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Author(s): W. Scott Armbruster and David A. Guinn

Source: *Journal of the Kansas Entomological Society*, Vol. 62, No. 4 (Oct., 1989), pp. 468-483

Published by: Allen Press on behalf of Kansas (Central States) Entomological Society

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The Solitary Bee Fauna (Hymenoptera: Apoidea) of Interior and Arctic Alaska: Flower Associations, Habitat Use, and Phenology

W. SCOTT ARMBRUSTER AND DAVID A. GUINN

Institute of Arctic Biology and Department of Biology and Wildlife,
University of Alaska Fairbanks, Fairbanks, Alaska 99775-0180

ABSTRACT: Over 40 species of solitary bees occur in interior and arctic Alaska. They are most diverse and abundant in open treeless habitats, especially in steppe on south-facing bluffs and early successional sites along large rivers. Solitary bees visit a large variety of plants for nectar and pollen and are important pollinators of many of these plants. There is a strong positive relationship between the length of a bee species' proboscis and the length of the corolla tube of the flower species it visits for nectar.

The abundance, diversity, and ecology of bumble bees in arctic and subarctic North America has been discussed by many authors (Hocking, 1968; Kevan, 1972, 1973; Richards, 1973; Macior, 1975; Michener, 1979; Williams and Batzli, 1982). In contrast, the solitary bee fauna has received little attention (Hurd, 1979; Danks, 1981; Sakagami and Toda, 1986). The literature suggests that nearly all apoid pollination in subarctic and arctic North America is effected by *Bombus*, and that solitary bees are generally rare or absent from all habitats of far northern North America. Field studies in Alaska during the past 8 years indicate that the solitary bee fauna of subarctic North America is fairly diverse, very abundant in certain habitats, and plays a major role in the pollination of many northern plants (Armbruster, 1983; Sakagami and Toda, 1986).

In this paper we report on the composition of the solitary bee fauna of interior and arctic Alaska. We also present data on phenology, distribution across habitat types, and flower use by solitary bees.

Materials and Methods

Thirty-two sites in interior Alaska and two sites in arctic Alaska were visited one to several times during the summers of 1981-1988 (Table 1). Solitary bees were observed on flowers or in other activities (flight, nesting, etc.). Voucher specimens were collected, pinned, and sent to authorities for determination (see acknowledgments for list of authorities). Vouchers are deposited at the University of Alaska Museum, University of Alaska Fairbanks.

Phenological data were collected by making repeated observations throughout the season (ca. 1 May-15 August) at intensive study sites along the Tanana River drainage within ca. 80 km of Fairbanks, Alaska. Data on bee distribution across habitats were collected by repeated sampling along transects located in a stratified random sampling scheme in open, successional habitats of river floodplains, closed-canopy aspen forest, and open grassy steppe on steep south-facing slopes and bluffs along the Tanana River. Additional data were derived from incidental collecting in a variety of other habitats.

Floral associations of bees were determined by repeated sampling using 4 m² quadrats placed along random transects. The presence of a bee on a flower species, or the visit of a bee to a flower species, was noted as an association event. When possible, notes were made on whether nectar or pollen was being collected. Additional data were derived from incidental observations of bees on flowers. The distance between the nectary and the throat (or end of floral tube) was measured for each flower species using dial calipers (0.05 mm scale) or an ocular micrometer on a dissecting microscope (smaller flowers only). The length of the proboscides of a sample of bees was measured by dissecting out the proboscis of recently killed or relaxed specimens, placing it on a micrometer slide, and measuring from the base of the prementum to the tip of the glossa. Since the vast majority of visits observed was by female bees, we measured the proboscides of females only. Males may have somewhat different proboscis lengths than reported here.

Results

FAUNISTICS AND BIOGEOGRAPHY: Forty-one species of solitary bees were collected from the study sites in interior and arctic Alaska; nearly half of these represent new records for the state (Table 2). The largest proportion (38%) of the solitary bee fauna of interior and arctic Alaska is comprised of species with cool temperate North American distribution (i.e., north of approximately the 45th parallel), followed by that for species with holarctic distribution (24%) (Table 2). Twenty-one percent of the bee species appears to be disjunct from temperate eastern North America (east of 100° longitude). Two species appear to be disjunct from montane western North America. These disjunctions may be artifacts of, or accentuated by, inadequate collecting in Canada.

HABITAT USE: While many of the solitary bee taxa are widely distributed across a large number of habitat types in interior Alaska (e.g., *Hylaeus* spp., *Andrena* spp., *Dialictus* spp.), others appear to be restricted to one or a few kinds of habitats (e.g., *Anthidium palliventre*, *Anthophora terminalis*; Table 3). South-facing bluffs have the greatest species richness of bees, followed by roadside and floodplain successional habitats (Table 3). Closed forests and alpine tundra have the lowest abundance and richness of solitary bee species. It should be noted, however, that the patterns depicted in Table 3 may have been accentuated by our more thorough collecting of bees on the bluffs and floodplain, where they were most abundant. The sampling intensities in steppe, aspen forest, spruce forest, bog, burns, roadsides, floodplains, alpine tundra, and arctic tundra conform approximately to the ratio: 10:3:2:1:1:3:5:1:1.

PHENOLOGY: Like the flowers they visit, solitary bees in interior Alaska follow a distinctive, consistent phenological sequence of emergence and flight. We have observed similar emergence dates for the common species of bees in each of the 8 years of observations. While all species appear to be univoltine, some (e.g., *Andrena* spp., *Evylaeus comagenensis*) emerge very early in the season, others (e.g., *Anthidium palliventre*, *Anthophora terminalis*) are active only very late in the growing season (Fig. 1).

In the species where the females overwinter as adults outside of the natal cell (*Evylaeus*, *Dialictus*, *Halictus*; see Stephen et al., 1969), only females were observed at the beginning of the season; males were collected only at the end of the season. In bees that overwinter in the natal cell as prepupal larvae (e.g., *Andrena*

Table 1. Dates of collection and location of collection sites in interior and arctic Alaska.

Collection site	Longitude & latitude	Habitat/vegetation type	Collection dates
Upper Tanana River Drainage			
1) Salcha River Bluff	146°57'W; 64°28'N	Steppe	May–July 1982; May–July 1985
2) Munson's Slough Bluff	146°59'W; 64°29'N	Steppe	May–June 1982; 28 May 1984; May–July 1985
3) Moose Creek Bluff	147°10'W; 64°42'N	Steppe	May–July 1982; May 1983; May–June 1985
4) Delta River Bluff	145°50'W; 64°10'N	Steppe	21 June 1984
5) Bluff at Mile 312 Richardson Hwy	146°55'W; 64°27'N	Steppe	24 May 1982; 24 May 1984
6) Shaw Creek/Richardson Hwy	146°08'W; 64°16'N	Roadside	24 May 1986
7) Mile 230 Richardson Hwy (Donnelly)	145°50'W; 63°40'N	Roadside shrub	6 July 1986
8) Harding Lake/Mile 310 Richardson Hwy	146°54'W; 64°25'N	Roadside shrub	11 June 1983
9) Delta Junction/Donnelly Dome	145°40'W; 63°55'N	Bog/roadside	24 May 1986
Middle Tanana River Drainage			
10) UAF Bluff (Fairbanks)	147°50'W; 64°51'N	Steppe/aspens	May–July 1982; May 1985
11) Rosy Creek Bluff	148°05'W; 64°46'N	Steppe	May and July 1982; May–July 1985
12) Bonanza Creek Bluff	148°15'W; 64°40'N	Steppe/bog	May 1981, May–Aug 1982; May–June 1983; June 1984; May–Aug 1985; May–Aug 1986
13) Whiskey Slough Bluff System	148°25'W; 64°41'N	Steppe/aspens	21–22 May 1985
14) Whiskey Slough Willow Floodplain (dry)	148°32'W; 64°40'N	Willows/ <i>Hedysarum</i>	May–July 1985
15) Rosy Creek Willow Floodplain (wet)	148°00'W; 64°44'N	Floodplain willows	June–July 1985
16) Fairbanks/Tanana River (campground)	147°57'W; 64°48'N	Floodplain willows	2 July 1985
17) Fairbanks/Tanana River (Cushman Street)	147°45'W; 64°48'N	Floodplain willows	May 1981; May–June 1982
18) Rosy Creek Burn	148°20'W; 64°45'N	Early upland succession (post fire)	June–July 1986
19) UAF, Fairbanks	147°50'W; 64°51'N	Roadside	April–May 1981; May–July 1982; 8 July 1985; 12 June 1986
20) Ester	148°00'W; 64°50'N	Roadside	16 May 1985
21) Sunrise Subdivision, Fairbanks	147°48'W; 64°53'N	Roadside willow/spruce forest	5 May 1982
22) Goldstream Valley	147°50'W; 64°55'N	Bog	5 June 1981
23) Aspen Forest Study Site (mature)	148°32'W; 64°40'N	Mature aspen forest	July 1985
24) Nenana/Parks Hwy	149°10'W; 64°35'N	Roadside	7 June 1981
25) Pedro Dome	147°30'W; 65°05'N	Alpine tundra	19 June 1983

Table 1. Continued.

Collection site	Longitude & latitude	Habitat/vegetation type	Collection dates
Yukon River Drainage			
26) Eagle Bluff	141°15'W; 64°48'N	Steppe	13-14 June 1982
27) Mission Valley, Eagle	141°12'W; 64°47'N	Spruce forest	13 June 1982
28) Calico Bluff	141°12'W; 64°54'N	Steppe	29 June 1982
29) Chicken Bluff	142°00'W; 64°05'N	Steppe	12 June 1982
30) Mile 114 Taylor Hwy	141°10'W; 64°10'N	Tundra/steppe mosaic	13 June 1982
31) Six Mile Bluff	141°06'W; 64°53'N	Steppe	27-28 July 1982
Porcupine Drainage			
32) Porcupine River Bluff System	142°00'W; 67°00'N	Steppe	June-July 1982
Arctic Slope			
33) Sagwon Bluff	148°45'W; 69°10'N	Arctic tundra	19 July 1982
34) Kakuktukruich Bluff	148°45'W; 68°50'N	Arctic tundra	20 July 1982

Table 2. Solitary bee taxa collected in interior and arctic Alaska and their biogeographic affinities. Abbreviations: AK = Alaska, CTNA = cool temperate North America, NA = North America, ENA = eastern North America, H = holarctic, WNA = western North America, CT/SANA = cool temperate/subarctic North America, MWNA = Montane Western North America.

Bee taxon	Distribution outside AK	New record for AK	New record for sub-arctic	Clepto-parasite/social parasite
<i>Colletes consors mesocopus</i> Swenk	CTNA	X		
<i>Hylaeus</i>				
<i>H. ellipticus</i> (Kirby)	CTNA			
<i>H. citrinifrons</i> (Cockerell)	NA	X	X	
<i>Andrena</i>				
<i>A. milwaukeensis</i> Graenicher	ENA	X	X	
<i>A. frigida</i> Smith	CTNA			
<i>A. clarkella</i> (Kirby)	H			
<i>A. thaspia</i> Graenicher	CTNA	X	X	
<i>A. costillensis</i> Viereck & Cockerell	MWNA	X	X	
<i>A. algida</i> Smith	WNA	X		
<i>A. salicifloris</i> Cockerell	WNA	X	X	
<i>A. barbilabris</i> (Kirby)	H			
<i>Panurginus ineptus</i> Cockerell	CTNA	X	X	
<i>Evylaeus comagenensis</i> Knerer & Atwood	CT/SANA			
<i>Dialictus</i>				
<i>D. disabanci</i> Knerer & Atwood	CTNA	X	X	
<i>D. ruidosensis</i> (Cockerell)	MWNA	X	X	
<i>D. nr. rohweri</i> (Ellis)	ENA	X	X	
<i>Sphecodes</i>				
<i>S. nr. prosophorus</i> Lovell & Cockerell	NA	X?	X?	X
<i>S. solonis</i> Graenicher	CTNA	X	X	X
<i>Halictus rubicundus</i> (Christ)	H			
<i>Megachile</i>				
<i>M. nivalis</i> Friese	CT/SANA			
<i>M. relativa</i> Cresson	NA	X		
<i>M. frigida</i> Smith	CTNA			
<i>M. giliae</i> Cockerell	CTNA			
<i>Osmia</i>				
<i>O. bucephala</i> Cresson	H			
<i>O. nigriventris</i> (Zetterstedt)	H			
<i>O. inermis</i> (Zetterstedt)	H			
<i>O. sp. nov.</i>	?	?	?	
<i>Anthidium palliventre</i> Cresson	WNA	X	X	
<i>Coelioxys sodalis</i> Cresson	CTNA			X
<i>Hoplitis</i>				
<i>H. albifrons</i> (Kirby)	CT/SANA			
<i>H. robusta</i> (Nylander)	H			
<i>Anthophora</i>				
<i>A. terminalis</i> Cresson	NA	X		
<i>A. bomboides</i> Kirby	NA	X		

Table 2. Continued.

Bee taxon	Distribution outside AK	New record for AK	New record for sub-arctic	Clepto-parasite/social parasite
<i>Epeolus</i> nr. <i>americanus</i> (Cresson)	CTNA	X	X	X
<i>Nomada</i>				
<i>N. aquilorum</i> Cockerell	CTNA	X	X	X
<i>N.</i> sp. 1	?	?	?	X
<i>N.</i> sp. 2	?	?	?	X
<i>N.</i> sp. 3	?	?	?	X
<i>N.</i> sp. 4	?	?	?	X
<i>N.</i> sp. 5	?	?	?	X
<i>Psithyrus fernaldae</i> Franklin	CTNA			X

spp., most Megachilidae) or adults (*Osmia*), males generally emerged first, followed by the females usually a week or two later (Fig. 1).

USE OF FLOWERS BY BEES: At least three distinct processes may contribute to a non-random pattern of utilization of flower resources by bee species: (i) Flowers and bees are structured by habitat; bees do not use flowers growing in a habitat they do not inhabit, (ii) Not all plant species have receptive flowers during the season of an insect's activity, and (iii) Bees may have morphological, physiological, or behavioral constraints and/or "preferences" which restrict their foraging to only certain members of the otherwise available flower pool (including, the effects of the dispersion of rewards, daily availability of rewards, quality of rewards, proboscis length, and floral morphology). The flower association data (Tables 4, 5) therefore may reflect the operation of all three processes and possibly others.

To investigate the role of morphological limitations, specifically proboscis length, in determining bee foraging patterns, we employed polynomial regression to relate the length of the corolla "tube" (throat to nectary) of flowers visited for nectar to the length of the proboscis of nectar-foraging bees (see Neter et al. [1985] for method). We used only bee-flower associations where we were certain nectar was being collected and we had ≥ 4 observed events. The results suggest a strong positive relationship between the length of a bee's proboscis and the tube-length of the flowers from which it collects nectar ($r^2 = 68.3\%$, $F_{2,28} = 30.2$, $P < 0.001$; Fig. 2). An exception to this trend was when bees of very small body size and with short proboscides (e.g., *Colletes*, *Dialictus*, *Evylaeus*; Table 5) collected nectar successfully from flowers with long but moderately broad tubes (e.g., *Silene williamsii*, *Apocynum androsaemifolium*) by crawling down the throat. We excluded these events from the statistical analysis but included them in Fig. 2.

Discussion and Conclusions

In interior Alaska solitary bees are abundant and fairly diverse in open sunny habitats at low elevations, especially in treeless subarctic steppe (on south-facing slopes) and early succession habitats along floodplains and roads. Unlike *Bombus*, they are relatively uncommon in closed-canopy boreal forests and alpine habitats (Table 3). Casual observations of the effects of weather conditions on bee activity

Table 3. Continued.

Bee taxon	Habitat								
	Sub-arctic steppe (bluffs)	Aspen forest	Spruce forest (openings)	Bog	Burn (prev. forested)	Roadside	Floodplain	Alpine tundra	Arctic tundra
<i>N. sp. 3</i> ¹						X			
<i>N. sp. 4</i> ¹	X								
<i>N. sp. 5</i> ¹						X			
<i>Psithyrus fernaldae</i>	X				X	X			
<i>Bombus</i> spp.	X	X	X	X	X	X	X	X	X
Number of species (excluding <i>Bombus</i>)	37	1	2	3	6	19	17	3	4

¹ Habitat distribution only from specimens determined by specialists. Distribution of unauthenticated specimens indicated in genus row.

suggests a cause for this distribution pattern. *Bombus*, which has a relatively large body size and dense pile and is endothermic (Heinrich, 1979), appears to be relatively insensitive to variation in air temperature and insolation. In contrast, most solitary bees are smaller, lack the dense pile, and may lack the ability to

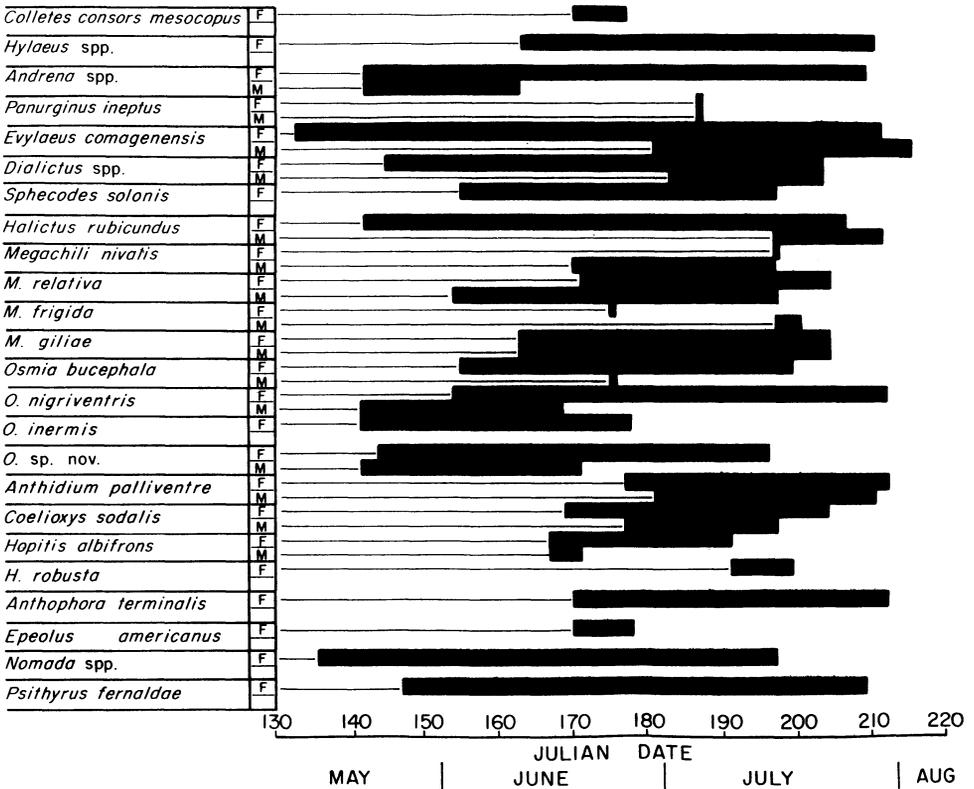


Fig. 1. Flight phenology of solitary bees based on 1985 and 1986 transects and collections. Symbols: F, female; M, male; bar indicates observation of active adults.

Table 4. Host plant taxa and their corolla depths (throat to nectary).

Plant species	Corolla depth
1) <i>Pulsatilla patens</i> (L.) Mill	0.0
2) <i>Arctostaphylos uva-ursi</i> (L.) Spreng.	5.8
3) <i>Ledum palustre</i> L.	0.0
4) <i>Arabis holboellii</i> Hornem.	5.0
5) <i>Erysimum cheiranthoides</i> L.	5.0
6) <i>Saxifraga reflexa</i> Hook.	0.0
7) <i>Saxifraga tricuspidata</i> Rottb.	0.0
8) <i>Rosa acicularis</i> Lindl.	0.0
9) <i>Amelanchier alnifolia</i> (Nutt.) Nutt.	0.0
10) <i>Fragaria virginiana</i> Duchesne	0.0
11) <i>Dryas octopetala</i> L.	0.0
12) <i>Potentilla pennsylvanica</i> L.	0.0
13) <i>Potentilla nivea</i> L.	0.0
14) <i>Potentilla hookeriana</i> Lehm.	0.0
15) <i>Potentilla fruticosa</i> L.	0.0
16) <i>Arnica alpina</i> (L.) Olin	6.5
17) <i>Aster sibiricus</i> L.	5.0
18) <i>Achillea millefolium</i> L.	1.5
19) <i>Taraxacum officinale</i> Weber ex Wiggers	5.0
20) <i>Erigeron glabellus</i> Nutt.	4.0
21) <i>Solidago multiradiata</i> Ait.	—
22) <i>Solidago canadensis</i> L.	2.0
23) <i>Solidago decumbens</i> Greene	3.0
24) <i>Silene menzeisii</i> Hook.	7.5 ^a
25) <i>Hedysarum boreale</i> Nutt.	7.0
26) <i>Hedysarum alpinum</i> L.	6.0
27) <i>Lupinus arcticus</i> Wats.	—
28) <i>Vicia cracca</i> L.	—
29) <i>Oxytropis viscida</i> Nutt. ex T. & G.	5.0
30) <i>Astragalus alpinus</i> L.	3.0
31) <i>Cnidium cnidiifolium</i> (Turcz.) Schischk.	0.0
32) <i>Zygadenus elegans</i> Pursh	0.0
33) <i>Salix</i> spp.	0.0
34) <i>Castilleja pallida</i> (L.) Spreng.	12.0
35) <i>Shepherdia canadensis</i> (L.) Nutt.	0.0
36) <i>Apocynum androsaemifolium</i> L.	6.0 ^a
37) <i>Cornus canadensis</i> L.	0.0
38) <i>Cornus stolonifera</i> Michx.	0.0
39) <i>Epilobium angustifolium</i> L.	0.0
40) <i>Phacelia mollis</i> Macbr.	0.0
41) <i>Galium boreale</i> L.	0.0
42) <i>Papaver nudicaule</i> ssp. <i>americanum</i> Rändel	0.0
43) <i>Mertensia paniculata</i> (Ait.) G. Don	6.5
44) <i>Cryptantha shackletteana</i> Higgins	3.5

^a Throat not highly constricted.

control their body temperatures endothermically. They appear to be adversely affected by low air temperatures. On cool days during much of the spring, they actively forage only when they are exposed to high levels of insolation. For the smaller bees early in the season, foraging and mating bouts are typically interspersed with periods of basking on the ground. This suggests that in the far north

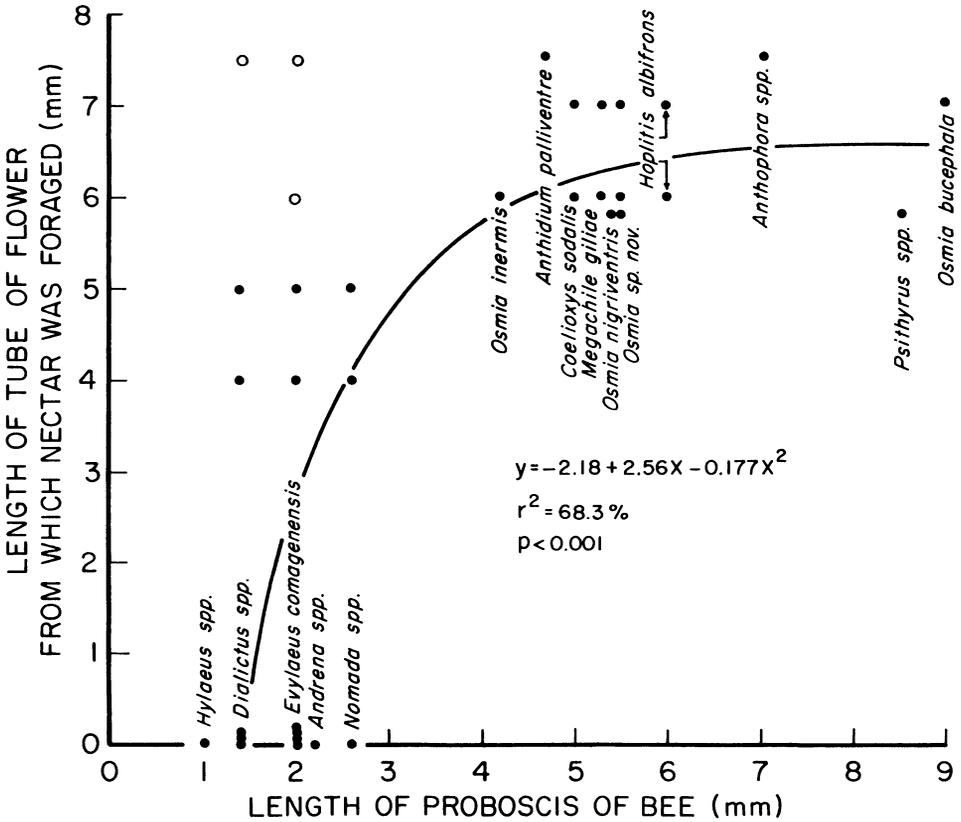


Fig. 2. Relationship between length of floral tube of flowers visited for nectar and proboscis length of visiting solitary bee. Each solid dot represents a species-by-species association of ≥ 4 observed events. Open dots were excluded from statistical analysis; these were cases in which the bee was small enough to crawl down the throat to the nectar. Curve fitted by hand.

most solitary bees require open habitats where they can bask in full sun on the warm ground or in flowers (see Kevan, 1975). Treeless habitats (e.g., steppe, successional habitats, bog, and tundra) are the only sites which provide these conditions. We are presently conducting studies on the thermal ecology of northern bees to address these hypotheses.

An additional factor affecting bee distribution may be their nesting biology. Many solitary bees in Alaska nest in the ground; those that do usually need bare, well-drained soil. We have observed *Colletes* sp., *Andrena* spp., *Evyllaes* sp., *Dialictus* spp., *Megachile frigida*, and *Anthophora* spp., as well as their parasites, nesting in soil in Alaska (see Stephen et al., 1969). Bare, well-drained soil is common on bluffs and in some early succession floodplain and roadside habitats, but rare in other habitats of the arctic and subarctic Alaska. However, this does not explain the diversity and abundance of stem and wood nesters in open sites. These include some *Megachile* spp., *Osmia bucephala*, *Hoplitis albifrons*, *H. robusta*, and some *Anthophora* spp. (Tepedino, pers. comm.; Armbruster, unpubl. ob.).

Table 5. Continued.

	Flower species																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Osmia</i>																				
<i>O. bucephala</i>																				
<i>O. nigriventris</i>		11 ^b						2 ^a	1								1			2
<i>O. inermis</i>		1 ^b						1 ^a				1								1
<i>O. sp. nov.</i>		12 ^b		1						1										
<i>Anthidium palliventre</i>		4.7 (2)																		1
<i>Coelioxys sodalis</i>		5.0 (2)																		2 ^b
<i>Hoplitis</i>																				
<i>H. albifrons</i>		6.0 (3)						1 ^a												
<i>H. robusta</i>		3.0 (1)									3 ^a			1 ^a						
<i>Anthophora terminalis</i>		7.0																		
<i>Epeolus nr. americanus</i>		3.3 (1)																		
<i>Nomada</i> ¹		2.7 (9)	1 ^b							1 ^b							1	9 ^b		8
<i>N. aquilarum</i>		—																1 ^b		
<i>N. sp. 1</i>		3.0 (6)																		1
<i>N. sp. 3</i>		—																		
<i>N. sp. 4</i>		—															1			
<i>N. sp. 5</i>		2.0 (3)																		
<i>Psithyrus fernaldae</i>		8.5 (4)	11 ^b							1										1 ^b

^a Pollen collected.

^b Nectar collected.

^c Both pollen and nectar collected.

¹ Flower associations are pooled for entire genus. Flower associations of species are only for specimens determined by taxonomic authorities.

The presence of a significant fauna of solitary bees in subarctic Alaska suggests that solitary bees may be important pollinators of flowering plants, at least in open habitats. Indeed, ongoing work suggests that many plants in interior Alaska are xenogamous (predominately outcrossing) and depend on solitary bees as pollen vectors (Armbruster, 1983; Armbruster and McGuire, unpubl.). Additional pollination studies and collection of bees in the arctic tundra may also show solitary bees to play a more important role in pollination there than was previously suspected.

It is interesting that such a tight relationship exists between the proboscis length of a bee and the lengths of the corolla tubes of the flowers from which it forages. The length of the bee's tongue probably sets the upper limit of the tube length of flowers from which it can forage nectar. There is nothing, however, preventing bees with long tongues from visiting open and short-tube flowers. The paucity of visits by long-tongued bees to open and short-tubed flowers (Fig. 2) is consistent with Inouye's (1980) observations that long-tongued bees are less efficient at handling open and short-tube flowers, and hence may avoid them when long-tubed flowers are available (see also Harder, 1983, 1988). Also the depletion of nectar in open and short-tubed flowers by the more numerous short-tongued insects (including flies and wasps, as well as bees) may cause long-tongued bees to forage more efficiently from the more restrictive long-tubed flowers.

The apparent long-distance disjunction from sites in temperate North America of nearly one-third of the solitary bee species in interior Alaska is probably at least partly an artifact of collecting patterns, although for some species it may reflect contraction of ranges that were larger in previous times. Many plants now found only on south-facing bluffs in interior Alaska show similar disjunctions (Batten et al., 1979; Edwards and Armbruster, 1989; Murray et al., 1986) as do several hemipterans (G. E. Scudder, pers. comm.) and at least one coleopteran (Smetana, 1986). The coleopteran has been suggested as a relict from warmer times in the Tertiary (Smetana, 1986). Whether the flora and fauna on south-facing bluffs in interior Alaska are relicts of warm and/or xeric periods of the Tertiary, Pleistocene, or early Holocene has been debated extensively and does not appear near immediate resolution (see Hopkins et al., 1982; Murray et al., 1983; Edwards and Armbruster, 1989; and references cited therein).

Acknowledgments

We wish to thank M. S. Arduser (*Sphecodes*), R. W. Brooks (*Anthophora*), G. C. Eickwort (Halictidae), T. L. Griswold (Megachilidae), W. E. LaBerge (*Andrena*), R. J. McGinley (*Evyllaesus*), C. D. Michener (*Panurginus*), F. D. Parker (Megachilidae), R. W. Rust (*Osmia*), R. R. Snelling (*Hylaeus* and *Nomada*) for determining specimens, A. D. McGuire for help in the field, and M. S. Arduser, M. E. Edwards, G. C. Eickwort, T. L. Griswold, W. E. LaBerge, C. D. Michener, R. W. Rust, R. R. Snelling, V. Tepedino, and W. T. Wcislo for comments on the manuscript. Support for this research was provided by the University of Alaska (Faculty Small Grants Program) and the National Science Foundation (BSR-8516864).

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