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Original Article

The Nesting Ecology of Social Wasps (Hymenoptera: Vespidae: Vespinae and Polistinae) in Northern Mongolia

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Abstract

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Observations on the nesting characteristics and colony life of Mongolian social wasps are essential to the field due to the peripheral locations of species distribution ranges and critical lack of such information. We found 35 nests of seven social wasp species, including three vespine species (*Dolichovespula saxonica, D. media* and *Vespula vulgaris*) and four polistine species (*Polistes snelleni, P. riparius, P. nimpha* and *P. biglumis*). Riparian woodland was the habitat where the most species (five out of seven) nests were found. Nests of *P. snelleni*, Baikal-Far Eastern species, were found only in river cut banks, in holes probably originally excavated by passerine birds most likely sand martin (*Riparia riparia*). Nesting sites of *D. saxonica* were the most diverse (bank hole, underground, aerial and birch stump/logs). Colony size of vespine wasps in northern Mongolia was relatively small (36-60 individuals). Nests of *Polistes* species (except *P. snelleni*) were found frequently on the branches of willow (*Salix sp.*) and wild rose (*Rosa acicularis)*. Other characteristics associated with each species nest were considered separately.

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Introduction

All Mongolian social wasps are included in the family Vespidae (Hymenoptera), and are divided in two subfamilies, Polistinae and Vespinae. These two subfamilies comprise nearly one-fifth of the total vespid fauna of Mongolia, consisting of 11 species of Vespinae and 8 species of Polistinae.

Polistine and vespine wasps are eusocial insects. Eusociality is defined by overlapping adult generations, cooperative brood care and a division of labor into reproductive (queen/foundress) and non-reproductive (workers) groups (Carpenter, 1991). The colony cycle of the social wasps in temperate regions is generally similar. After overwintering as an adult, the queen establishes her nest in late spring and rears the first workers. After workers emerge, the queen concentrates on intensive oviposition, while the workers carry out other duties such as brood care, nest extension, protection of the nest, and foraging for food. Males and future queens are produced and copulate through mid to late summer. In late autumn, only future founder queens remain to overwinter, while the workers and males die. The nest of a vespine wasp mainly consists of multiple combs (layers of cells for

brood rearing) and their protective envelopes outside the nest, whereas polistine nest consists of an exposed comb without envelop.

Distribution ranges of the Mongolian vespine species are generally wide, ranging from trans-Eurasian (*e.g., Dolichovespula saxonica*) to cosmopolitan (*e.g. Vespula vulgaris*). This contrasts with the polistine species, which are found across the entire western and central Palaearctic region (*e.g. Polistes biglumis*, *P. nimpha*) as well as the Baikal–Far Eastern area (*e.g.*, *P. snelleni, P. riparius*) (Buyanjargal *et al*., 2016).

Nesting biology and ecology of species with wide ranges have been described in detail due to their pivotal value in understanding insect sociality (Bromley, 1931; Spradberry, 1973; Archer, 2006; Edward, 1980; Greene, 1991) as well as their economic importance with respect to environmental impact and the success of pest control activities (Steffan-Dewenter, 2002; 2003; Souza *et al*., 2010). Nesting characteristics and related studies on the more restricted species of the Baikal–Far Eastern distribution have been studied by Japanese researchers (e.g. Yamane, 1969; 1971; Yamane & Kawamichi, 1975; Makino, 1989; Yamane *et al*., 1999). However, nesting ecology of social wasps has not been characterized for species in the peripheral areas of their distributions in Mongolia.

Herein, the nesting site preferences and biological characteristics of social wasps are identified for seven species in northern Mongolia.

Materials and Methods

The Tarvagatai Valley is a one of the southern valleys of Mountain Khantai (1600-1800 m) which is belonged to Khangai Mountain Range in Mongolia. It is located within the Province Bungan (*aimag*) and east of the District Teshig (*soum*). The Tarvagatai River and its branches flow through this valley, approximately 70 km in length (Fig. 1). River Tarvagatai originates from Khantai Mountains and flows to Eg river, one of the largest rivers in northern Mongolia. The area is classified as mountain forest-steppe and represents southern edge of Siberian taiga. Climate of the region is characterized by cold winters and humid, cool summers. Average perennial air temperature is -4°C and mean annual precipitation is 300-400 mm (National Atlas of Mongolia, 2009).

Six habitats were identified as suitable nesting sites for social wasps, which represent almost all of the habitat types occurring in the valley (Table 1). Ground searches were undertaken to locate social wasp nests in these habitats during a two-week of period, in late June and early August 2018.

After locating a nest, the following variables were evaluated: nest attachment (plant, rock or earth), location, distance above ground (if nest is

Table 1. Habitat descriptions of study area in Tarvagatai Valley.

Habitat groups	Description
Coniferous forest	Siberian larch (*Larix sibirica*) dominated forest (N49.78249 E103.47212)
Mixed forests	Siberian larch (*Larix sibirica*) and Silver birch (*Betula platyphylla)* dominated forest with stony herb-festuce-shrub (*Cotoneaster*, *Spiraea*, pea-shrub) (N49.78041 E103.47423; N49.77949 E103.47508)
Forest openings	Mountain meadows with a variety of herbaceous plants (N49.85246 E103.23969; N49.77433 E103.57618; N49.82035 E103.36539)
Riparian woodlands	Riverside meadows mainly with willow (*Salix sp.*), shrubs of wild roses (*Rosa acicularis*) and other herbaceous plants (N49.79033 E103.24296; N49.81732 E103.49444; N49.77251 E103.46561)
Cut banks	River side cut banks with many variously sized holes made by the passerine bird (*Riparia riparia*). Height of the banks varied from 2-6 meters (N49.790153 E103.48395; N49.75611 E103.16292; N49.57608 E103.16317).
Mountain Steppe	The habitat characterized by short vegetation, mainly with *Carex sp*., and stony, south-facing mountain slopes (N49.49388 E103.22463).

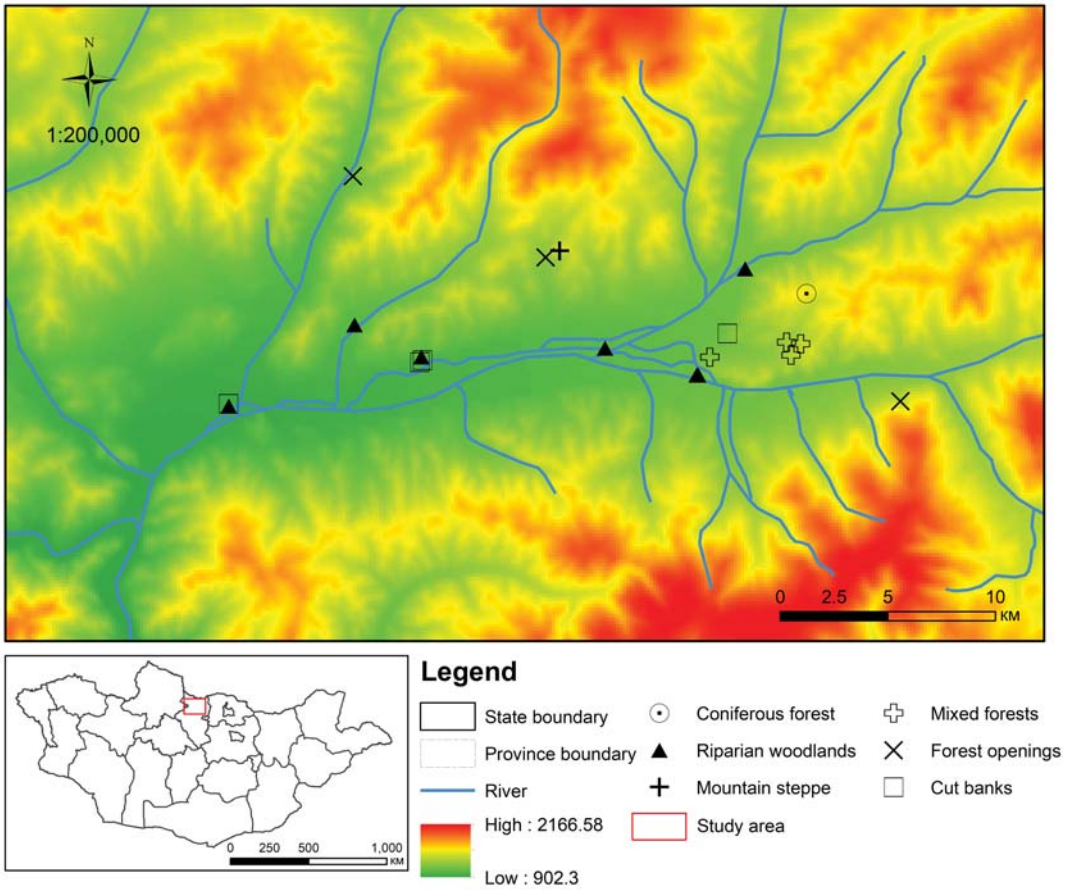

Figure 1. Study area, Tarvagatai Valley in northern Mongolia.

not underground), nest entrance direction, petiole location, number of cells and broods (for *Polistes* nests), number of individuals (females, males), and nest size (cm).

During the data collection, the open nests of the *Polistes* were not disturbed during cell and brood counting. This was not possible for the enveloped vespine nests. Representative individuals from each nest were captured and preserved in ethanol (70%) for confirming the species identification.

Result

Thirty-five nests of seven species were located in six habitats (Table 2). The most common species, nesting in four of six habitats, was *Dolichovespula saxonica*. Nests of other species were found in one or two habitats only (Table 2). The seven nests of *Polistes snelleni* were found in the holes of cut banks along the river. These cut banks have many holes where colonies of the passerine birds, sand martin (*Riparia riparia*) had nested. Several vespid nests were found in smaller holes, which were not occupied by any other animal. However, most of the vespids nested in the riparian woodland (Table 2).

Nests of *D. media* (2 nests) and *V. vulgaris* (1 nest) were found only in riparian woodlands. Nests of *Polistes* species (except *P. snelleni*) were confined to two habitats. Therein, nests of *P. biglumis* and *P. riparius* were located in forest openings and riparian woodlands, whereas the nests of *P. nimpha* were found in cut banks and mountain steppe (Table 1).

Observed nesting sites and nest characteristics were considered for each species as follows:

***Dolichovespula saxonica* nests**: Eleven nests were found at separate nesting sites in four habitats (Table 2; Fig. 2). In the *Betula-Larix* mixed forest, nests were found in the hollows of rotting birch stumps or fallen birches (18%) as well as underground near bush root systems, such as *Rosa acicularis.* Nests in that habitat were found at the beginning of August. Colony

Table 2. Social wasp species and their nest locations in the Tarvagatai Valley habitats.

Subfamily	Species	No. of nest	Nest location	Habitats					
				Coniferous forest	Mixed forest	Forest openings	Riparian woodlands	Cut banks	Mountain steppe
Vespinae	*Dolichovespula saxonica*	11	Aerial, underground, in the hollow of or under the dead trees, in the hole of river cut bank	+	+		+	+	
	D. media	2	Aerial (on the plant stem)				+		
	Vespula vulgaris	1	Undergound				+		
Polistinae	*Polistes biglumis*	7	Dried plant stem, branches of Salix sp. and *Dasiphora fruticosa*			+	+		
	P. nimpha	3	In the hole of cut bank, under rock					+	+
	P. riparius	4	Dried plant stem, branch of *Dasiphora fruticosa*			+	+		
	P. snelleni	7	In the hole of cut bank					+	

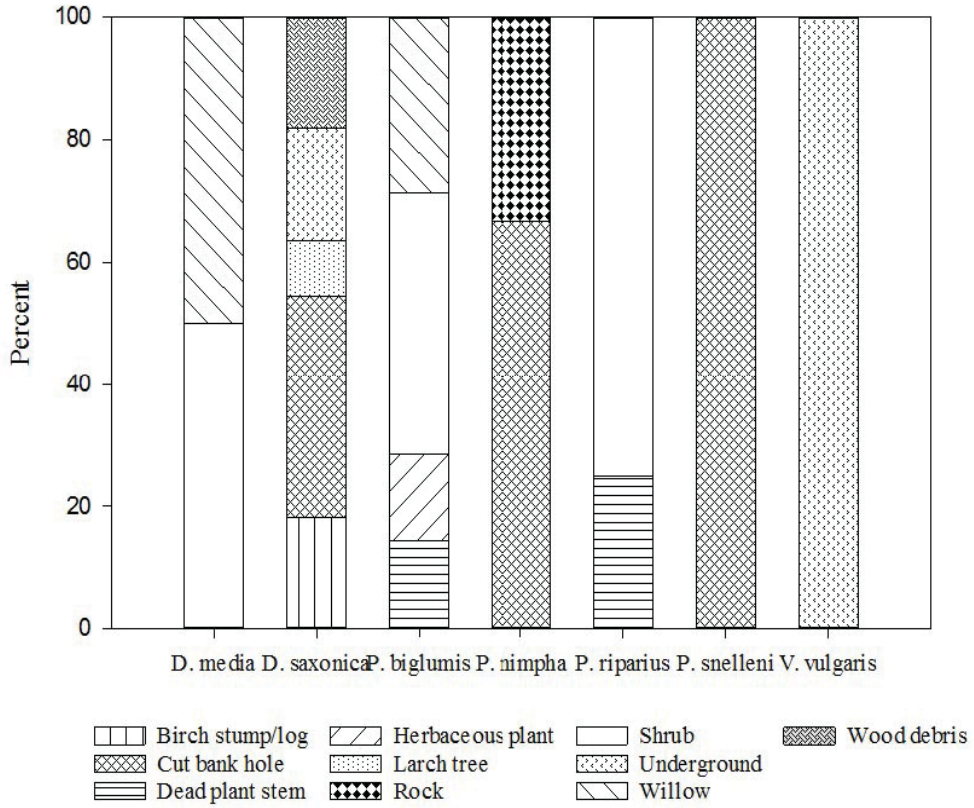

Figure 2. Percentage of nesting sites by wasp species.

Figure 3. Nests of *Dolichovespula saxonica* (a). Underground nest in root system of *Rosa acicularis* bushes; (b). Aerial nest on *Larix sibirica*; (c). Cut bank nest in the earth hole. (d). Nest under a tree debris (held with forceps).

size based on adult wasps ranged from 36 to 60 individuals, and nest size was 8-20 cm in width and 10-20 cm in height for four nests (Fig. 3a).

Nests in the cut banks (36%) were located inside the holes at distances of 10 and 35 cm from the hole-entrance for two nests; two other nests were not exposed (Fig. 3c). Height of the holes from the ground level was 80-100 cm.

An aerial nest of *D. saxonica* was located at the edge of coniferous forest on the southern slope of a mountain. This nest was attached to a *Larix sibirica* branch at 210 cm above the ground. The nest entrance was directed to the south, and nest size was 15 cm in width and 25 cm in height (Fig. 3b).

The remaining two (18%) nests of this species were found in riparian woodlands under fallen tree debris (Fig. 3d). The entirety of each nest was inserted in the earth, with colony size for one of the nests of 70 individuals.

***Dolichovespula media and V. vulgaris* nests:** Two aerial nests of *D. media* and one underground nest of *V. vulgaris* were located in the riparian woodland habitats. One of the aerial nests of *D. media* was attached to the branch of a willow *(Salix sp.*) (Fig. 4a). This nest was found at the end of June; only the queen was captured for identification. The nest hung about in three meters above the ground with a diameter of 5 cm; the entrance length was 2 cm. The second aerial nest was located amidst the branches of thickset shrubs of *Dasiphora fruticose* (Fig. 4b). The nest hung at 56 cm above ground, and the nest width was 9 cm and height 12 cm. We counted 16 individuals in this colony.

An underground nest of *V. vulgaris* was found in another riparian woodland. The nest appears only as a hole in the ground beneath a willow (Fig. 4c). The hole was directed to the northwest.

***Polistes* nests:** Twenty-one nests of 4 species of *Polistes* wasps occurred in four habitats (Table 1). The most common nests belonged to

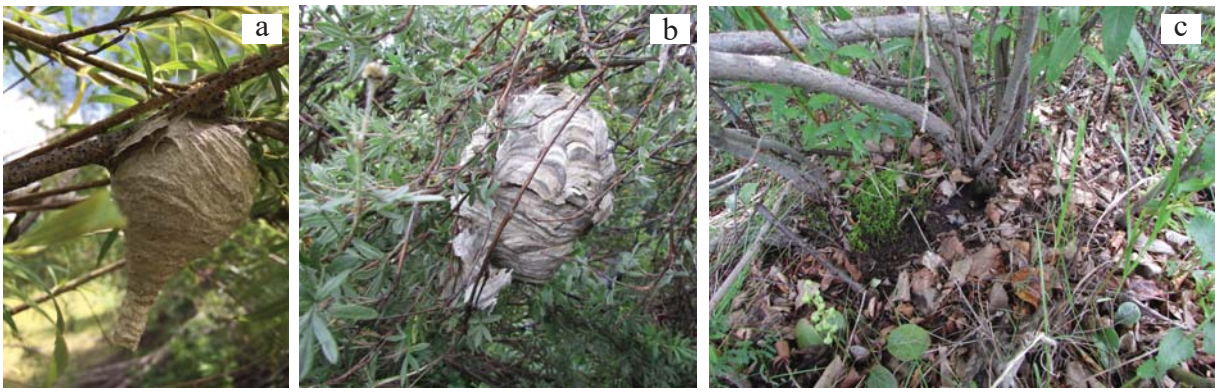

Figure 4. Nests of *Dolichovespula media* (a- nest in late June; b- nest in late August) and *Vespula vulgaris* nest entrance beneath a willow (c).

P. snelleni and *P. biglumis*. The seven nests of *P. snelleni* found in holes of cut banks were each attached to the roof of the hole. The cut bank holes where *P. snelleni* nested were facing south or southeast, and located at 100-200 cm above ground level (average 134 cm). The nests were located 5-10 cm inside the hole-entrance. Most of the nests were discovered in late June. At that time, only the founder queens and few workers were observed in the nests (Fig. 5a). The average cell number was 34.7 (26-47). Combs of the *P. snelleni* nests always faced the floor of the holes; therefore, their broods were not visible in the cells without disturbing the nests.

Most nests of *P. biglumis* were found on the branches of shrubs (*Dasiphora fruticose*) (43%)

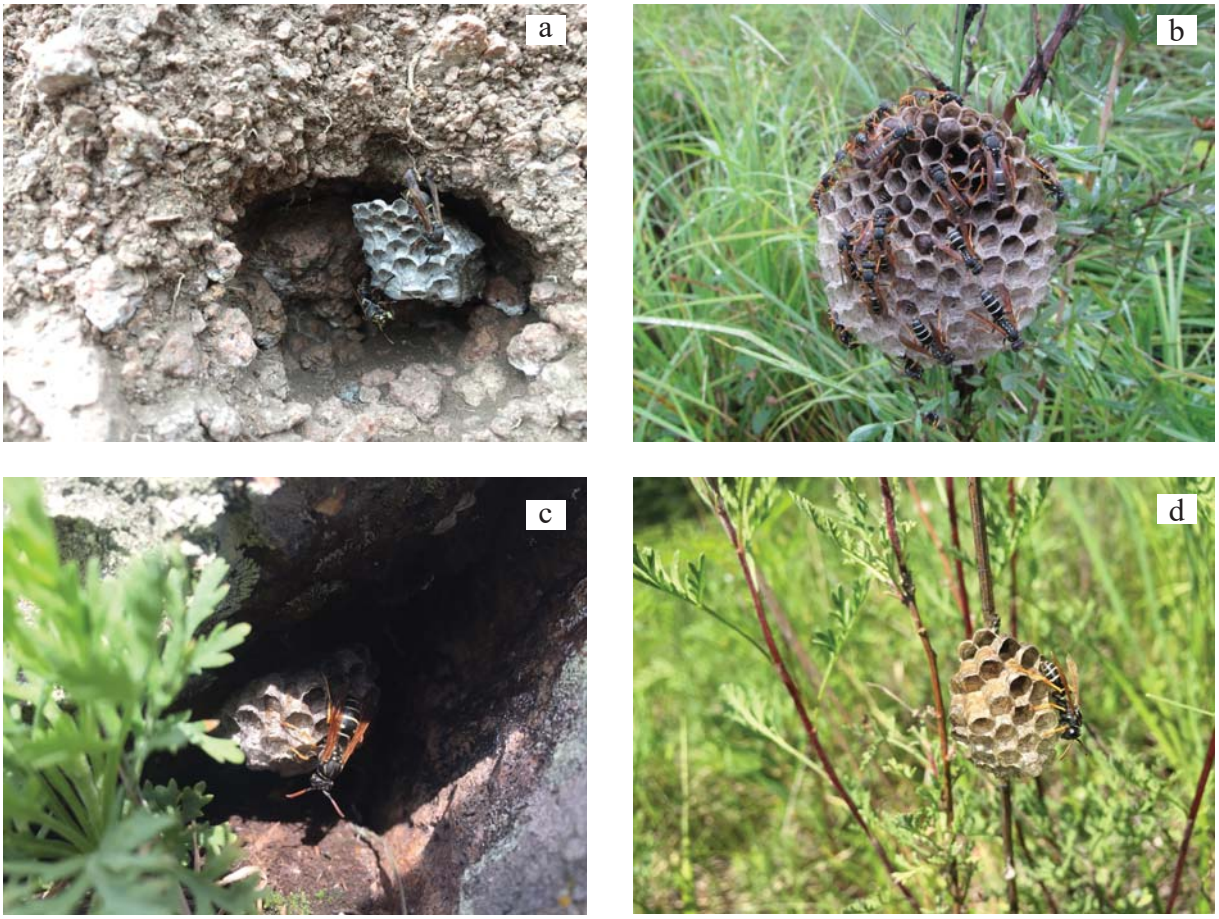

Figure 5. Representatives of the nests of *Polistes* species: (a) *P. snelleni*, (b) *P. biglumis*, (c) *P. nimpha*, and (d) *P. riparius.*

and willows (29%) (Fig. 2). The nests were located at 30-70 cm above ground in riparian woodlands and forest opening habitats (Table 1). In these habitats, one nest was found on a dried buttercup (*Ranunculus japonicus*) stem and the other one on a living buttercup stem at approximately 15 cm above ground. All nests faced to the south or southeast, probably to maximize sun exposure. Most nests were observed in early August. The largest nest had at least 22 individuals including 9 males (Fig. 5b). The average cell number in a comb was 61, and ranged from 24 to 89. The nest petiole, or stalk, was built in the upper side of the nest, and for the most nests, broods were located in cells on the upper side of the comb (Fig. 5b). Broods were mostly in the cocoon stage, as it was late in the colony cycle, and the number of cocoons in the cells ranged from 6-19. Only one or two larvae were observed in each nest.

Only three nests of *P. nimpha* were observed, located in cut banks and mountain steppe habitat. One nest in the mountain steppe was located under small rock with only a founding queen (Fig. 5c). The two other nests were found in the holes of a cut bank, one in late June and the other in early August. The holes were located at approximately 100 cm high above ground level and directed to the southeast. The nest petiole originated from the center of a comb. Three nests of *P. riparius* were found on the branches of *Dasiphora fruticose* shrubs in riparian woodlands at heights of 50 and 75 cm above ground, and on a dried plant stem in the forest opening habitat at 10 cm height (Fig. 5d). Nests faced to the south and southeast. Cell numbers of the first two nests were 36 and 49 respectively, found in August. The other nest, on a dried plant stem, had 26 cells with 2 eggs, 2 larvae, 3 cocoons and a founder, found in late June (Fig. 5d). In the August nests, broods were represented only by a few cocoons, and the colonies were small with 9-10 individuals, including one or two males.

Discussion

Vespine species in the current study represent 50% of the recorded species in northern Mongolia, however, other vespine species such as *V. germanica, V. rufa* and *D. sylvestris* were captured in our study area by the sweep net method, especially near cut bank areas.

Nests of *D. saxonica* were more likely to associated with the birch stumps or fallen logs in the forests, because the wood debris is easily accessible for nest building material (Bromley, 1931). Many other observations of wasps nesting in dead wood have been recorded (Morato & Martins, 2006). Therefore, preserving dead or dying trees in the forest ecosystem will serve to conserve wasp populations as well as other invertebrates inhabiting these environments.

European *D. saxonica* usually nests in aerial settings in shrubs and trees (Archer, 2006), whereas in Mongolia, the species is more likely to build subterranean nests. This behavior is probably influenced by the unstable weather conditions in Mongolia since aerial nests face a much greater challenge from strong winds and difficulties with thermoregulation in contrast with protected nests (Greene, 1991). However, their choice in nesting site is also demonstrated by flexibility, observed in the current study as occurring in several habitats. Nonetheless, *D. media* is inflexible with respect to the aerial nesting habit. In England, it builds nests at 1-5 m above ground (Edwards, 1980), and in the current observations, nests were found at 0.5 meters and 3 meters.

The numbers of adult *D. saxonica* in the colonies were relatively few compared to other populations within its distribution range. For instance, in northern Japan at the same season (early August), 97-228 adult individuals were noted in three nests (Makino, 1982), whereas in northern Mongolia we found 36-60 adults in four nests. In general, *Dolichovespula* species tend to have comparatively small colonies in temperate areas, probably related to the shorter period of colony life. This can last from 15 to 17 weeks for many species; furthermore, the foraging options may be limited in comparison with large-colony species (Greene, 1991).

The root systems of the shrubs of *Rosa acicularis* and *Salix sp.* provide supporting points to the subterranean nests of *D. saxonica* and *V. vulgaris*. This is a minimum requirement for a nest site (Spradbery, 1973) and does not prevent nest expansion due to interference of root growth into nest construction (Fig.3a).

Kemper (1960) determined five factors that influence nest site choice: atmospheric and nest site humidity, temperature, overhead cover,

wind-shields, and light intensity during the day. These factors were not measured for the nests of *V. vulgaris*; however, *Vespula* species appear to require extremely low level of light intensity, as indicated by the selection of very long and curved holes. In contrast, *D. media* prefers a considerable amount of light intensity, which in turn influences the selection of their nest sites (Edward, 1980). However, these variables may have roles only in the early stage of the nest development, since Archer (1988) found no correlation between the variable and mature colony size of *V. vulgaris*. Moller *et al*. (1991) argued that sunny sites and proximity to water are the more important variables for *V. vulagris* colony success.

Nests of *Polistes* species, except for *P. snelleni*, were predominantly built on the branches of *Dasiphora fruticose* and *Salix sp*., and rarely on dead plant stems or tall buttercup (*Ranunculus japonicas*) stems in the region. Kozyra *et al*. (2016) recorded 30 species of 11 plant families on which *P. nimpha* had built their nests in western Poland. In Tarvagatai Valley, this species nested under rocks and in cut bank holes. *Polistes nimpha* tends to build nests closer to the ground than other species. The average height of the nest location was 17-20 cm in Poland (Kozyra *et al*., 2016), and maximum nest height was recorded as 60 cm above the ground in Italy (Cervo & Turillazzi, 1985).

Another widely distributed species, *P. biglumis* is a mountainous species and able to persist cold climate in Alps (Lorenzi & Turillazzi, 1986). This species usually builds its nest on the sides of small stones scattered in meadows at the height of 3-25 cm (Lorenzi & Turillazzi, 1986). However, in northern Mongolia, nests were found on the branches of shrubs (*Salix sp*. and *D. fruticose*) at the height of 30-70 cm. Average cell number was 61 in Tarvagatai, markedly more numerous than the alpine populations (45). Nonetheless, the colony size (less than 30 individuals) and colony activity period (from late May to late September) were similar since Mongolian climate is cold and severe. Broods located upper half of the comb cells may receive more insolation than lower cells which are often shaded. This brood distribution pattern was also observed for *P. riparius* in early nests in Japan (Yamane & Kawamichi, 1975).

Nesting habitat, attached substrate, direction and above ground height of *P. riparius* nests in northern Mongolia were similar to those of northern Japan. There, they nested in open fields of riparian woodlands, attached to dead herbaceous plants and on branches of shrubs or young trees (Yamane, 1969; Yamane & Kawamichi, 1975; Makino, 1989; Yamane *et al*., 1999). When comparing cell number and broods in an early colony of *P. riparius* to Japanese colonies of similar period, cell number was twice fewer; in addition, the broods were much fewer in the Mongolian colony (Yamane, 1971). However, the peripheral long cells of the *P. riparius* nest structure that serve a thermoregulatory function are observed as a vespine envelope (Yamane & Kawamichi, 1975) in populations of both countries.

In northern Mongolia, *P. snelleni* chooses cut bank holes as a nesting site. This type of nesting site has never been described in previous publications. In Japan, this species nests in hilly areas, predominantly in cavities under rocks. At both positions, whether in a hole or under rock, nests do not receive direct sunlight, although the heat absorbed into the rock or the ground during daytime warms nest during cooler periods (Yamane, 1969), as well as being protected from the wind.

The nest comb of *P. riparius* is built vertically with horizontal petiole. In contrast, for *P. snelleni*, the comb is built horizontally with a vertical petiole (Yamane *et al.*, 1999).

Mortality of *Polistes* wasp nests in the pre-emergence phase is often high (58-85%) because of attack by birds, mammals or other reasons (Cervo & Turillazzi, 1985; Lorenzi & Turillazzi, 1986; Makino, 1989; Kozyra *et al*., 2016). Only two (14%) of fourteen nests found in late June at Tarvagatai, survived until August. Therefore, this period is the most important part of wasp colony life. The nesting site choice of the *Polistes* wasp primarily depends on the thermal condition of the habitat (Rau, 1929; Yamane & Kawamichi 1975; Reed and Vinson, 1979), since more rapid development of brood was observed to occur in warm sites than in cool sites (Jeanne and Morgan, 1992).

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