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EVOLUTIONARY ASPECTS OF GEOGRAPHICAL VARIATION IN COLOR AND OF
PREY IN THE BEEWOLF SPECIES *PHILANTHUS ALBOPILOSUS* CRESSON

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ABSTRACT

Prey selection and aspects of life history were studied in a population of Philanthus albopilosus Cresson, near Empress Alberta, and compared with published data reported about other populations. A disproportionately large number of sphecoid wasps was used as prey in comparison with prey used by more southern populations. Females did not hunt at flowers, but appeared to hunt suitable apocritans found around the Empress dune, or captured male apocritans which pursued them as potential mates. False burrows appeared to function as visual aid in orientation to the nest. Relative absence of other species of Philanthus implies specialization of wasps of P. albopilosus for life on sand dunes.

Differences in prey selected, nest structure and colour of adults suggest geographic isolation and differentiation during Pleistocene glaciations. The Nebraska Sand Hill region is proposed as a northern refugium where differentiation of the dark race, P. albopilosus, occurred during the Wisconsinian glacial stage. A southern refugium in the American Southwest is proposed for the ancestral stock of the pale race, P. albopilosus manuelito a newly described subspecies (type locality Monahans, Ward County, Texas).

RÉSUMÉ

Cette étude porte sur la sélection des proies et sur divers autres aspects de l'histoire naturelle d'une population de Philanthus albopilosus Cresson vivant près d'Empress en Alberta. Les résultats sont comparés à d'autres données déjà publiées se rapportant à d'autres populations de cette espèce. Le régime de proies de la population étudiée comprenait une proportion anormalement élevée de guêpes sphécides comparé au régime de populations plus méridionales. Les femelles ne chassaient pas sur les fleurs, mais semblaient plutôt capturer les hyménoptères apocrites convenables trouvés dans les parages de la dune d'Empress. Elles capturaient aussi les mâles apocrites qui les poursuivaient en vue d'un accouplement. Les faux terriers semblaient servir de repères visuels dans l'orientation vers le nid. L'absence relative d'espèces de Philanthus autres que P. albopilosus implique que les guêpes appartenant à cette espèce sont spécialisées pour vivre sur les dunes de sable. Des différences dans les proies sélectionnées, la structure des nids et la coloration des adultes suggèrent y a eu isolation géographique et différenciation pendant les glaciations du Pléistocène. La région de Nebraska Sand Hill pourrait avoir servi de refuge septentrional où la différenciation de la forme foncée, P. albopilosus albopilosus, aurait eu lieu au cours du stade glaciaire wisconsinien. Le sud-ouest américain pourrait avoir servi de refuge méridional aux populations ancestrales de la race pâle, P. albopilosus manuelito, une sous-espèce nouvellement décrite (localité du type: Monahans, comté de Ward, Texas).

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INTRODUCTION

Wasps of the genus *Philanthus*, have aroused new interest of researchers. Classical studies by Tinbergen (1932, 1935) using *P. triangulum* focused on orientation by females to their concealed nests. In North America little work was done on the genus until about the 1950's. Early workers recorded habitats and prey of various *Philanthus* species (Rau and Rau 1918, Peckham and Peckham 1905). Reinhard (1924) reasoned that because of the observed specificity of females of *P. gibbosus* (Fabricius) to a particular group of bees (Halictidae) and the occurrence of another family Andrenidae represented in the prey records, that these families should be combined. However most members of the genus *Philanthus* are not specific to a few species or families of bees. Other workers (Alcock 1974, Armitage 1965 and Cazier and Mortenson 1965, Evans 1966b, 1970, 1975, and others) report that bees are preferred prey, but females of some species (*P. pulcher* Dalla Torre, *P. crabroniformis* Smith, *P. zebratus nitens* (Banks), *P. pacificus* Cresson, and others) take many sphecids. Armitage (1965) explored aspects of prey quality, Alcock (1974) experimented with visual clues used in hunting and Evans (1970) investigated some areas of competition between species for prey.

Most studies of beewolves have been ethological. Little information is available about historical factors which have shaped behaviour. Lorenz (1967) stated that behaviour "...must never be regarded as a product of change or taken as a matter of course when behaviour is found to be adapted to a corresponding point of the species environment". In this study behavioural and structural features are features used to document relationships of populations against a background of Pleistocene and Holocene changes in environmental parameters, and to recognize a new subspecies. Different populations have experienced different selective pressures and these may be manifested in differences in life history and behaviour. Analysis of colour variation allows interpretation of dispersal patterns and hypotheses about relations between populations (Freitag 1965). This permits speculation about evolutionary events which may be responsible for differentiation of various facets of life history and behaviour.

STUDY SITE

The study site was 11 km south of Empress, Alberta, east of the Alberta-Saskatchewan boundary (50° 51' 30" north, 109° 59' 27" west; Figure 1). The dune field straddles the provincial boundary and active dunes are on both sides (Whitaker and Christiansen, 1972). The Empress dunes are more or less an eastern continuation of the Middle Sand Hills.

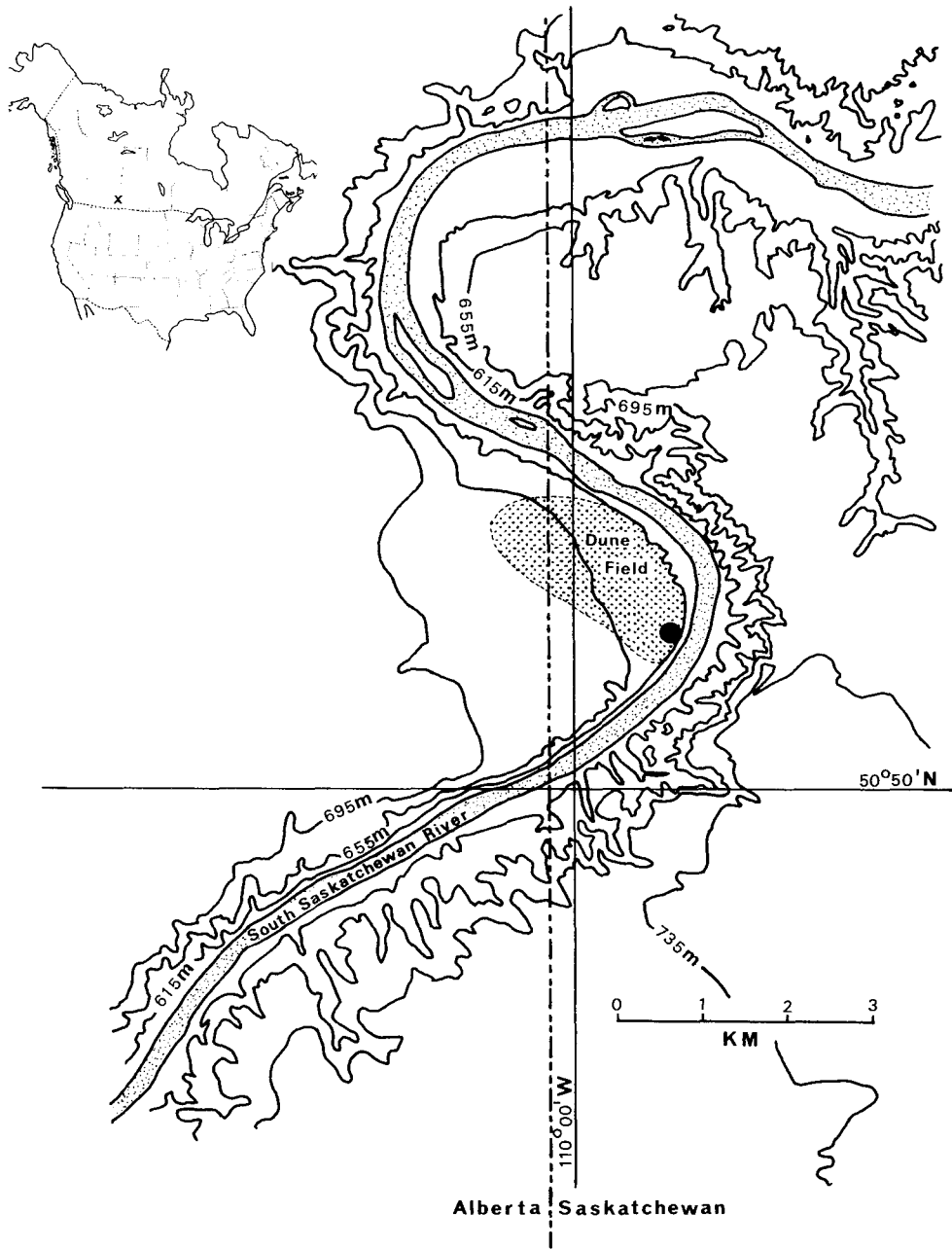


Figure 1. Map of study area. ● marks the study dune. The inset shows the relative position of the study site in North America

The study dune was the crest of a low bluff overlooking the South Saskatchewan River. Sand from the eastern edge of the dune blows down the bluff into the gallery forest near the river. The Empress dune field is on a layer of glacial till intermixed with lacustrine deposits. All of these overlie the Judith River formation¹ which is exposed along the river valley. The undulating terrain of the dunes, variety of substrates and close proximity to the river combine to create a varied physical habitat permitting many species of insects to occupy a small area.

Climate of the study site is related to continental position, absence of modifying bodies of water, a mid-northern latitudinal location, and rainshadow influence of the Rocky Mountains (Coupland 1950). Average annual precipitation is low, 22.55 cm at the town of Empress (1975 Climate of Alberta Report). Evaporation rate from free standing water in the Great Sand Hills of Saskatchewan to the east is approximately 75 cm during the frost free season (Hulett *et al.* 1966). The Empress area is the most arid region in Alberta and may be drier than any area in Saskatchewan. Aridity of the region probably permits continued movement of the sand dune by limiting vegetation cover.

The Empress dunes appear to have similar plant associations to those recorded by Hulett *et al.* (1966) for the Great Sand Hills (about 60 km due east). The dunes are inhabited by several species of xeric plants (*Oryzopsis hymenoides* Ricker, *Psorealea lanceolata* Pursh and *Sporobolus cryptandrus* A. Gray) which are commonly found further to the south or on sand dunes in the Great Basin (Chadwick and Dalke 1965).

Philanthus albopilosus shares the Empress area with five other species of *Philanthus*. *Philanthus psyche* Dunning nests on the sand dunes near nesting areas of *P. albopilosus*, *Philanthus solivagus* Say, *P. ventilabris* Fabricius, *P. gibbosus* (Fabricius), and *P. gloriosus* Cresson were found near, but did not nest on the open sand of the sand dune.

Fauna of the Prairie Provinces is of comparatively recent origin. The majority of organisms currently found within the provincial boundaries entered from refugia in the south following melting of Wisconsinan Ice. Major glacial advances during the Wisconsinan eliminated all previous living assemblages. Summaries of events of Wisconsinan age are presented by Flint (1971), Wright and Frey (1965), and Mitchell (1979).

The Wisconsinan Glacial Stage is postulated to have begun about 55,000 years B.P. and achieved the maximum southward expansion of the ice sheet at about 17,000 years before present. It is generally accepted that, with the southward movement of the ice, the faunal zones were either overrun (Löve 1959) in part or were displaced (Wright 1969) to the south. Extent of displacement is still a matter of much speculation. Martin (1958) argued for a wide band of tundra and taiga. Ross (1970) shows a boreal type forest abutting with the ice front, but Frenzel (1973) portrays the tundra merging with the steppe on the Great Plains which splits the boreal forest into eastern and western components. Many groups of animals dependent on plant associations may have had their populations split into two main groups (Freitag 1965, Mengel 1970).

Much of the insect fauna at the study site appears to be dependent on a sandy substrate. Post-glacial colonization and subsequent development of the fauna is dependent on past events and conditions.

¹Bearpaw formation is present above the Judith River formation and beneath the glacial till a few km to the east or west. The Bearpaw formation was eroded away by a periglacial river at the site of the Empress dunes.

At the zenith of the Wisconsin stage, a large ice sheet moved southward from the Hudson Bay region. Soil and rocks were crushed, then ground and transported, eradicating evidence of preglacial floras and faunas.

During melting of the Wisconsin ice sheet, a large mass of ice impeded drainage of water to the north. Various glacial lakes developed. Some were very large, such as glacial Lake Agassiz (Mayer-Oakes 1967). However, most were smaller transient lakes, which formed in ice-impeded river drainage basins, giving rise to extensive areas of lacustrine deposits (Edmunds 1962, Klassen 1972) comprised of clay, silt and sand deposits. Wind, reworking sandy lake bottoms and deltaic deposits, gave rise to recent dune sands (Mitchell *et al.* 1974).

Requirements for development of sand dunes are: (1) a source of sand and (2) a wind to move the sand (Flint 1971). Other factors may modify availability of sand such as geologic history of the area and climate. Geologic events control presence or absence of sand, whereas climate controls transport of sand. Xeric environments tend to develop sand dunes more readily than mesic areas. Sand dunes are in regions where sand is available for transport (e.g. active dunes occur at Brule Lake, Alberta in the boreal forest, Dowding 1929).

The period of dune formation probably occurred in two major phases. The first began shortly after recession of the ice, before mineral soils could be stabilized by encroaching pioneer vegetation (Ashwell 1966). This phase may have lasted for a short period. Subsequently, boreal type forest may have developed and moved north across the plains (Bryson and Wilson 1967), Wright 1969). The climate ameliorated, allowing expansion of prairie northward, beyond its present limits, reaching a maximum about 7,000 years before present. During the Hypsithermal renewed dune building would have occurred. Increased aridity reduced vegetation cover allowing increased aeolian erosion. During this warm dry period many of the xeric-tolerant and sand-adapted insects would have migrated north into new unoccupied habitats. Along with cooling since the Hypsithermal, Boreal forest has reinvaded much of the northern prairie regions and continues to slowly encroach (Löve 1959).

MATERIALS AND METHODS

Study material included 39 adults of *P. albopilosus*, collected at the study site, 46 specimens collected in the south-western United States, and 195 borrowed specimens. The latter are from the following collections: CAS

- CAS California Academy of Sciences, San Francisco, Calif. 94118
- CNC Canadian National Collection, Ottawa, Ontario. K1A 0C6
- CSU Colorado State University, Fort Collins, Colorado. 80521
- CUM Cornell University, Ithaca, N.Y. 14853
- GH G. Hilchie, Edmonton, Alberta. T6E 4B5
- MCZ Museum of Comparative Zoology, Cambridge, Mass. 02138
- SEM Snow Entomological Museum, Lawrence, Kan. 66045
- UAS University of Alberta, Strickland Museum, Edmonton, Alta. T6G 2E3
- UCB University of California, Berkeley, California. 94720
- UCD University of California, Davis, California. 95616
- USNM United States National Museum, Washington, D.C. 20560

Behavioural Study

During the summer of 1977, nesting behaviour of *P. albopilosus* was studied in detail. More cursory data from previous years have been incorporated with data from the 1977 season.

Early in the season, nests of *P. albopilosus* were left undisturbed. Nests were located by watching a potential nesting area for prey-laden female wasps and locating false burrows. Nesting areas often had males patrolling and landing on the sand. Each nest was marked with a stake.

In conjunction with marking nests, individual female wasps were marked with small dabs of Testors model paint on the scutum. Five colours were used in two positions (right and left side). Males of *P. albopilosus* were not studied at the Empress site.

Nests were initially observed while recording prey brought back by females. Toward the end of July, in an effort to determine the prey species more accurately, many staked nests were sacrificed in the evening when the female was inside with a day's capture of prey. Prey and beewolf were collected and preserved in 75% alcohol solution. Voucher specimens are in the Strickland Museum (University of Alberta).

Potential prey available at the site was sampled by sweeping vegetation around the dune in potential hunting areas. Bees and wasps were collected from blossoms of *Psoralea* and *Solidago*. Other dune-inhabiting bees and wasps were collected as they were encountered. Notes about relative abundance were made for some of the common species.

In 1978, several additional populations of *P. albopilosus* were observed at Roggen, Colorado (Evans' study site) and Little Sahara Recreation Area, Utah. The Roggen dunes were very similar to the Empress dunes in appearance.

Taxonomic Study

Trends were examined through use of a Compound Character Index (Brown and Wilson 1956), because of lack of a single consistent diagnostic character or group of characters.

Colour is important in species discrimination, and it is sometimes necessary to rely heavily upon colour (Evans and Matthews 1973). Colour is subject to variation in hue and extent in many species. Trends may be correlated to environmental gradients, such as moisture (*Bembix variabilis*, Evans and Matthews 1973), and thus may be ecophenotypic. When trends in colour do not follow evident environmental gradients, with markedly contrasting (divergent) populations occupying neighbouring areas and intermediate masculated forms in peripheral zones, differences may be taken as a measure of genetic differentiation and thus of taxonomic significance.

Character states used are as follows.











Females. – Eleven characters were studied (Table 1.) whose states were constant in a given locality, but varied geographically. Many additional characters such as pubescence length and density were examined but they varied within localities. Variation in density of pile may result from age of the wasp and variable abrasion by sand.

1. Frons: An estimate of percentage of area marked with yellow was made. The area considered was delimited at the apex of the head by a line on the microscope ocular grid positioned at the base of the median ocelli and extending to contact both compound eyes. Estimates of coloured area were made to the nearest 5%. Maximum ranking was given a value of 99%. The border between the clypeus and frons was dark and assumed to be 1%.

2. Clypeus: The clypeus was scored in a similar manner with a maximum score of 99%. The area was delimited by the dorsal suture with the frons and the ventral suture with the labrum.

Table 1

Compound character index values assigned to selected character states in female wasps of *Philanthus albopilosus*.

Character \ Index value	0	1	2	3	4	5	6	7	8	9
1. frons	*0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
2. clypeus	*0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
3. vertex of head	black	-	o o	-			-		-	
4. scutellum	black	-	o o	-	oo	oo	-		-	
5. mesonotum	black	-	. .	-	-	o o	-	-	-	
6. pronotal collar	black	-	o o	-	-		-		-	
7. scutum	*0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49
8. propleuron	*0-7	8-15	16-23	24-31	32-39	40-47	48-55	56-63	64-71	72-79
9. abdominal tergite 1	*0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99
10. abdominal tergite 2	*20-27	28-35	36-43	44-51	52-59	60-67	68-75	76-83	84-91	92-99
11. abdominal sternal spots	0	-	1	-	-	2	-	3	-	4

*Denotes percentage area of light colored maculations. Diagrams denote relative size and shape of maculation, anterior is towards top of column.

3. Vertex of Head: Colour pattern was given index values ranging from 0 for no maculations to 9 for a solid bar.

4. Scutellum: Character states ranged from entirely black through two spots to a single large median spot with index values of 0 to 9 respectively.

5. Mesonotum: Three character states were recognized; black, two lateral spots and a single transverse band with index values of 0, 5 and 9 respectively.

6. Pronotal Collar: Five character states were recognized: black, small lateral spots, large oblong lateral spots, broken band and a continuous transverse band which were assigned index values of 0, 2, 5, 7 and 9 respectively.

7. Scutum: An estimate of percentage colour was made. Range was from 0% to 50%. Estimates were to the nearest 5%.

8. Propodeum: An estimate of percentage colour was taken, which ranged from 0% to 80%. Maculations on the dorsal and lateral aspects were used in the estimate. Posterior exposure of the propodeum was excluded from estimates because it was obscured by the abdomen in many specimens.

9. First Abdominal Tergum: An estimate of the area of light colour was made from the dorsal aspect. Values varied from 0% to 95%. Estimates were made to nearest 5%.

10. Abdominal Tergum Two: Colour was estimated as for the first abdominal tergum with values ranging from 20% to 99%.

11. Abdominal Sternal Spots: These are on the lateral portion of the sternal sclerites, one spot per sclerite per side. Total number of spots on the right side were recorded and assigned an index value.

Low values were assigned to black or minimum colour and high values to the maximum amount of yellow. All character states were given equal weighting.

Males. – Males varied less than females. Five characters were studied (Table 2.).

1. Pronotal Collar: Maculations varied from solid black to a continuous bar of yellow.

2. Scutellum: Only two character states were recognized; presence or absence of two yellow spots.

3. Colour of Abdomen: Most frequent colour for males is bright lemon yellow, tinted in some with orange, in others the colour is a rich orange to red. The red or darker colour is assigned an index value of 0 and yellow the index value of 4.

4. Pronotal Lobe: Presence or absence of colour was noted and given a value of 0 (no colour) or 4 (colour).

5. Fourth Abdominal Tergum Maculation varied from a single median spot (index value 0), a series of spots, median and lateral (index value of 2) and a band spanning the width of the tergite (index value 4).

A score of 0 typified the extreme dark male and a score of 20 the extreme light male.

No taxonomically useful differences were found in the male genitalia. Bohart and Grissell (1975) and Strandtmann (1946) also report that variability in male genitalia is of little or no taxonomic importance in *Philanthus*.









RESULTS

Life History

At Empress, *P. albopilosus* is closely associated with a dune environment. Females typically nested on margins of broad, flat bare areas of the sand dune. Nests were in a zone of lightly

Table 2

Compound character index values assigned to selected character states in male wasps of *Philanthus albopilosus* Cresson.

Character \ Index Value	0	1	2	3	4
1. pronotal collar	black	o o			
2. scutellum	black	-	-	-	
3. abdominal colour	orange	-	orangish yellow	-	yellow
4. pronotal lobe	black	-	-	-	
5. abdominal band on tergite 4		-		-	

Diagrams denote relative shape and size of maculation.

drifting sand, away from vegetation.

A nest is of elaborate design (Evans, 1975). The entrance of a new nest is concealed by a sand closure and a number of false burrows (0 to 6) may be present. They are constructed immediately following completion of a nest at the time of initial closure, but are not maintained, and some fill with loose sand in a few hours. From the nest entrance a horizontal or nearly horizontal vestibule extends for about 25 cm. The vestibule terminates at the beginning of a vertical gallery. Vertical galleries extend 25 to 30 cm in depth. Provisioned cells were not located. Prey is stored in the vestibule until a cell is provisioned.

Females occupied their nest for a relatively short time, usually one or two days. Nests were provisioned from late June through July into early August. Life span for adults of *P. albopilosus* is as yet undocumented but females of *P. gibbosus* (Reinhard 1924) and *P. crabroniformis* (Alcock 1974) live and provision their nests for about three weeks.

Males in the Empress area typically perched on the sand in alert positions. They often flew after passing insects and frequently grappled with females (prey-burdened) about to enter their nests. In 1980 copulating wasps were observed resting on the dune surface.

Comparisons with Other Populations

At Roggen, Colorado, male *P. albopilosus* behaved as reported by Evans and as observed on the Empress dunes. No females were sighted or nests located. In contrast, 19 males and 5 females were captured at Little Sahara, Utah. No males were seen patrolling and no nests were found in "suitable" areas. All beewolves were captured foraging on flowers along the dune edges in the vegetation belt.

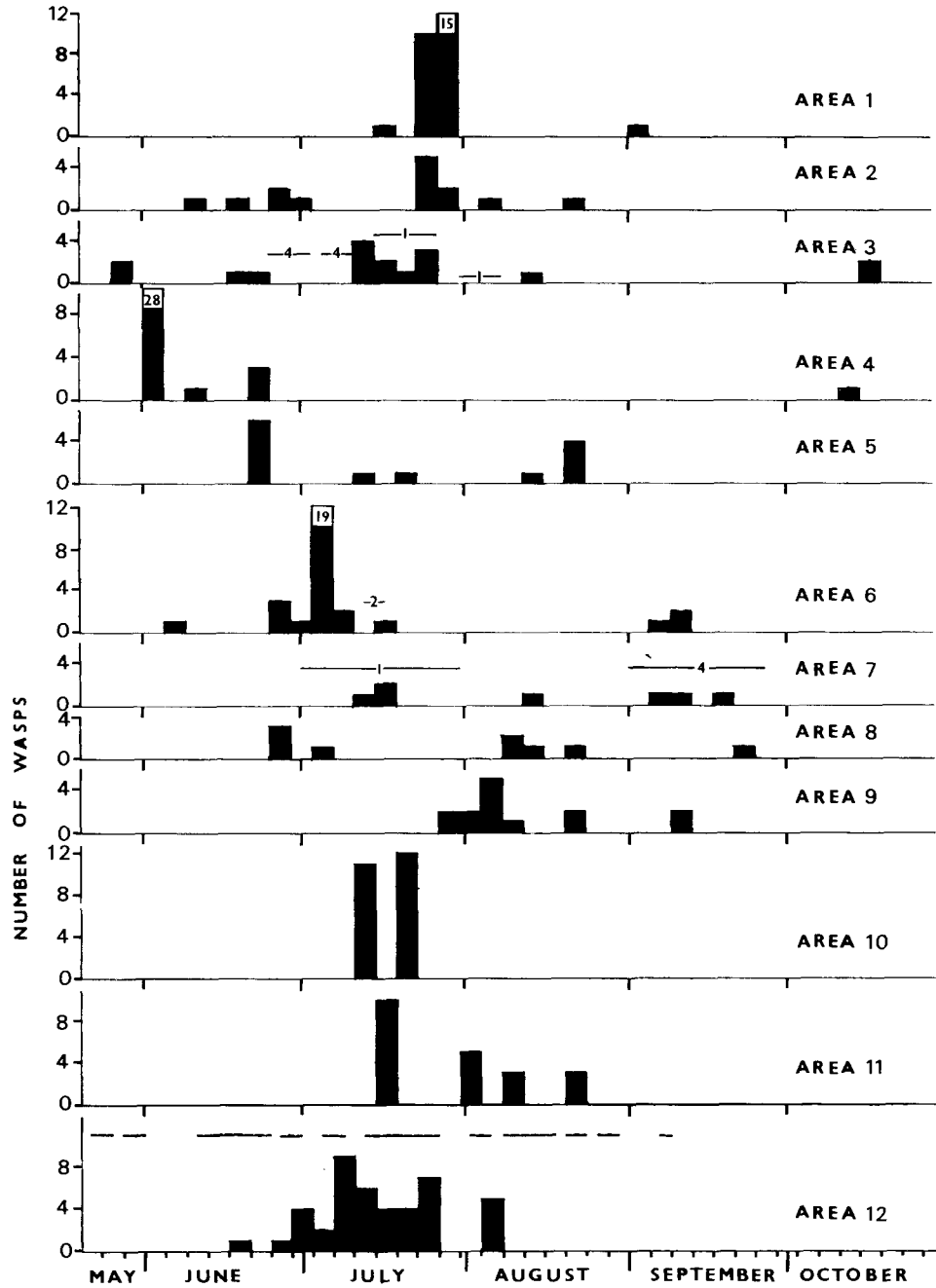


Figure 2. Temporal distribution of adult *Philanthus albopilosus* Areas are those illustrated in Figure 3. Dashed line above histogram for Area 12 (Empress) indicates collecting dates at the study site.

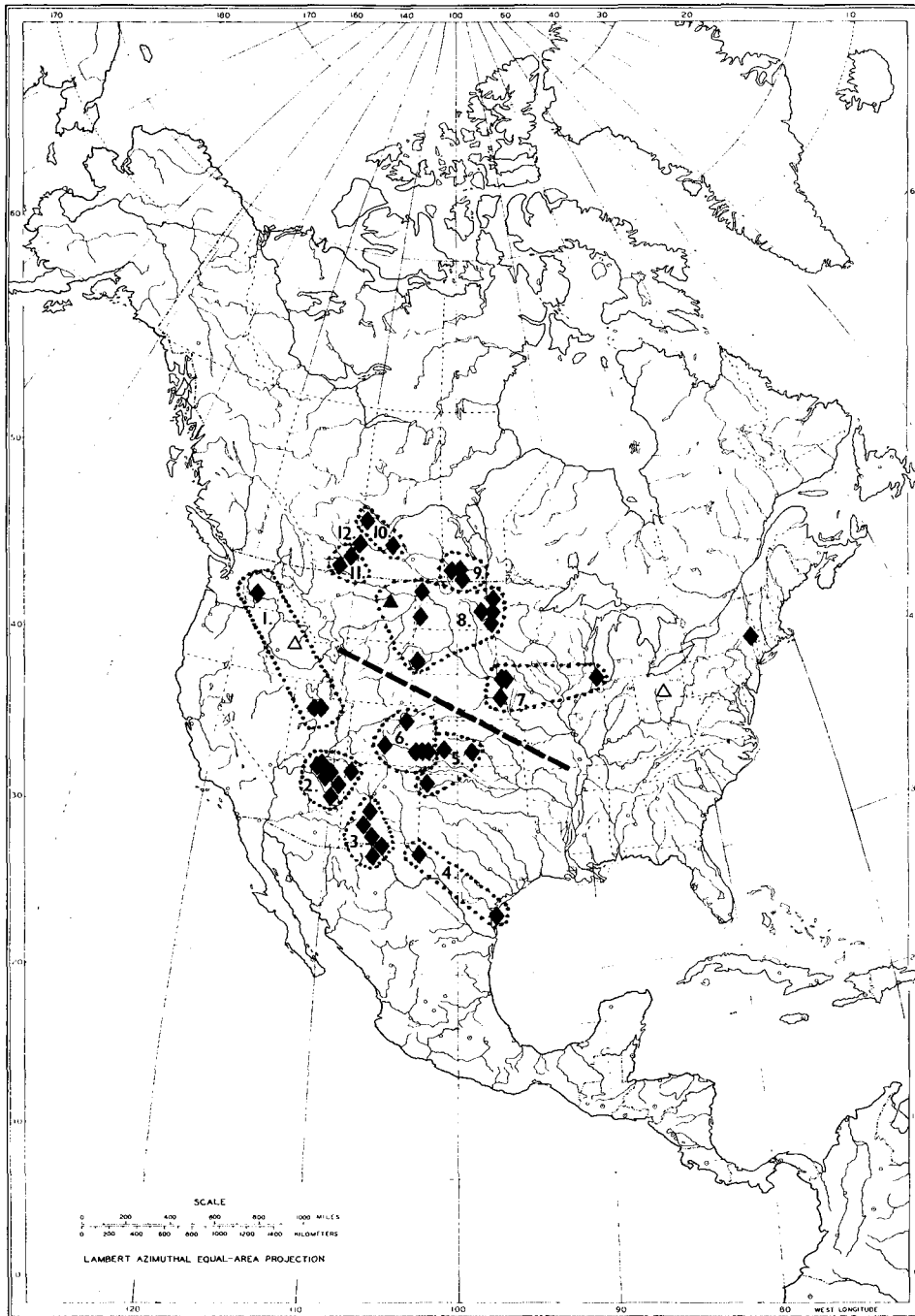


Figure 3. Distribution of *Philanthus albopilosus*. Numbers shown are used in the text to refer to the localities enclosed by the dotted line. The dark race *P. albopilosus albopilosus* occurs northeast of the dashed line, and the light race *P. a. manuelito* to the south west. Symbols used: ◆ locality record (specimens seen); ▲ state record (specimens seen); △ state record (published).

Evans (1975) reported that cells at the terminal end of burrow galleries averaged about 2.5 times deeper in Colorado populations than in those studied near Albany, New York. Vertical gallery depths at Empress compare favourably with those at Albany, New York.

If depth of the burrow reflects past evolutionary interactions and with diminished response to local conditions, presence of shallow burrows in the northern populations may reflect adaptation to past climatic stress. Cells closer to the surface ought to experience warming earlier in the season. This permits a longer period of development, which would allow colonization of areas with a shorter growing season. The opposite may be true in southern areas: intense heating of the sand by the sun may be lethal to cells near the surface (Chapman *et al.* 1926) which would select for deep nests.

Data about periods of adult activity were obtained from locality labels; dates were consolidated into four day units and illustrated in Figure 2 using the area groups illustrated in Figure 3. Northern populations (Areas 7 to 12) appeared to have one main generation active during July, and in some (Areas 7, 8, and 9) there appears to be a smaller second generation in early September. Among southern populations, collection dates range from May 27 to October 17, indicating the possibility of several generations per year.

Data obtained at Empress (Area 12), provide a more unbiased indication of activity of adults. Collecting dates and number of beewolves collected are both presented so that negative evidence is an indicator of when beewolves were not present.

Females at the Empress study site appear to occupy nests for a short duration comparable with Colorado and New York populations (Evans 1975). Evans reports that of 26 marked nests in Colorado only a few were active after a few days. In the New York Sample of marked nests ($n=5$), two were active three days later (Table 3).

The Empress population is not distinctly different from the New York population. However Colorado females dig deeper galleries than observed in the two more northerly populations.

Table 3. Duration of nest occupancy on the Empress dunes in comparisons with Evans' (1975) study sites.

Locality	Day				
	0	1	2	3	4
Empress, Alberta	15	2	0	–	–
Albany, New York	5	–	–	2	–
Roggen, Colorado	26	–	–	–	few

Numbers refer to the nests observed. Day zero refers to when the nests were first observed.

PREY SELECTION

Prey specificity in *Philanthus* is a result of evolutionary interactions and environmental factors expressed as a mosaic of different wasp populations using different complexes of prey species (Evans 1966c). Precise entrainment to a particular group may be detrimental because prey species are subject to fluctuations in relative abundance; a plastic response to a complex of prey groups may be a more successful evolutionary strategy.

Females of philanthine genera use various apoids and, to a lesser degree, other wasps. Females of most species of *Philanthus* show a preference for halictid bees, with a marked tendency of some species to use sphecids as prey (Armitage 1965, Evans 1970). Females of *Aphilanthops* prey exclusively on ants of the genus *Formica* (Bohart and Grissell 1975). Remarkably, females of most species of *Cerceris* and those of all species of *Eucerceris* prey on beetles. (Bohart and Menke 1976). This is exceptional among philanthines, but illustrates the sorts of differences among groups included in a single subfamily. These last two genera are closely related to one another, but are quite distantly related to *Philanthus* (Menke 1976).

The Empress Dunes Populations

Females of *P. albopilosus* captured a varied group of prey including members of three families of wasps and three families of bees. Twenty six male and four female wasps used as prey were members of nine species. *Aphilanthops frigidus* (F. Smith) males were the most common wasps used as prey (17 individuals). The 48 male and two female bees captured as prey were members of seven species. Most of the prey records were divided between males of two species, *Halictus rubicundus* (n=23) and *Colletes* sp. (n=19). Overall, 37.5% of the prey were wasps and 92.5% were male apocritans. Prey ranged in length from 5 to 11 mm with a few wasps measuring 14mm and 19.5 mm. The most commonly used prey ranged from 8 to 11 mm.

General collecting of wasps was done in the study area to establish a basis for comparing what prey was taken with what was available. Table 7 contains data about apocritans whose adults seem to be within the size range preferred by females of *P. albopilosus*.

Table 4. Provisioning rates for selected females of *Philanthus albopilosus* .

Individual	Leaving Time h	Returning Time h	Time Elapsed
004	1325	1330	5 min.
006	1335	1342	6 min.
007	before 0858	1030	92 min.
	1036	1050	14 min.
014	1250	1345	55 min.
019	1158	1220	22 min.

Time intervals are from when the female left the nest to when she returned with prey.

Table 5. Number of prey per nest.

Date	Number of nests	Number of prey
20:VII:76	1	4
16:VII:77	2	11
25:VII:77	5	24
5:VIII:77	5	27
	13 nests	66 prey records

Calculations are based on nests dug after 1800 h when no further hunting was expected. The average number of prey per nest is 5.1 individuals.

Rates of provisioning were variable (Table 4). One wasp (#004) returned in five minutes with prey; another wasp completed the task in 55 minutes. Females captured about five prey for each cell provisioned (Table 5).

On August 4 I observed a female *P. albopilosus* attack and capture prey. A beewolf cruising about 50 to 60 cm above the sand near a colony of *Microbembex monodonta* (Say) wasps, dived to the ground, attacked and captured one of the *Microbembex*. The latter individual was either flying near or resting on the sand. I did not see it until the beewolf made contact. Females of *Microbembex monodonta* nested along the edges of the sand dune.

Throughout the 1977 field season, neither sex of *P. albopilosus* was observed at flowers. If female *P. albopilosus* did hunt at flowers, I would expect that number of female bees taken as prey would increase or exceed number of males captured. Females of several species of bees of the correct approximate size to be used as prey were quite common on flowers on or near the dune.

Comparisons with Other Populations of *P. albopilosus*

Evans (1975) reported a prey capture pattern similar to the Empress population of *P. albopilosus* from Albany, New York. Females in the Albany population captured wasps of two families (Sphecidae and Eumenidae) and captured bees of three families (Colletidae, Halictidae and Andrenidae). Prey records of wasps comprised 17.3% of the total catch, and of male Apocrita, 79.1%

Prey data for the Colorado population of *P. albopilosus* are different. Number of species and families of Hymenoptera decline, for 73 prey records include only four species of two families of bees (Halictidae and Colletidae). A single nest of *P. albopilosus* in Tuba City, Arizona contained one halictid and four anthrophorid bees (Evans and Lin 1959). Because few populations were examined, difference may be due in part to sampling error.

Many authors (Armitage 1965, Evans 1966b, 1970, Reinhard 1924, Tinbergen 1935, and others) have reported female *Philanthus* hunting at flowers. Pinned specimens of *P. albopilosus* from several localities bear flower capture data. These are as follows: Colorado, on *Tamarix*; Arizona, on *Poliomintha* and on *Parvella*. There are no data for capture at flowers for any northern localities.

DISCUSSION

Selection of prey. – Data presented show that prey selected by females of *P. albopilosus* at Empress is typical for philanthines. A mixture of bees and wasps is taken, and this is consistent with Evans' (1975) observations of a colony of *P. albopilosus* in New York. However, information of this sort is only the first step toward understanding the general phenomenon of prey selection for this species.

In an organism specializing on a particular group of prey species, many factors influence choice. Physical constraints of the predatory apparatus and behavioural restraints control which type of prey are suitable. Behavioural restraints may also regulate where the organism hunts, type of prey, and quality of prey acceptable (Armitage 1965, Alcock 1974, Tinbergen 1935). Availability of suitable prey and its relative abundance will affect what is caught by the predator.

Certain parameters may be useful in predicting whether or not a particular species of bee or wasp will be exploited. Evans (1970) used length of prey, and despite some disadvantages I use also body length to estimate prey acceptability. Adult apocritans whose minimum body length is 5 mm and maximum length is 11 mm for stout forms and 20 mm for slender forms, are regarded as potential prey.

Prey selected by female *P. albopilosus* on the Empress dunes consists of mostly bees and sphecid wasps (Table 6). Table 6 lists apocritan species found in the study area whose adults are of a suitable size to serve as prey for females of *P. albopilosus*. As an indicator of where females of *P. albopilosus* hunt, notes are included about locations and relative abundance of potential prey.

Proportions of bees and wasps differed between prey used (Table 6) and potential prey (Table 7) ($X^2=3.84$, $p>0.05$). Females specialized on a few common species occurring near dune margins. Surprisingly, dune dwellers are underrepresented among prey used. There is also heavy bias toward males of the dominant species of prey. Males of many species of bees and wasps frequent flowers or positions near flowers while seeking potential mates.

Hunting females flew swiftly from the nesting area into vegetation surrounding the dune, where they were quickly lost from sight. In view of the prey captured, I think that two different methods of hunting are employed. The first is to attack and capture any apocritan seen, of appropriate size. This would produce a wide spectrum of prey and would not be biased toward a particular species or sex. A number of apocritans not commonly encountered in large number would be used. A second method of prey capture may be to attack and capture male bees or wasps that trail the female beewolf, as a potential mate. Male bees and wasps which are much larger or smaller than females of *P. albopilosus* may detect the error at greater distance; those whose females are of similar size and colour would likely continue pursuit and may possibly grapple with the beewolf. The three species of prey captured in the greatest number were males of *Aphilanthops frigidus* (F. Smith) *Colletes* sp. and *Halictus rubicundus* Christ.. Females of the three prey species approximate the size and appearance of female *P. albopilosus*. Neither the *A. frigidus* wasps nor the *Colletes* sp. and *H. rubicundus* bees were very abundant around the dunes.

Prey selected by female *P. albopilosus* (Empress dunes) is consistent with data from a population examined by Evans (1975) at Albany, New York, but is inconsistent with data from the population examined by him at Roggen, Colorado. This may suggest a genetic basis, which is behaviourally manifested in either, 1) site of prey capture, or, 2) acceptability of potential prey after contact has been made: or, 3) prey selection is the result of opportunism.

Table 6. Prey records for wasps of *Philanthus albopilosus* Empress study site.

	♂	♀
Ichneumonidae		
genus species	1	0
Eumenidae		
<i>Stenodynerus anormis</i> (Say)	0	1
Sphecidae		
<i>Aphilanthops frigidus</i> (F. Smith)	0	17
<i>Crabro denningi</i> R. Bohart	0	1
<i>Diodontus</i> sp.	1	3
<i>Mellinus abdominalis</i> Cresson	0	1
<i>Microbembex Monodonta</i> (Say)	1	1
<i>Podalonia violaceipennis</i> (Lep.)	0	1
<i>Tachysphex tarsatus</i> (Say)	1	0
<i>Tachysphex exsectus</i> W. Fox	0	1
10 species of wasps; 30 prey records		
Halictidae		
<i>Agapostemon</i> sp.	0	1
<i>Halictus rubicundus</i> Christ	0	23
<i>Halictus</i> sp.	1	0
<i>Lasioglossum</i> sp.	0	2
<i>Sphecodes</i> sp.	0	3
Colletidae		
<i>Colletes</i> sp.	0	19
Megachilidae		
<i>Osmia</i> sp.	1	0
7 species of bees; 50 prey records		
total prey records for each sex	6	74

Change in prey selected, may have occurred as a result of populations of *P. albopilosus* becoming isolated in different refugia during the Wisconsin glaciation. In a northern refugium (i.e. Nebraska Sand Hills, see below) changes in faunal composition coincident with changing climate may have led to a shift in prey selection. Decreasing abundance and number of suitable species of bees, may have selected populations of *P. albopilosus* that used increasing proportions of wasps. Selection of sphecids over other groups of wasps may be in part, due to prevalence of dune nesting species with similar environmental tolerances, relative abundance around dunes and a suitable body size.

False burrows. – A false burrow or accessory burrow is defined by Evans (1964b) as “any burrow started from the soil surface in close proximity to the true burrow and made by the same individual”. Evans suggests that these burrows serve to dupe nest parasites into ovipositing in an inappropriate place or to divert parasites into exploring empty holes where there are no hosts. Wasps which maintain or repair false burrows dig them early in the history

Table 7. Some taxa of Hymenoptera collected in the Empress area which are available as potential prey* to the beewolf *Philanthus albopilosus*.

Taxa	Abundance	Association	Specimens collected	
			♂	♀
Sphecidae				
<i>Ammophilla</i> spp.	a	nest on dune	35	14
# <i>Aphilanthos frigidus</i> (Smith)	c	on dune, scurf pea	2	4
<i>Astata</i> sp.	nc	on dune	–	2
<i>Cerceria echo</i> Mickel	nc		2	–
# <i>Crabro denningi</i> R. Bohart	a	on dune	?	9
<i>Crabro</i> spp.	a	on dune, scurf pea	12	–
<i>crabronids</i> , other	nc		1	–
# <i>Diodontus</i> sp.	nc	on dune	–	2
<i>Gorytes</i> sp.	nc		1	1
# <i>Mellinus abdominalis</i> Cresson	a	sweeping, on dune	–	7
# <i>Microbembex monodonta</i> (Say)	a	on dune in colonies	20+	10+
<i>Oxybelus</i> sp.	nc	on dune	1	2
# <i>Podalonia violaceipennis</i> (Lep.)	c	nest on dune	1	5
<i>Podalonia</i> spp.	a	nest on dune	10+	20+
<i>Psenulus</i> sp.	nc	on dune	–	1
# <i>Tachysphex tarsatus</i> (Say)	a	on dune	9	12
# <i>Tachysphex</i> spp.	a	on dune	3	5
<i>Tachytes</i> sp.	nc		–	1

(continued on next page)

Table 7 (continued)

Taxa	Abundance	Association	Specimens collected	
			♂	♀
Eumenidae				
<i>Cephalodynerus</i> sp. 1	c	on dune scurf pea	1	5
<i>Cephalodynerus</i> sp. 2	nc	on dune	-	1
# <i>Stenodynerus</i> sp.	nc		-	1
Halictidae				
# <i>Agapostemon</i> sp.	a	on dune sweeping, scurf pea	6	4
# <i>Halictus rubicundus</i> Christ	nc	on dune	1	-
# <i>Halictus</i> spp.	nc	on dune, on plants	2	1
# <i>Lasioglossum</i> sp.	nc	sweeping	-	1
# <i>Sphecodes</i> sp. 1	a	on dune, goldenrod	4	2
<i>Sphecodes</i> sp. 2	nc	on dune	1	-
Colletidae				
# <i>Colletes</i> sp.	a	sweeping	-	1
Andrenidae				
<i>Perdita</i> sp.	nc	sweeping	-	1

(continued on next page)

Table 7 (continued)

Taxa	Abundance	Association	Specimens collected	
			♂	♀
Anthrophoridae				
<i>Nomada vicina</i> Cresson	a	on dune	5	—
Megachilidae				
<i>Anthidium</i> sp.	a	on scurf pea	5	—
<i>Megachile</i> sp.	c	sweeping, scurf pea	3	—
# <i>Osmia</i> sp.	nc	on dune	2	—
Mutillidae				
<i>Dasymutilla bioculata</i> (Cresson)	a	on dune	20+	10+
Ichneumonidae				
<i>many species</i>	—	in vegetated areas	5	2

*This list is a sample of potential prey defined Apocrita Hymenoptera from 5 to 11mm if heavy bodied or a maximum of 20 mm if slender bodied and active during the months of June, July and August. This list is a guide and many species and genera have been overlooked because of sampling procedures. I assume that those missed do not compromise a large portion of the potential spectrum of prey species. Symbols used: a. abundant; c. common; nc. not common; # taxa used as prey but excluding prey records.

Table 8. Occurrence of accessory burrows in the Sphecidae

Taxon	Number of false burrows	Type of false burrow	Duration of false burrow	Type of provisioning	Care of false burrows	First occurrence of false burrow	notes	Investigation
<i>Philanthus albopilosus</i>								
Cresson	0-6	lt	sh	ma	nm	er	-	Evans 1975
<i>P. lepidus</i> Cresson	1-5	lt	lo	ma	mt	er	-	Evans 1964a
<i>P. cornatus</i> Fabricius	1	-	-	ma	-	-	-	Tsuneki 1943
<i>Sphex argentatus</i>								
Mocsary	2-3	lt	lo	-	mt	er	-	Tsuneki 1963
<i>Stinus pulcherrimus</i>								
Smith	2-4	lt	lo	-	mt	er	-	Tsuneki 1943
<i>Bembix sayi</i> Cresson	2	bh	sh	pr	nm	la	-	Evans 1964b,1966a
<i>B. texana</i> Cresson	0-2	lt	sh	pr	nm	cr	cc	Evans 1964b,1966a
<i>B. troglodytes</i> Handlirsch	0-1	lt	sh	pr	-	-	-	Evans 1964b,1966a
<i>B. pruinosa</i> Fox	1	lt	-	-	-	-	-	Evans 1964b,1966a
<i>B. amoena</i> Handlirsch	0-1	fu	-	pr	-	at	fc	Evans 1964b,1966a
<i>B. niponica</i> Smith	?	ho	-	pr	-	-	fc	Tsuneki 1956

Symbols used: at- any time; bh- back hole; cc- cell cleaning; er- early; fc- fill for closure; fu- furrow; ho- hole; la- late; lo- long; lt- lateral; ma- mass; mt- maintained; nt- not maintained; pr- progressive; sh- short.

of the nest, usually during or after initial closure. The habit is thought to have evolved from quarrying soil for a closure of the nest. Maintaining false burrows would simply entail use of one or a few of the holes as a source of soil for later closures. Maintenance of false burrows may provide continued protection from nest parasites. Females of *P. albopilosus* construct accessory burrows after completion of the nest.

Associated with species which dig false burrows early, but do not maintain them, are various behavioural features which may reduce the effect of nest parasitism (Table 8). Females of *Bembix* provision their nests progressively. If parasites enter the nest the female may be able to supply enough prey, permitting survival of both larvae and parasites. This tactic may remove some of the selective advantage of maintaining false burrows.

Females of one species, *B. texana* Cresson, construct false burrows during final closure. Debris is removed from the nest and parasites may be swept out during this process. False burrows prepared at this time may offer protection from invasion by parasites, at least until environmental effects obliterate all traces of the burrow.

Construction and failure to maintain false burrows in a mass-provisioning species such as *P. albopilosus* is unexpected. The association of provisioning and nesting behaviours has changed, I propose that false burrows made by *P. albopilosus* serve as visual markers aiding in initial orientation to the nest in a habitat with an unstable substrate. A large premium would be placed on learning the correct location of the nest without advertising its true entrance during the first orientation flight. This would permit the female to take bearings on distant land marks and visually relate the location of her nest (van Iersel 1964). After orientation, false burrows would no longer have a function, and so they would not be maintained. A similar land mark function has been attributed to the mound building activities of *Bembix littoralis* Turner. Evans and Matthews (1975) reported *B. littoralis* females building a mound of soil at the entrance of their burrow, which may serve as a species specific marker identifying the nest location when other species of sand wasps were present.

GEOGRAPHICAL DISTRIBUTION AND VARIATION

Known Range and Locality Data,

Philanthus albopilosus is almost transcontinental in distribution with the most eastern known locality at Albany, New York (Evans 1975) and the western most at Hatton, Washington. The most northern locality is 175 km north of Empress at Rutland, Saskatchewan. It is doubtful that the range extends much further north. The southern known extreme is on Padre Island, Texas, but the range probably extends into central Mexico.

Localities of material studied are listed below. Numbers following locality names indicate the number of females examined followed by the number of males examined. Acronyms represent collections from which the material was borrowed.

Material examined:

CANADA. Alberta: Empress (11 km south), 31, 8 (GH); Medicine Hat, 6, 14, (CNC, UAS); Orion, 0, 2, (UAS). Manitoba: Aweme, 2, 8, (CNC, UCD); Harteny 0, 1, (SEM); Onah, 3, 0, (CNC). Saskatchewan: (see Empress, Alberta) Elbow, 5, 6, (CNC, UCD); Rutland, 3, 8, (CNC, UCD).

MEXICO. Chihuahua: Samalyuca, 0, 1, (UCD).

UNITED STATES. Arizona: Coconino County: Tuba City, 1, 0, (CUM); Navajo County: Hotenvilla, 1, 1, (UCD); Indian Wells (16 miles south), 1, 0, (UCD); Judito Trading Post, 1, 2, (UCD); Joseph City, 0, 1, (UCB); Kayenta (19 miles southwest), 2, 0, (CAS); Colorado: Alamosa County: Great Sand Dunes National Monument, 0, 2, (CSU); Bent County: Caddoa (9 km east), 3, 16, (GH); Hasty, 1, 1, (CSU); Prowers County: Carlton, 1, 3, (CSU); Lamar (10 miles west), 0, 2, (CSU); Weld County: Roggen, 10, 1, (CSU, GH). Idaho (Strandtmann 1946). Iowa: Woodbury County: Sergeant Bluff, 1, 1, (USNM); Sioux City, 0, 1, (USNM). Illinois: Cook County: Chicago, 2, 5, (MCZ). Kansas: Kearny

County: McKinney Lake, 0, 1, (MCZ); Stafford County: Salt Flats, 2, 4, (CUM, CNC, MCZ). Minnesota: Polk County: Muskoda, 0, 1, (CUM). Montana: 0, 2. Nebraska: Cumming County: West Point, 1, 2, (USNM). New Mexico: Dona Ana County: Las Cruces, 0, 2, (CAS, SEM); Otero County: White Sands National Monument, 0, 5, (MCZ, UCD); San Juan County: Shiprock (near), 0, 1, (USNM); Socorro County: La Joya Wild Life Preserve, 8, 14, (CSU, MCZ, GH). New York: Albany County: Albany (Evans 1975); Colonie 3, 0, (CSU). North Dakota: Billings County: Medora, 0, 1, (MCZ); Ransom County: McLeod, 1, 1, (UCB), Sheldon, 2, 1, (CUM, MCZ); Richland County: Walcott (11 miles west), 1, 0, (UCD); Williams County: Williston, 1, 2, (MCZ). Ohio (Strandtmann 1946). South Dakota: Fall River County: Hotsprings, 1, 0, (MCZ). Texas: El Paso County: Fabens, 0, 2, (CAS, SEM); Hartley County: Romero, 2, 4, (SEM, UCD); Nueces County: Padre Island, 0, 1, (UCD); Ward County: Monahans State Park, 10, 22, (CSU, MCZ). Utah: Juab County: Eureka, 0, 1, (UCB); Little Sahara Recreation Area, 5, 19, (GH); Utah County: Utah Lake, 0, 1, (CUM); Millard County: Oak City (18 km north), 0, 1, (GH). Washington: Adams County: Hatton, 0, 1, (USNM).

In total 234 specimens were examined, 100 females and 134 males. Positions of localities are mapped in Figure 3. Dotted lines define groups of populations which were united and treated as a single population to increase sample sizes for statistical purposes. Populations were grouped naturally using existing geographical barriers as boundaries.

Most localities are in semi-arid to arid regions of the Great Plains with clusters in desert regions. A range extension appears to follow the arid interior into the Great Basin. Three eastern localities - Chicago, Illinois; Ohio and Albany, New York - are disjunctive. Beewolves are not found in regions where annual precipitation exceeds 91.5 cm (36 inches). Moisture may affect presence or absence of suitable habitats rather than having a direct influence on the species. Activities by man permit colonization of disturbed sites such as sand and gravel pits and road cuts.

Geographical Variation in Colour Pattern

Interpretation of species limits for many *Philanthus* wasps is based on maculation and punctuation patterns in adults. Several closely related species of *Philanthus* were once thought to be subspecies of *P. politus*. Recognition was in part based on coloration of tibiae, femora, and punctuation and shape of metanotal lamina. In *P. zebratus nitens* (Banks) several forms once recognized as distinct species have been united and given subspecies status. Diagnostic characters were maculations and punctures. In this paper specimens of *P. albopilosus* are placed in recognizable groups based on colour patterns.

Results of analysis with a compound character index are shown in Figure 4 for females and in Figure 5 for males. To give some perspective to the index values used, Figure 6 a, b and d illustrate some aspects of a dark northern female. The total compound character index value for the specimen is zero. Figure 7 a, b and d illustrate a southern female which has a total compound character index value of 93. Figure 8 illustrates the typical frontal maculation of the head and an abdomen of a northern male. This male received a total index value of four.

Figure 4 illustrates variation in maculation patterns in females. In the north (Areas 7, 8, 9, 10, 11 and 12) index values are concentrated toward the low range, indicating populations comprised of dark individuals. Most of the specimens received index values below 30. A few maculate specimens (Figure 7c) were present but index values did not exceed 70 units.

Females from more southern localities (Areas 4, 5 and 6) had extreme expansion of the yellow markings and few specimens were assigned index values less than 70. No populations are known to have intermediate index values.

Females from mountain regions of the southern United States (Areas 1, 2 and 3) are intermediate in coloration, with index values between 30 and 70. These groups are the most geographically distant populations from those in the northern areas.

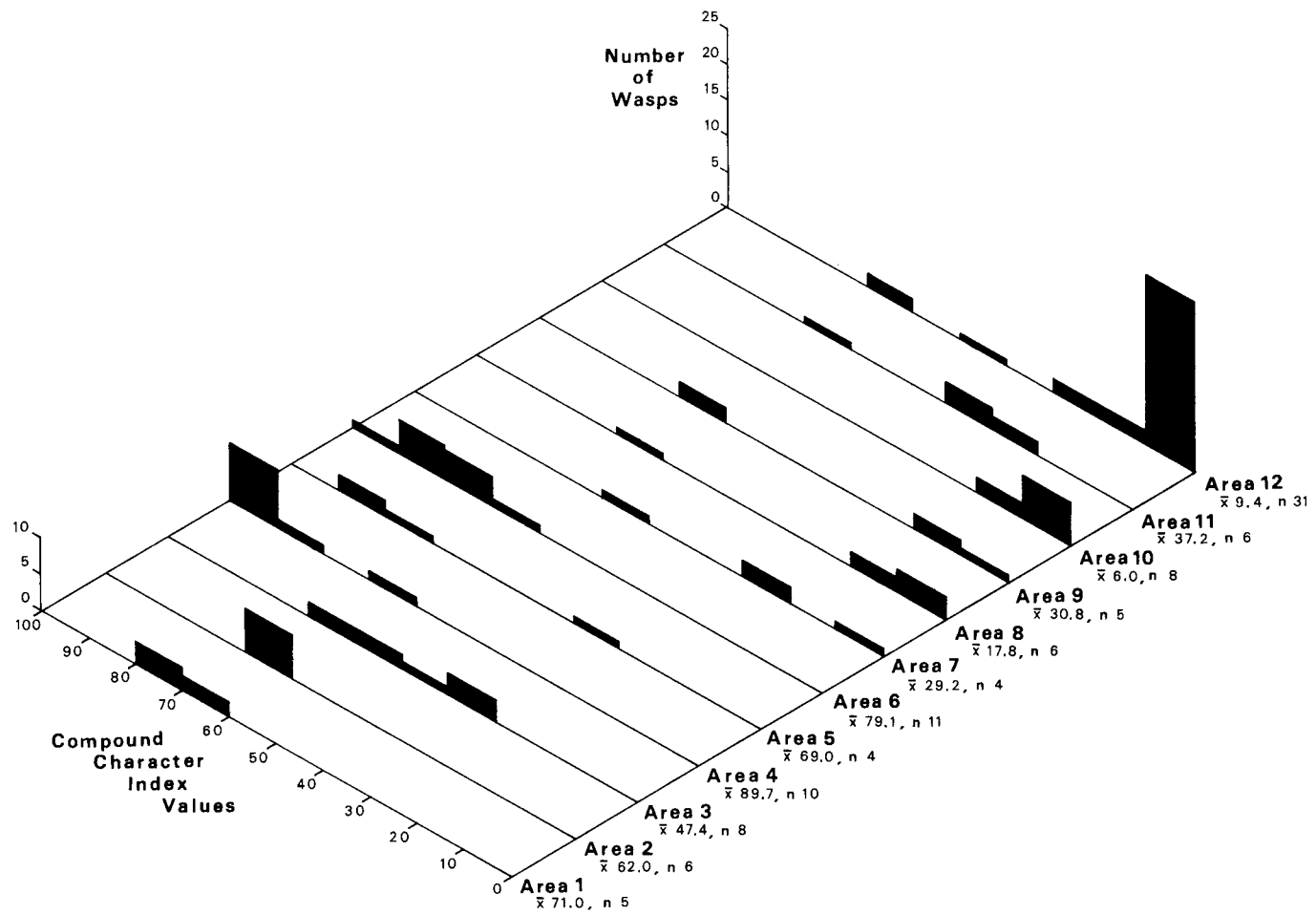


Figure 4. Compound character index values for females of *Philanthus albopilosus*. Area numbers refer to those illustrated in Figure 3.

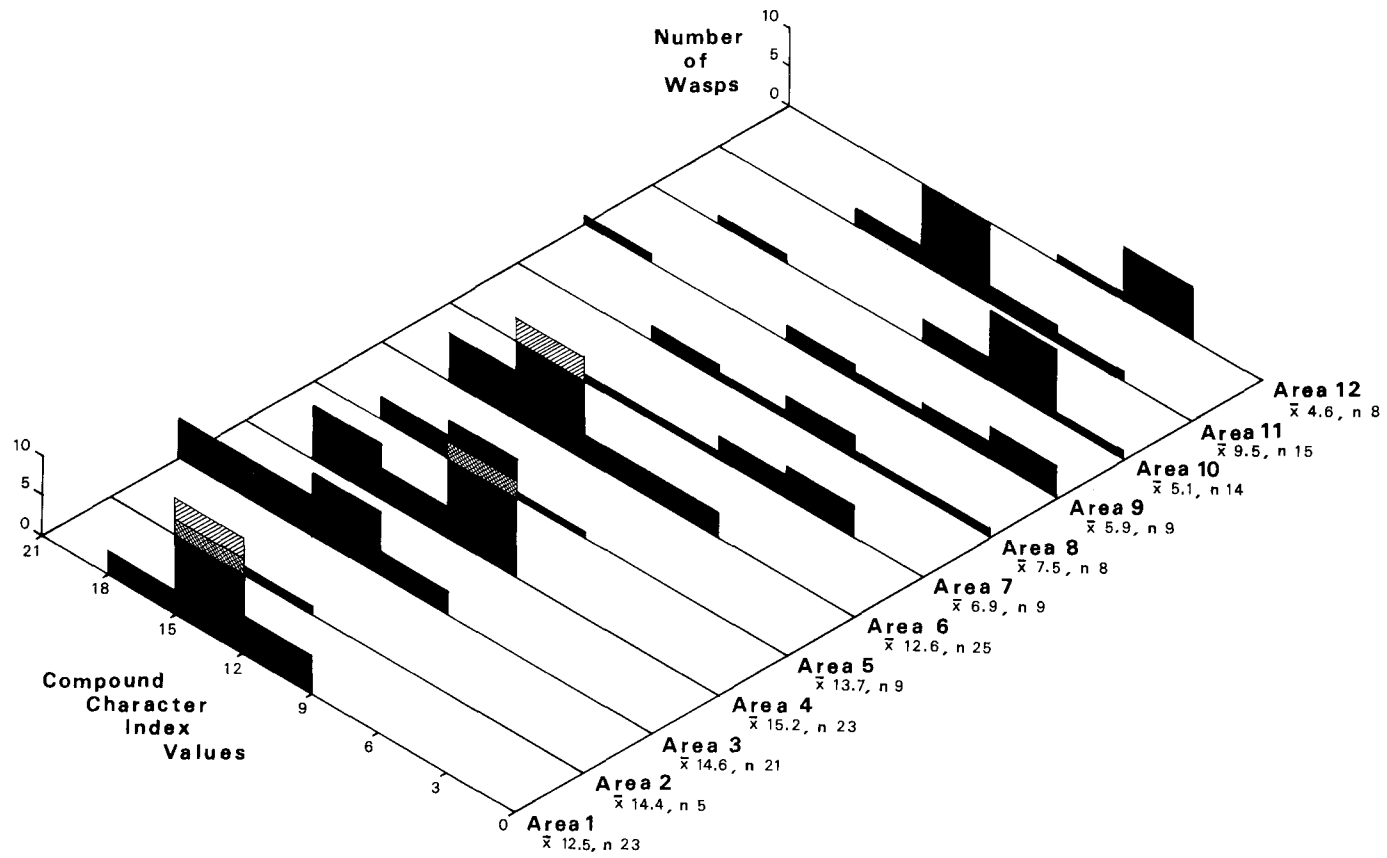


Figure 5. Compound character index values for males of *Philanthus albopilosus*. Area numbers refer to those illustrated in Figure 3.

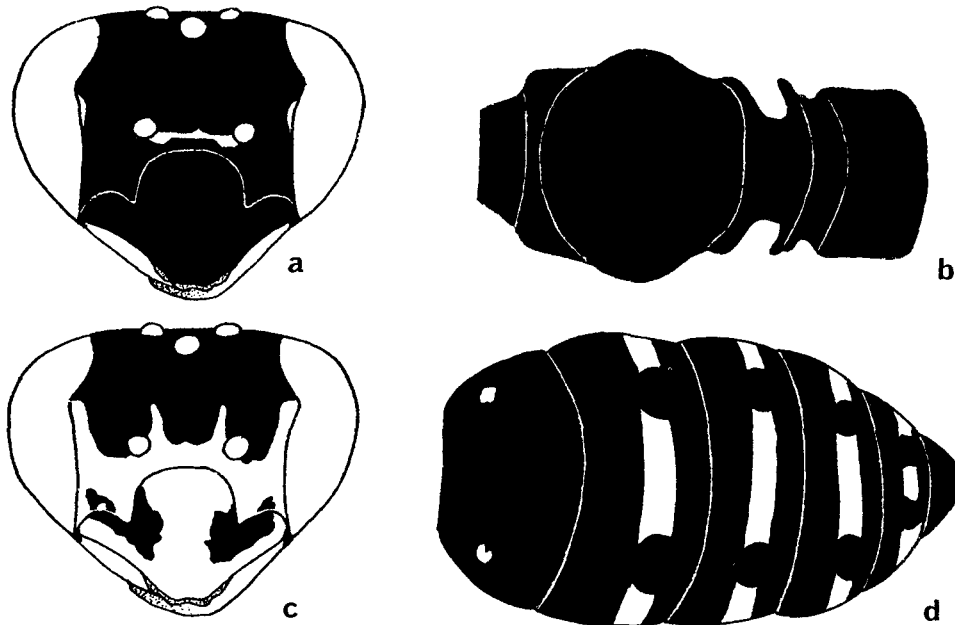


Figure 6. Typical and maculated specimens of female *Philanthus albopilosus* (northern race). Figures 6a, 6b, and 6d, head, thorax and abdomen of a dark specimen from Empress, Alberta. Figure 6c, head of maculate specimen of the dark race at Medicine Hat, Alberta.

Males of *P. albopilosus* also exhibit some trends in colouration (Figure 5) but these are not as distinctive. Individuals from northern populations (Areas 7 to 12) tended to be darker (Figure 8). Males from southern and western areas (Areas 1 to 6) tended to be pale. There is not a discrete break in index values but a trend to shift to darker forms in the northeast and lighter forms in the southwest.

Index values for each area were averaged, female index values were plotted against male index values (Figure 9). The points form loose clusters: northern groups separate together, in contrast to southwestern populations and geographically intermediate populations. The points illustrate a break in variation, with the largest break occurring between the geographically intermediate group and the northern group. The phenotypically intermediate groups are the extreme southwestern populations which may grade into the geographically intermediate group.

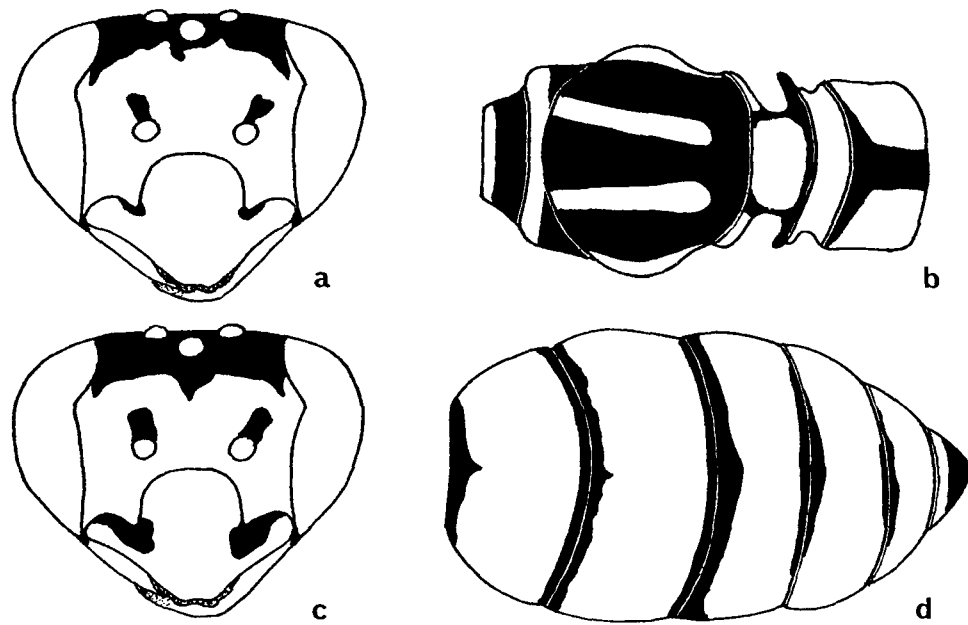


Figure 7. Typical specimens of females of the light race *Philanthus albopilosus manuelito*. Figures 7a, 7b, and 7d head, thorax and abdomen of specimen from Monahans, Texas. Figure 7c, head of specimen from Roggen, Colorado.

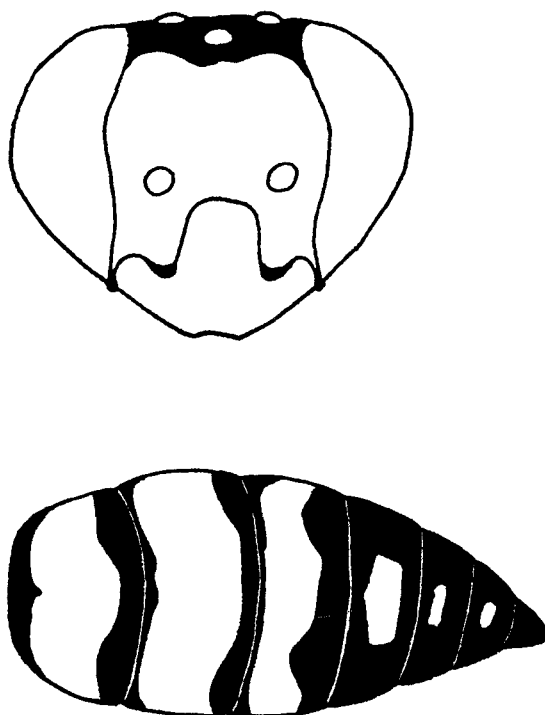


Figure 8. Head and abdomen of male *Philanthus albopilosus* wasp from Empress, Alberta showing typical maculation pattern for most males.

Taxonomic Interpretation

The beewolf species *P. albopilosus* includes two major groups of populations. Populations of the dark form appear to form a cohesive geographic unit across the northern United States and southern Canada (Areas 7, 8, 9, 10, 11 and 12). Slight differences among northern populations may be due in part to “ founder effect ” (MacArthur and Wilson 1967), associated with invasion of new areas by few individuals. Physiographic barriers are not evident. However sand dune habitats are islands in a sea of grassland or forest, unsuitable for *P. albopilosus*. Therefore, these latter habitats serve as barriers.

The southern light form is a slightly less coherent grouping. In Areas 2 and 3, an intermediate colour form is present, which is partly isolated by mountain divide systems from populations of the extreme yellow form found in Areas 4, 5 and 6.

It appears that there has been a break in gene flow between northern populations and southern populations (Figure 9) for an extended period of time (probably since the Wisconsin glaciation). At present, gene flow is interrupted between some populations in the southern race by physiographic barriers. On the Great Plains gene flow appears restricted between northern areas (7 and 8) and southern areas (5 and 6). No populations of intermediate coloration were found between these areas, even though *P. albopilosus* is highly vagile and should have dispersed, forming intermediate populations. This pattern suggests character displacement.

Character displacement occurs between ecologically similar sibling species, many pairs of which exhibit narrowly parapatric distribution. Lack of a physiographic boundary separating species indicates contact has recently occurred (Vuilleumier 1971). Taxonomists often

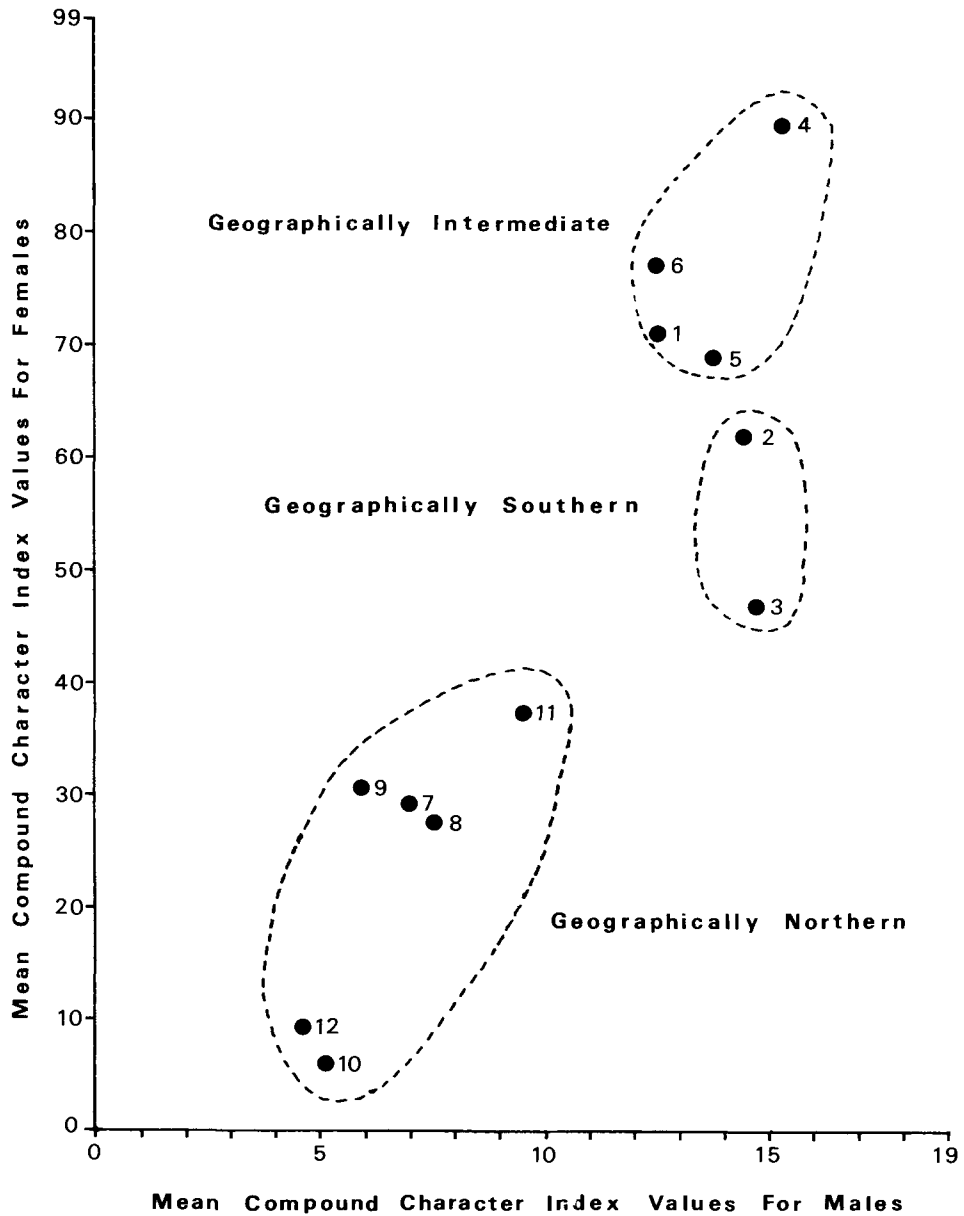


Figure 9. Compound character index value comparisons of means for colour variation in wasps of *Philanthus albopilosus*. Numbers refer to areas illustrated in Figure 3.

experience difficulty deciding between displacement and hybridization (Brown and Wilson 1956). Races of *P. albopilosus* might be specifically distinct, and thus cryptic species.

The premise that the races have come into recent contact implies a barrier at some phase in the species history. Populations in Area 4 may be relatively recently derived from yellow populations further to the north which are in contact with the northern race. Origin from Areas 1, 2 or 3 is less likely because of mountain divide systems. A north-south movement on the

Great Plains is more probable because of relative lack of geographic barriers.

The major isolating event separating the northern from the southern race was probably the Wisconsin glacialiation. Isolation of the lineages may have occurred late in the Sangamon interglacial stage. This would place the dichotomy at about 60,000+ years B.P. Whitehead (1972) suggested that speciation occurs at a rate of about one dichotomy per 3,000,000 years. On the basis of this hypothesis, races of *P. albopilosus* may not have been isolated long enough, to have evolved into separate species.

Regardless of what actually happened in the past, populations of *P. albopilosus* may be grouped into definable races on the basis of phenotypic variation and these groups are restricted to geographic regions. For a few populations additional evidence is supplied by variation in aspects of life history and behaviour.

Subspecies of *Philanthus albopilosus*

In a species divided into various populations which are more or less isolated over time, when do the variants warrant taxonomic recognition? Many authors have considered the subspecies concept and each has a slightly different idea of what the limits should be; some are for recognition, others are against. I prefer the argument given by Willis (1976)“ . . . if subspecies reflect to some degree the actual pattern of variation, as well as being convenient ‘handles’ for reference, their value seems sufficient to justify their recognition”.

In philanthines, character differences in head shape, punctation, placement of ocellus and most importantly maculation patterns, provide useful tools for species recognition. In members of *Philanthus albopilosus* two major groups can be recognized. In certain regions, some specimens feature character states not characteristic of the population mean. Most female specimens (95%) and the majority of males can be assigned to one subspecies group or the other consistently on the basis of maculation patterns.

***Philanthus albopilosus albopilosus* Cresson** *Philanthus albopilosus*, Proc. Ent. Soc. Phila., 5, 91, 1865 (♂). *P. simillimus* Cresson, Proc. Ent. Soc. Phila., 5, 95, 1865 (♀). For a complete synonymy see Strandtmann 1946.

Female. – Length 10 to 13 mm. Black, marked with yellow as follows: clypeus 0 to 50% yellow, frons 0 to 40% yellow (Fig. 7a,c), vertex at most five yellow spots, antennae scape black above yellow below, pedicel black, flagellum black above infuscated below, thorax black to black with maculations (Fig. 6b), coxae black or black with apical spot, femora black apices yellow, tibiae yellow with black spot, tarsi pale to testaceous, sterna black may have lateral spots, tergum 1 with two lateral spots, terga 2 and 3 with biemarginate band, tergum 4 with broken band, tergum 5 with three spots, pygidium black.

Male. – Length 7 to 11 mm. (Fig. 8). Yellow, frons yellow, vertex black, scape black above, pedicel black, flagellum with basal three yellow ventrally dorsally black infuscated toward tip, thorax black, pubescence white, apices of femora yellow, tibiae yellow, tarsi infuscated propodeum black, abdominal sterna black, terga 1,2, and 3 with yellow band, terga 4, 5, and 6 with elongate yellow spot; tergum 7 with or without elongate yellow spot.

Type locality. – Illinois.

Range. – CANADA: Alberta, Manitoba, Saskatchewan.

UNITED STATES: Illinois, Iowa, Montana, Nebraska, New York, North Dakota, Ohio, South Dakota.

***Philanthus albopilosus manuelito* new subspecies**

Female. – Length 10 to 13 mm. Yellow, marked with black, clypeus yellow, frons 10 to 20% black near vertex (Fig. 7a, c), vertex with five yellow spots or solid yellow band, antennae as in *Philanthus albopilosus albopilosus*, collar yellow, mesonotum with two longitudinal yellow bands, scutum yellow, scutellum yellow, propleuron large lateral yellow spots (Fig. 7b), apices of coxae yellow, femora 30 to 50% yellow abdominal sterna with lateral spots, with or without medial spots, terga yellow with black along apical and basal margins (Fig. 7d).

Male. – Length 8 to 11 mm. Similar to *Philanthus albopilosus albopilosus*, most specimens with additional maculations on scutellum, collar and tubercle of thorax and with or without additional spot on tergum 7.

Type material. – Holotype; UNITED STATES: Texas, Ward County, Manahans State Park, 1-2 vi 1974, H. Evans and W. Rubink (female) [USNM]. Paratypes; 9 females, 22 males with same data.

Range. – MEXICO: Chihuahua

UNITED STATES: Arizona, Colorado, Idaho, Kansas, New Mexico, Texas, Utah.

Derivation of specific epithet. – Manuelito was a Navaho chief, who with the aid of other chiefs, persuaded the United States government in 1868 to let the Navaho return to their home lands. The bee wolf *Philanthus albopilosus manuelito* nests on reservation land.

EVOLUTIONARY CONSIDERATIONS

Evolution of the Geographic Pattern

The occurrence of geographical races of *P. albopilosus* Cresson indicates fragmentation of the ancestral range of the species, and hence, isolation of populations. At least two major refugia seem to be indicated, one in northeastern Nebraska, and the other in southwestern Arizona-New Mexico. Each region contained unique biotic and abiotic features. Divergence in structure and behaviour are related to historical events which might have been causative.

Because of similarities between subspecies, they are of relatively recent origin. The Sangamon interglacial stage between Illinoian and Wisconsinan glaciations may serve as a reference point. Flint (1971) argued that conditions during the Sangamon probably ranged from arid in the southwest to cool and moist in the east. Thus climate and plant biomes may have been comparable with today's. Dune habitats would have been present in many areas where they are currently found. During the early part of the Sangamon interglacial stage, populations of *P. albopilosus* Cresson were probably widespread (Figure 10a).

Toward the end of the Sangamon interglacial (about 70,000 B.P.) the climate began to cool eventually giving rise to the Wisconsinan glaciation (from 55,000 to 10,000 B.P.). Cool wet conditions induced reforestation of much of the Great Plains, and of the northern Great Basin and Mohave Desert (Martin and Mehringer 1965). Increased moisture also caused reduction of sand dunes as ground cover increased, with consequent widespread extinction of and disruption of range of *P. albopilosus* Cresson. During this isolation, morphological and ecological differentiation occurred.

In large dune fields, however, porosity of the sand would locally induce aridity and thus blowouts may have developed. Thus populations of *P. albopilosus* Cresson (s.l.) in the large dune fields may have survived (Figure 10b).

Toward the end of the Wisconsinan glacial stage, climate ameliorated, lifezones move north and up mountain slopes. Many stabilized dunes would have become active by loss of their plant

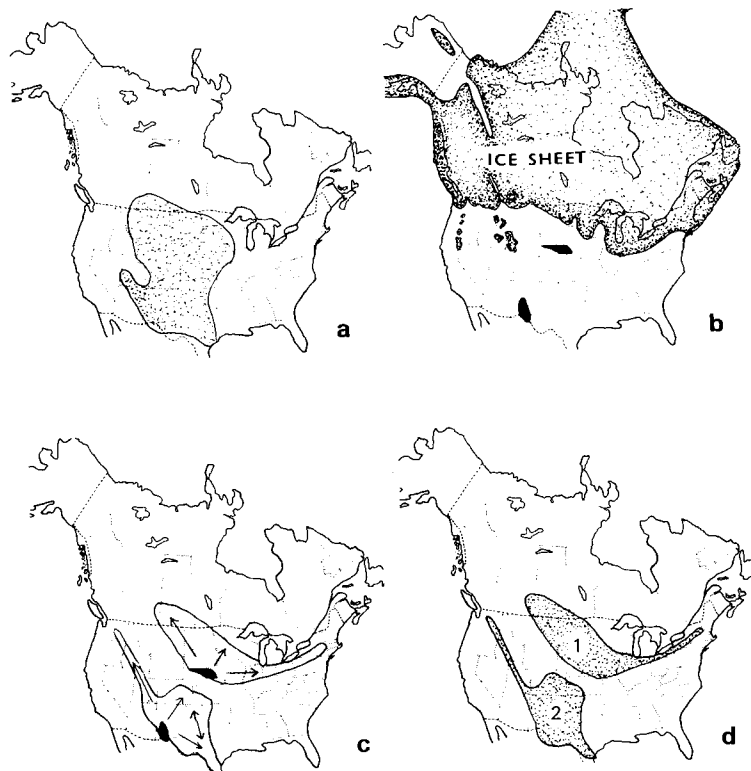


Figure 10. Distribution patterns of *Philanthus albopilosus* through time. a) 70,000 B.P. hypothetical range of ancestral stock. b) Ca. 17,000 B.P. geographic isolation of ancestral stock at the zenith of the Wisconsinan, c) Ca. 7,000 B.P. expansion of ranges from refugium. d) recent distribution of (1) *Philanthus albopilosus albopilosus* (dark race) and *P. a. manuelito* (pale race).

cover and being subject to wind erosion. Maximal rates of range extension may have occurred during the Hypsithermal due to increased dune and blowout development.

In the southwestern United States, arid regions may have persisted during Wisconsinan glaciation, permitting dune fields to remain active. Sonoran Desert floras were derived relatively recently (Axelrod, 1979). The great diversity is due to a 'vacuum' effect, floristic elements from surrounding zones which adapted to increasing aridity and temperature, provide the bulk of taxa. A rise in rainfall of 250 to 300 mm would eliminate the Sonoran Desert as a regional lowland. This would allow an oak-conifer association to cover much of the lowland. Axelrod's data suggest that taxa survived on the driest sites in bordering zones.

A portion of the American southwest is proposed as a refugium for the southern subspecies, *P. albopilosus manuelito*. Very few sites suitable for a northern refugium are available east of the Mississippi River (Thorp *et al.*, 1952). Most of eastern North America was cloaked in a continuous forest (Ross 1970, Martin 1958, Freitag 1973, and others). On the Great Plains, several sand dune areas were probably active during portions of the Wisconsinan glaciation. Smith (1965) demonstrated that there were several periods of dune building on the Nebraska Sand Hills, based on past movement of stabilized dunes. This large dune area may have served

as a refugium for sand dwelling organisms which were able to adapt to a cooler climate. Willis (1967) proposed survival of at least five species of tiger beetles (*Cicindela*: Cicindelidae) in the vicinity of the Nebraska Sand Hills.

Following Wisconsin glaciation, many sand dunes developed and older ones became reactivated. Figure 10c illustrates proposed dispersal patterns for *P. albopilosus* Cresson from refugia.

Expansion of *Philanthus albopilosus manuelito* onto the Great Plains should have allowed rapid colonization of most prairie sand dunes. Northward expansion may have been limited by presence of *Philanthus albopilosus albopilosus* acting as a cryptic species, genetically distinct, yet morphologically similar. Rare occurrence of *Philanthus albopilosus manuelito* in the Great basin may be the result of relatively recent post-Pleistocene dispersal.

EVOLUTION OF COLOUR PATTERN AND BEHAVIOURAL FEATURES OF *P. ALBOPILOSUS*

Colour pattern features of *P. albopilosus*

Ancestral *P. albopilosus* were probably similar to *P. a. manuelito*. Extensive yellow contrasted with black, in typical warning maculation pattern, is similar to that seen on other sand dune sphecids (e.g. *Microbembex*, *P. psyche*).

Adaptation to a cooler climate during Wisconsinan glaciation may have been the major evolutionary reason for differentiation by populations in the northern refugium. Females of northern, *P. a. albopilosus* are dark: this may be a functional adaptation for absorbing radiant heat, which may prolong the length of time per day in which they could hunt. Males may not require much darkening, as they could restrict their activities to the hot microenvironment of the sand dune surface.

The very pale form of *P. a. manuelito* of the great plains is somewhat of a puzzle: Character displacement was suggested, but does not adequately explain populations of area 4, unless, there is considerable gene flow between populations on the plains. Mountain barriers would buffer populations in Areas 2 and 3 from influx of extreme pale forms.

Present distribution of *P. a. albopilosus* is the result of post-Pleistocene dispersal into new dune habitats. Eastern and northwestern expansion of range has occurred. Southward expansion may have been blocked by *P. a. manuelito*. There may be enough genetic and behavioural differences reducing the tendency for the two groups to hybridize (cryptic species). A few northern populations contain well marked individuals. This may be the result of reversed selection toward a form with typical warning colouration pattern or they may represent remnants of the ancestral gene pool or limited introgression.

The above discussion is primarily based on variation in the females; trends are present in males but are less marked.

Behavioural features of *P. albopilosus*

Evolutionary adaptations exhibited by *P. albopilosus* are similar to other digger wasps living in sand dune environments. Parallel evolution in development of false burrows originated from nest parasite pressures, which are intense in open environments. Orientation to the nest is difficult for females, as landmarks near the nest may change in an unstable dune environment. Use of distant landmarks is important, but fixation to these requires seeing the nest site while orienting and keeping nest parasites out. False burrows may serve both of these functions.

Short occupancy time of the nest as compared to other species of *Philanthus* may be due to friable soil. Little time is spent digging in comparison to species which dig in hard soils. Few cells per nest would be a function of the ephemeral occupancy coupled with slow provisioning. A relatively long adult life span, nest location in areas devoid of vegetation and anti-parasite nest building behaviours may reduce selection pressures for the production of large numbers of offspring ("k" selection).

Reduction in number of generations per year in northern populations is probably a result of shorter growing seasons either presently or during the species evolutionary history.

Change in prey specificity from the ancestral limits may be a response to reduction in number and species of bees available during Wisconsinan time. Alternate prey species would be incorporated from other groups of Apocrita.

These facets of life history serve to characterize *P. albopilosus* as a whole. This also serves in part, as a start in characterization of the northern fauna of *Philanthus*.

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REFERENCES

- Alberta Environment, 1975. Climate of Alberta, tables of temperature, precipitation and sunshine. 90 pp.
- Alcock, J. 1974. The behaviour of *Philanthus crabroniformis* (Hymenoptera: Sphecidae). *Journal of Zoology*. London 1973: 223-246.
- Armitage, K.B. 1965. Notes on the biology of *Philanthus bicinctus* (Hymenoptera: Sphecidae). *Journal of the Kansas Entomological Society*. 38: 89-100.
- Ashwell, I.Y. 1966. Glacial control of wind and soil erosion in Iceland. *Annals of the Association of American Geographers*. 56:529-540.
- Axelrod, D. I. 1979. Age and origin of Sonoran Desert vegetation. *Occasional Papers of the California Academy of Science* No. 132, 74 pp.
- Bohart, R.M. and E.E. Grisell. 1975. California wasps of the subfamily Philanthinae (Hymenoptera: Sphecidae). *Bulletin of the California Insect Survey*, Vol. 19, 92 pp.
- Bohart, R.M. and A.S. Menke. 1976. Sphecid wasps of the world, a generic revision. University of California Press 695 pp.
- Brown, W.L.jr. and E.O. Wilson. 1956. Character Displacement. *Systematic Zoology*, 5:49-64.

- Bryson, R.A. and W.M. Wendland. 1967. Tentative climatic patterns for some late glacial episodes in Central North America pp. 279-297. In Mayer-Oakes, W.J. (Editor), Life, land and water. University of Manitoba Press, Winnipeg.
- Cazier, M.A. and M.A. Mortenson. 1965. Studies on the bionomics of the sphecoid wasps II. *Philanthus gibbosus* (Fabricius) and *Philanthus anna* Dunning (Hymenoptera: Sphecidae). Bulletin of the Southern California Academy of Sciences 64: 171-206.
- Chadwick, H.W. and P.D. Dalke. 1965. Plant succession on dune sands in Fremont County Idaho. Ecology 46: 765-780.
- Chapman, R.N., C.E. Mickel, J.R. Parker, G.E. Miller, and E.G. Kelly. 1926. Studies in the ecology of sand dune insects. Ecology 7:416-426.
- Coupland, R.T. 1950. Ecology of the mixed prairie in Canada. Ecological Monographs 20: 271-315.
- Danks, H.V. (Ed.) 1979. Canada and its insect fauna. Memoirs of the Entomological Society of Canada. No. 108. 573 pp.
- Dort, W and J.K. Jones (Ed.). 1970. Pleistocene and recent environments of the Central Great Plains. Department of Geology, University of Kansas Special Publication 3, University of Kansas Press.
- Dowding, E.S. 1929. The vegetation of Alberta III. The sand hill areas of central Alberta with particular reference to the ecology of *Arthrobium americanum* Nutt. Journal of Ecology 17: 82-105.
- Edmunds, F.H. 1962. Recession of Wisconsin Glacier from central Saskatchewan. Saskatchewan Department of Mineral Resources, Report No. 67.
- Evans, H.E. 1964a. Notes on the nesting behaviour of *Philanthus lepidus* Cresson (Hymenoptera: Sphecidae). Psyche 71: 142-149.
- Evans, H.E. 1964b. The accessory burrows of digger wasps. Science 152: 465-471.
- Evans, H.E. 1966a. The comparative ethology and evolution of the sand wasps. Cambridge, Harvard University Press pp. 526.
- Evans, H.E. 1966b. Nests and prey of two species of *Philanthus* in Jackson Hole, Wyoming (Hymenoptera: Sphecidae). Great Basin Naturalist 26: 35-40.
- Evans, H.E. 1966c. The behavior of solitary wasps. Annual Review of Entomology 11: 123-154.
- Evans, H.E. 1970. Ecological-behavioural studies of the wasps of Jackson Hole, Wyoming. Bulletin of the Museum of Comparative Zoology 140: 451-511.
- Evans, H.E. 1975. Nesting behavior of *Philanthus albopilosus* with comparisons between two widely separated populations. Annals of the Entomological Society of America 68: 888-892.
- Evans, H.E. and C.S. Lin. 1959. Biological observations on digger wasps of the genus *Philanthus* (Hymenoptera: Sphecidae). Wasmann Journal of Biology 17: 115-132.
- Evans, H.E. and R.W. Matthews. 1973. Systematics and nesting behavior of Australian *Bembix* sand wasps (Hymenoptera, Sphecidae). Memoirs of the American Entomological Institute, No. 20, 387 pp.
- Evans, H.E. and R.W. Matthews. 1975. The sand wasps of Australia. Scientific American 233(6): 108-115.
- Flint, R.F. 1971. Glacial and quaternary geology. J. Wiley and Sons Inc. 892 pp.
- Frenzel, B. 1973. Climatic fluctuations of the Ice Ages. The Press of Western Reserve University, Cleveland and London. 306 pp.

- Freitag, R. 1965. A revision of the North American species of the *Cicindela maritima* group with a study of hybridization between *Cicindela duodecimguttata* and *oregona*. *Quaestiones Entomologicae* 1: 87-107.
- Hulett, G.K., R.T. Coupland and R.L. Dix. 1966. The vegetation of dune sand areas within the grassland region of Saskatchewan. *Canadian Journal of Botany* 44: 1307-1331.
- Iersel, J.J.A. van 1964. Orientation in the digger wasp *Bembix rostrata*. *Animal Behaviour* Supplement 1: 145-162.
- Klassen, R.W. 1972. Wisconsin events and the Assiniboine and Qu'Appelle valley of Manitoba and Saskatchewan. *Canadian Journal of Earth Sciences* 9: 554-560.
- Lorenz, K. 1967. *Evolution and Modification of Behavior*. University of Chicago Press, 121 pp.
- Löve, D. 1959. The postglacial development of the flora of Manitoba: a discussion. *Canadian Journal of Botany* 37: 547-585.
- MacArthur, R.H. and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, 203 pp.
- Martin, P.S. 1958. Pleistocene ecology and biogeography of North America. In Hubbs 1958, p. 375-470.
- Martin, P.S. and P. J. Mehringer. 1965. Pleistocene pollen analysis and biography of the Southwest. In Wright and Frey (Ed.) 1965, p. 433-451.
- Matthews, J.V. 1979. Tertiary and Quaternary Environments. Historical background for an analysis of the Canadian insect fauna. In Danks (Ed.) *Canada and its insect fauna*. *Memoir of the Ent. Soc. of Canada* No. 108 p. 31-86.
- Mayer-Oakes, W.J. 1967. *Life land and water*. University of Manitoba Press, Winnipeg.
- Mengel, R.M. 1970. The North American central plains as an isolating agent in bird speciation. In, Dort and Jones 1970, p. 279-340.
- Mitchell, J., H.C. Moss and J.S. Clayton 1974. Soil survey of southern Saskatchewan, from township 1 to 48 inclusive. Soil survey report No. 12. University of Saskatchewan College of Agriculture.
- Peckham, G.W. and E.G. Peckham. 1905. *Wasps, social and solitary*. Houghton Mifflin and Co., New York, 311 pp.
- Rau, P and N. Rau. 1918. *Wasp studies afield*. Princeton University Press, Princeton, New Jersey 372 pp.
- Reinhard, E.G 1924. The life history and habits of the solitary wasp *Philanthus gibbosus*. *Annual Report Smithsonian Institution*, 1922: 363-376.
- Ross, H.E. 1970. The ecological history of the Great Plains, evidence from grassland insects. In, Dort and Jones 1970, pp. 225-240.
- Smith, H.T.U. 1965. Dune morphology and chronology in central and western Nebraska. *Journal of Geology* 73:557-578.
- Strandtmann, R.W. 1946. A review of the North American species of *Philanthus* north of Mexico. Ohio State University Press, 126 pp.
- Thorp, J., H.T.U. Smith, *et al.* 1952. Pleistocene eolian deposits of the United States and parts of Canada. *Geological Society of America*, map, scale 1: 2,500,000.
- *Tinbergen, N. 1932. Über die Orientierung des Bienenwolfes (*Philanthus triangulum* Fabr.). *Z. Vergleich. Physiol.* 16: 305.

- *Tinbergen, N. 1935. Über die Orientierung des Bienewolfes II. die Bienejagd. Z. Vergleich. Physiol. 21: 699-716.
- *Tsuneki, K. 1943. On the habit of *Stizus pulcherrimus* Smith. Mushi 15: 37-37.
- *Tsuneki, K. 1956. Ethological studies on *Bembix niponica* Smith, with emphasis on the psychobiological analysis of behavior inside the nest II. experimental part. Mem. Fac. Lib. Arts, Fukui Univ., Ser. II., Nat. Sci. 6: 77-172.
- *Tsuneki, K. 1963. Comparative studies on the nesting biology of the genus *Sphex* (s. l.) in east Asia. Mem. Fac. Lib. Arts, Fukui Univ., Ser. II., Nat. Sci. 13: 13-78.
- Vuilleumier, B.S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771-780.
- Whitaker, S.H. and E.A. Christiansen. 1972. The Empress Group in southern Saskatchewan. Canadian Journal of Earth Sciences 9: 353-360.
- Whitehead, D.R. 1972. Classification, phylogeny and zoogeography of *Schizogenius putzeys* (Coleoptera: Carabidae: Scaritini). Quaestiones Entomologicae 8: 131-348.
- Willis, H.J. 1967. Bionomics and zoogeography of tigerbeetles of saline habitats in central U.S.A. University of Kansas Science Bulletin 47: 143-313.
- Wright, H.E. jr. (Ed.). 1969. Quaternary geology and climate. National Academy of Sciences, Publication 1701.
- Wright, H.E. and D.G. Frey (Ed.). 1965. The Quaternary of the United States. Princeton University Press, Princeton, N.J. 922 pp.

²*References not seen