup> were occasionally utilized when present. When the flower blossoms were ~~wide~~ <sup>fully</sup> open the bees usually settled near the base of the stamens with their body perpendicular to and curled around them. However, as the blossoms gradually closed the bees adjusted their position until finally they were oriented parallel to the stamens and faced outward. As with H. regularis the males exhibited a tendency toward gregariousness with two or very rarely three in the same blossom. Even more interesting, a degree of constancy appeared to occur since ~~individual~~ <sup>marked</sup> males ~~(marked distinctively with~~ <sup>marked</sup> ~~paint)~~ were observed returning to the same clump of flowers several nights in succession (fig. 11). Males of H. pellucida were also observed to sleep in the ground. As with H. regularis these males constructed their own shallow, ephemeral tunnels <sup>(1)</sup> which they closed. However, closing of the entrance was accomplished in a different manner from that reported by Burdick







~~Burdick and Torchio for H. regularis. Males of H. pellucida dug straight forward into the sand at a shallow angle kicking it back beneath their abdomen. As the digging continued the entrance gradually filled until only a slight depression could be seen externally.~~

#### Hesperapis peninsularis Stage

~~The only other species in which sleeping behavior of the males has been more than casually studied is H. peninsularis. Observations on it were made first by Dr. Paul Arnaud, Jr. and subsequently by my wife and I at the huge nest site of that species near San Felipe, Baja California. Probably at least half of the males slept exposed above the ground on almost any terminal part of any plant in the vicinity of the nest site. Many were sleeping singly, in pairs or in small groups but probably the greatest number were in homogeneous aggregations filling the terminal branches of certain Lycium bushes with as many as 300 individuals (fig. 8) although relatively large aggregations were also on other plants such as Croton. Males were variously oriented but they always grasped the substrate with all six legs and never with the mandibles. Even though they were often closely adjacent to one another in an aggregation they always perched on parts of the plant and never on each other forming clusters or balls. It is not known whether individual males had a tendency to return to the same~~



aggregation they always perched on parts of the plant and never on each other <sup>to</sup> forming clusters or balls. It is not known whether individual males had a tendency to return to the same aggregation on successive nights since the few males marked ~~to~~ ~~determined this~~ were not recovered. The aggregations themselves tended to remain in the same locations on the same bushes during the week of our observations but the size of the individual aggregations varied, sometimes considerably. These facts could be interpreted as evidence indicating individual males were not consistent in their choice of sleeping sites. However one cannot safely draw any conclusion on this point since so many other factors were involved, i.e., ~~my~~ disturbance to the aggregation while marking the males, ~~the~~ heavy predation by a mocking bird at the aggregation sites, as well as the general end of season decline of the male population which was evident at the time. Those males which did not sleep on the vegetation apparently slept underground. In one instance a male was found in the nest of a female however, in most cases, the males sleeping in the ground were in separate burrows apparently used exclusively for that purpose. The best evidence that these burrows were exclusively used by males comes with an examination of their contents and structure. Wire cone traps placed over the entrance <sup>s</sup> ~~of these~~ at night regularly yielded from one to a dozen males emerging from single burrows in the morning although ~~up to 36 males may occasionally use a single burrow.~~ ~~even more were found occasionally. Thirty-six was the maximum~~



CAP ~~recorded~~ ~~These~~ 2 male sleeping burrows were easily distinguished from the active female nests because they had no tumulus and they usually were aggregated loosely in local areas where the sandy soil had a thin but hard surface crust. Those excavated were completely unlike the nests of the females. They were shallow, generally ~~from 6.5 to~~ <sup>- (dash) deep,</sup> 2 20 cm with a maximum recorded depth of 25 cm. CAP ~~while~~ 2 nest burrows of the females varied from 140 to 234 cm in depth. Male sleeping tunnels ~~erratically~~ <sup>no change</sup> twisted and turned, often fused with adjacent ones and occasionally enlarged into cavities as wide as 5 cm. ~~On the other hand~~ those of the female <sup>s</sup> were nearly straight and vertical most of their length, uniform in diameter and contained no cavities other than <sup>/i</sup> the terminal cells. The absence of a tumulus around the male sleeping burrows can probably be attributed <sup>/t</sup> to long use of the burrows without continuous excavating activity. As a result there is ample time for the tumulus to be washed or blown away leaving only the hard surface crust exposed around the burrow entrance.

From the above we see that the sleeping behavior of the males of H. peninsularis is basically similar to that of the species studied in the subgenus Panurgomia, viz., H. regularis, H. wilmattae, H. nitidula, and H. pellucida. In each, part of the population <sup>e</sup> slep above the ground while the other part <sup>e</sup> slep below and in each <sup>species</sup> there was a tendency toward gregarious



sleeping. However, except for those gross similarities their habits differ enormously. In the species of Panurgomia the ground sleeping males slept individually in very shallow, epnemerical burrows which they usually constructed <sup>anew</sup> ~~freshly~~ each night while in H. peninsularis the ground-sleeping males usually slept gregariously in complex excavations which were probably used the entire season. The above-ground sleeping segment of the populations of the species studied in Panurgomia usually slept singly or in small groups in flowers that closed around them at night although under certain circumstances some would also sleep exposed on the stems of various plants. In comparison the above-ground segment of the <sup>male</sup> ~~population of males~~ of H. peninsularis <sup>A</sup> slept singly or in various sized, often very large, aggregations exposed on the terminal parts of various plants. It would be interesting to know if the males of H. peninsularis would behave like the species of Panurgomia if large, night-closing flowers were readily available to them.

Hesperapis rhodocerata (Cockerell)

*The senior author*  
I observed one male of H. (Carinapis) rhodocerata sleeping in the late afternoon on an open flower of Baileya pleniradiata near Rodeo, Hidalgo County, New Mexico. It was under the flower



clinging to the clayx with all six legs and oriented perpendicularly to and somewhat curled around it.

Hesperapis rufipes (~~Ashmead~~)

6/5

On another occasion <sup>6/5</sup> I observed seven males of H. (Hesperapis) rufipes sleeping in a local area in dry grass near their nest site at Tanbark Flat, Los Angeles County, California. They were oriented in different ways with some on the grass stems and others on the grass heads although all held on with all six legs (fig. 9).

~~Xeralictoides mentzeliae~~  
~~Hesperapis laticeps rufiventris~~ Stage

The sleeping habits of X. mentzeliae ~~H. laticeps rufiventris~~ have been observed by Dr. C. Don MacNeill (verbal communication) at the type locality near Parker Dam, San Bernardino County, California. As with the species of Penurgomia these males slept in the blossoms of their host flower, Mentzelia.

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Hesperapis larreae ~~Cockerell~~

Male sleeping behavior of H. larreae was recorded by ~~Mr.~~  
P.H. Timberlake at a site 18 miles west of Blythe, California.  
A series of seven males collected by him ~~from that site~~ all bear  
the label "asleep on grass".

Hesperapis arenicola ~~Crawford~~

*The junior author collected*  
~~Mr. Roy R. Snelling (in litt.) reported that he collected~~  
males of H. arenicola sleeping exposed in the open blossoms of  
their host species, Geraea canescens, in the early morning near  
Indio, Riverside County, California. As with several of the  
other species there was a gregarious tendency with two or three  
males often on a single blossom.

## Female sleeping behavior

Sleeping habits of the females of Hesperapis were first  
reported by Burdick and Torchio (1959) after making observations  
on the population of H. regularis at Arroyo Seco. Here females  
slep in the ground, usually in their establishment ~~burrows~~ but *//d*  
sometimes in shallow burrows ~~which they newly constructed~~ *evidently* *for that purpose*. The

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entrance was plugged by sand from within ~~the tunnel~~ in the same manner as that described for the males. Subsequent to the above work <sup>we</sup> have had the opportunity to observe sleeping behavior for the females of H. <sup>hermosa</sup> ~~kayella~~, H. ilicifoliae, H. nitidula, H. regularis, H. pellucida and H. peninsularis. The last three species were observed many times at various sites. In ~~all~~ these species the females usually slept underground in their established burrows which were sealed at the entrance. The only exceptions to this occurred either early in the season before the females had established nests or when ~~I had disturbed~~ <sup>had been disturbed</sup> their nests by excavating or when females were trapped on flowers away from their nests as a result of abrupt weather changes. In the first and second cases ~~the~~ females without burrows usually slept in a manner typical for the males of their species while in the third case the trapped females remained where they were trapped.

Even with such incomplete comparative data available it is evident that great variation exists in sleeping behavior of Hesperapis. Yet in spite of this, certain aspects of the behavior exhibited within each species are rather consistent. Thus, degree of gregariousness, ratio of above to below ground sleeping males in a population, structure and closure of burrows, length of use of burrows, and use of night closing flowers may all prove to be useful systematic characters when more is known of the rest of the species.



Entirely too little is known about the sleeping behavior of Hesperapis to permit any generalizations concerning the whole genus. However a few generalizations can be made regarding the sleeping behavior of the three well studied species. First, except under special circumstances females sleep in their nests which they seal at night. Second, males show great plasticity in choice of a sleeping site with part of a population often underground in burrows of their own construction and the other part above ground in or on vegetation. Third, males sleeping on vegetation use all six legs but not their mandibles to cling to the substrate. Fourth, males exhibit a tendency toward gregarious sleeping.



TABLE 2

Observed duration of territorial behavior by individual marked males of Hesperapis pellucida

Laguna Puerea - 1960		Lobos Creek - 1963	
Number of Days	Number of Males <sup>1</sup>	Number of Days	Number of Males <sup>1</sup>
1	4	1	10
2	3	2	1
3		3	6
4		4	
5	1	5	4
6		6	
7		7	
8	1 <sup>2</sup>	8	
9		9	1
10		10	
11		11	1 <sup>3</sup>
12		12	1

<sup>1</sup> Each male is counted only opposite the number that represents its maximum time.

<sup>2</sup> Between the fifth and eighth day the observation post of this male shifted 24 cm.

<sup>3</sup> On the seventh day the observation post of this male shifted 30 cm. to a new location where it stayed through the eleventh day.



TABLE 3

Data on the tunnels of the nests of some of the species of *Hesperapis*

Species	Locality	Length of tunnel <sup>1</sup>	Depth of terminal cell <sup>1</sup>	Depth of tunnel dichotomies <sup>2</sup>			Diameter of tunnel near surface <sup>1</sup>	Diameter of tunnel near cell <sup>1</sup>
<i>H. kayella</i>	Wadsworth	26.0 cm	9.0 + cm				5.0 - 10.0 mm	3.0 mm
		13.0	6.0				6.0	3.5
<i>H. rufipes</i>	Tanbark Flat	18.5	9.0 ?	5.5 cm	8.5 cm	8.5 cm	3.0	3.0
<i>H. ilicifoliae</i>	Santa Margarita	28.0	22.0	6.5	7.5	10.5	6.0 - 7.0	3.0
		33.0	20.5				5.0	3.5
<i>H. pellucida</i>	San Francisco	30.0	18.5	2.0			9.0 = 14.0	5.0
		37.0	19.0				8.0	5.0
		39.0	21.0				10.0	5.0
		41.0	23.0				9.0	4.5
		49.0	24.0				12.0	5.0
<i>H. regularis</i>	Antioch	59.0	33.0	2.5			12.0	6.5
							12.0	7.0
							10.0	6.5
<i>H. peninsularis</i>	San Felipe	220.5	193.0				11.0	8.0
		190.0 +	175.0 ?				9.0 - 14.0	8.0
		207.0	180.0 ?				14.0	8.0

<sup>1</sup> All measurements have been rounded to the nearest half unit.



TABLE 4

Summary of data on the cells of some species of *Hesperapis*

Species	Locality	Cell length in mm <sup>1</sup>		Cell width in mm <sup>1</sup>		Cell height in mm <sup>1</sup>		Depth of cells in cm <sup>1</sup>	
		Number measured	Average Range	Number measured	Average Range	Number measured	Average Range	Number measured	Average Range
<i>H. kayella</i>	Wadsworth	2	6.0 6.0	3	4.0 3.5-5.0	3	4.0 3.5-5.0	13	12.5 6.0-19.0
<i>H. rufipes</i>	Tanbark Flat	5	7.5 7.0-7.5	5	5.0 5.0-5.5	5	5.0 5.0-5.5	4	12.0 10.0-15.0
<i>H. bicifoliae</i>	Diablo Range							15-20 ?	12.0-18.0
<i>H. margarita</i>	Santa Margarita	2	5.5 5.0-6.0	2	4.5 4.5-5.0	2	4.5 4.5-5.0	2	21.0 20.5-22.0
<i>H. pellucida</i>	San Francisco	5	10.0 10.0-11.5	5	8.5 7.5-9.0	5	8.0 7.5-8.5	28	20.0 15.0-25.0
<i>H. nitidula</i>	Eaton Wash	1	15.0	2	7.0 7.0	2	7.0 7.0	11	10.5 7.5-15.0
<i>H. regularis</i>	Antioch Isabell Creek	1	13.0	1	10.0	1	11.0	12 6	36.0 19.0-49.5 14.0 11.5-18.0
<i>H. peninsularis</i>	San Felipe	9	22.5 21.0-24.0	16	13.0 10.0-15.0	23	9.0 7.0-12.0	111	187.0 140.0-234.0

<sup>1</sup> All measurements have been rounded to the nearest half mm.



TABLE 5

Vertical distribution of cells, clay and sand at the nest  
excavation of Hesperapis peninsularis

Depth of cells in cm	Number of Cells	Soil profile	
0-14		sand	15 cm
15-24		clay	25 cm
25-34			
35-44		sand	
45-54			
55-64			73 cm
65-74			
75-84		clay	
85-94			
95-104			114 cm
105-114			
115-124		sand	
125-134			
135-144	1 (140 cm)		
145-154	6		153 cm
155-164	16	clay	
165-174	6		173 cm
175-184	23		
185-194	17		
195-204	21	sand	
205-214	14		
215-224	6		
225-234	1 (234 cm)		228 cm
235-244		clay	
245-254			
255-			



TABLE 6

Pollen ball size for various species of Hesperapis

Species	Locality	Number measured	Average diameter <sup>1</sup>	Range of diameter <sup>1</sup>
<u>H. rufipes</u>	Tanbark Flat	3	3.0	2.6-3.3
<u>H. ilicifoliae</u>	Diablo Range	8	3.3	3.0-3.5
	Santa Margarita	3	3.0	3.0-3.0
<u>H. regularis</u>	Antioch	7	5.7	5.3-6.0
	Isabell Creek	3	5.7	5.4-6.1
<u>H. peninsularis</u>	San Felipe	25	7.1	6.8-7.5

<sup>1</sup>Measurements are in millimeters

TABLE 7

Results of gut analyses of representatives of eleven species of Hesperapis

Species	Locality	Pollen source	Gut contents	
			Pollen not present	Pollen present
<u>H. kayella</u>	Wadsworth, Nevada	<u>Coldenia nuttallii</u>	1	1
<u>H. pulchra</u>	Yuma, Arizona	<u>Coldenia palmeri</u>	1 , 1	
<u>H. rufipes</u>	Tanbark Flat, California	<u>Navarretia hamata</u>	1	1
<u>H. ilicifoliae</u>	Diablo Range, California	<u>Adenostoma fasciculatum</u>		1 , 1
<u>H. leucura</u>	San Felipe, Baja California	<u>Dalea mollis</u>	1 , 1	
<u>H. regularis</u>	Antioch, California	<u>Clarkia unguiculata</u>		1 , 1
<u>H. nitidula</u>	Baywood Park, California	<u>Eschscholtzia californica</u>		1
<u>H. pellucida</u>	San Francisco, California	<u>Eschscholtzia californica</u>	1	
<u>H. sphaeralceae</u>	Las Cruces area, New Mexico	<u>Sphaeralcea angustifolia</u>		2
<u>H. peninsularis</u>	San Felipe, Baja California	<u>Encelia californica</u>		2 , 2
<u>H. macrocephala</u>	San Felipe, Baja California	<u>Dalea mollis</u>	1	

<sup>1</sup>Identity of the pollen source is based on comparison of pollen grains from the gut and the scopa of each bee with that from anthers of appropriate pressed flower specimens. In all these cases the females ate the same kind of pollen they collected and the males ate the same as their females.