

Snow-surface activity of California Snow Scorpionfly, *Boreus californicus* (Mecoptera: Boreidae), in western Montana, USA

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Abstract

The flightless California Snow Scorpionfly (*Boreus californicus* Packard) has rarely been studied, and knowledge of its distribution and activity on snow remains fragmentary. I found it on snow surfaces in western Montana, USA, from valley grasslands to subalpine conifer forests and above the tree line. At lower elevations (991–1500 m), *B. californicus* was present on snow from early November to early March, at higher elevations (1800–2850 m), from early October to early January as well as late June. The species has now been documented in western Montana over an elevation gradient of nearly 2000 m and is probably active somewhere on snow in most months except in mid- and late summer. When the insect was present on snow, surface temperatures ranged from -5.0°C to 5.5°C . Pairs *in copula* ($n = 26$) were found when snow surface temperature was -0.5°C to 5.5°C . Mating occurred on snow at low elevations from November to late February, at high elevations in late June. The mating period in subalpine habitat, and probably above the tree line, includes early summer as well as late autumn to spring because of the colder temperatures and lingering snow in spring and earlier snowfall in autumn. Temperature and snow-cover characteristics affect the snow-surface ecology of *B. californicus* across its range in western Montana. Mating on a snow cover is likely related to greater mobility (ability to jump) on snow surfaces, aiding the search for mates and contributing to greater dispersal of eggs and reduced inbreeding.

Key words: *Boreus californicus*; California Snow Scorpionfly; ecology; mating; Mecoptera; Montana; snow cover; supranivean; temperature; winter

Introduction

Among the dark specks scattered on snow in winter landscapes is the occasional snow scorpionfly of the genus *Boreus* Latreille (Mecoptera: Boreidae), which constitutes a relatively little-studied group of winter-active insects with a holarctic distribution (Penny 1977). Where snow can persist for several months during winter, *Boreus* lay their eggs during winter in the subnivean space among low-stature mats of bryophytes (mosses and club mosses), where larvae pupate and where adults also occur; both larvae and adults feed mostly on mosses (Penny 1977). Adults are occasionally active on the snow surface throughout winter when temperatures are near 0.0°C (Sömme and Östbye 1969; Courtin *et al.* 1984; Aitchison 2001; Hågvar 2001), a capability attributable in part to elevated concentrations of trehalose, glycerol, and perhaps additional compounds in the hemolymph (Husby and Zachariassen 1980; Vanin *et al.* 2008). Adults exhibit additional adaptations to “supranivean” (snow surface) living, such as long legs, dark exoskeletons (for absorbing incident long- and short-wave radiation), flightlessness, and an ability to jump

(Courtin *et al.* 1984; Roff 1990; Hågvar 2010).

Most studies describing the ecology, reproductive biology, and winter physiology of *Boreus* have focussed on just a few species, such as Mid-winter *Boreus* (*Boreus brumalis* Fitch) in eastern North America, and *Boreus hyemalis* (L.) and *Boreus westwoodi* Hagen in Europe (e.g., Crampton 1940; Fraser 1943; Sömme and Östbye 1969; Courtin *et al.* 1984; Maier 1984; Hågvar 2001; Vanin *et al.* 2008). Far less is known about the ecology of other species, including most of those inhabiting western North America. Much of the information on the latter species has been obtained by passive sampling through use of pitfall traps and sticky boards (Maier 1984; Schmidt and Lockwood 1992; Looney *et al.* 2019). The presence and mating ecology of most western North American *Boreus* species on snow is poorly described, especially as related to ambient conditions, and merits additional study.

California Snow Scorpionfly (*Boreus californicus* Packard) is relatively widespread, ranging from British Columbia and Alberta in Canada to California, Nevada, and Arizona (Penny 1977) in the United

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States, but little has been published regarding the species' ecology other than the summary in Penny (1977) and the accounts of Chapman (1954) from western Montana, USA, and Looney *et al.* (2019) from south-central Washington, USA. I expand on Chapman's (1954) brief observations of snow-surface ecology of adult *Boreus unicolor* Hine, now considered a junior synonym of *B. californicus* (Penny 1977). I describe the annual phenology of activity by adult *B. californicus* across a range of elevations in western Montana, temperature and weather conditions as they relate to adults on snow and the occurrence of mating pairs (Figure 1), and the behaviour and rate of dispersal on snow as they may relate to mating. I place my observations in the context of literature on *B. californicus* and other *Boreus* species and speculate on why *B. californicus* sometimes occurs on snow. Less frequently, I encountered a second species, Reduced Snow Scorpionfly (*Boreus reductus* Carpenter), but will not discuss it further.

Methods

Observations were made west of the continental divide in Montana, mostly from 1994 to 1998 on transects ($n = 50$) that I walked or skied at eight locations in the lower mountains surrounding Missoula, Missoula County, Montana, <15 km from downtown (46.868°N, 113.997°W). A few transects were farther from Missoula: at Lolo Pass (46.635°N, 114.565°W) on the Montana–Idaho state line ($n = 4$) and at Willow Mountain (46.320°N, 113.910°W) in Ravalli County ($n = 1$). Maximum elevations varied from 991 to 1433 m above sea level (asl) for the eight transects near town, 1800 m at Lolo Pass, and 2432 m at Willow Mountain. I also include opportunistic observations at Ward Mountain (46.183°N, 114.245°W, 1830 m; Ravalli County) in 1994, Lolo Pass area (1875 m) in

2000, Saint Mary Peak (46.512°N, 114.244°W, 2758–2850 m; Ravalli County) in 2000, and near Polebridge Ranger Station in Glacier National Park (48.776°N, 114.272°W, 1122 m; Flathead County) in 2013. All transect lengths and elevations are from topographic maps.

Forested habitat at lower elevations included Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), Ponderosa Pine (*Pinus ponderosa* Douglas ex P. Lawson and C. Lawson), and Western Larch (*Larix occidentalis* Nuttall), with Lodgepole Pine (*Pinus contorta* Douglas ex Loudon), Subalpine Fir (*Abies lasiocarpa* (Hooker) Nuttall), and Engelmann Spruce (*Picea engelmannii* Farrar) at subalpine locations and Whitebark Pine (*Pinus albicaulis* Engelmann) and Subalpine Fir krummholz above the tree line. One location near Missoula was open grassland dominated by Flat-stem Bluegrass (*Poa compressa* L.) with a diversity of dried forbs projecting above the snow.

I conducted transects mostly from 1994 to 1998 between 5 November (1996, the earliest) and 12 March (1997, the latest), except at Willow Mountain on 22 June 1995. Transects were on established trails or old forest service roads, generally when fresh snow (2–40 cm) covered the ground; fresh snow was often on top of older, firmer snow up to 80 cm thick. Transect lengths were 1.2–6.4 km (mean 3.2 km) and ended when I reached a turn-around point or completed a loop, traversed at a pace of ~1–2 km/hr when walking or skiing. I recorded ambient temperature <1 cm above the snow surface using a pocket thermometer accurate to 0.5°F with the thermometer bulb shaded, similar to the method of Chapman (1954), with readings later converted to °C. Thermometer readings were made at several locations on each transect then averaged or recorded when I encountered *B. californicus* opportunistically.

I used a non-parametric Spearman rank correlation to examine the relation between numbers of mating pairs and ambient temperature near the snow and a non-parametric Wilcoxon rank sums test or a two-sample *t*-test (if variances were similar) to examine differences in sample mean values of temperature when *B. californicus* was present or absent on the snow or when mating pairs were or were not present. Values are means \pm SD; statistical significance was assumed if $P < 0.05$. All statistical analyses were conducted using Statistix 8 (Analytical Software, Tallahassee, Florida, USA).

Results

Boreus californicus was widespread, both in habitat and elevation, occurring in mixed grassland and lower-elevation mixed conifer forest as low as 991 m asl but also subalpine mixed conifer



FIGURE 1. Mating pair of California Snow Scorpionfly (*Boreus californicus*) near Polebridge Ranger Station, Glacier National Park, Flathead County, Montana, 13 February 2013. Male (below) grasping female to his back with modified wings; individuals are ~4.0 mm in length. Photo: P. Hendricks.

forests of Lodgepole Pine, Subalpine Fir, and Engelmann Spruce, and above the tree line near margins of Whitebark Pine and Subalpine Fir krummholz at the summit of Saint Mary Peak (2849 m) in the Bitterroot Mountains. The species was also present in a six-year-old Lodgepole Pine burn on Ward Mountain (Bitterroot Mountains) and a regenerating pole-sapling Lodgepole Pine stand in a 25-year-old stand-replacement burn near Polebridge Ranger Station in Glacier National Park.

Boreus was not encountered on 19 snow transects between 27 November to 12 March (all years combined; mean distance travelled: 3.4 ± 1.2 km) when ambient temperature averaged $-6.2 \pm 3.4^\circ\text{C}$ (range -13.0 to -1.0°C). On transects when *B. californicus* was detected on snow between 5 November to 22 June (all years combined; $n = 28$), the ambient temperature averaged $0.4 \pm 2.2^\circ\text{C}$ (range -5.0 to 5.5°C), significantly warmer than when they were absent (Wilcoxon rank sums test: $P < 0.001$). Between 5 November and 22 February (all years combined), I found 24 mating pairs on 12 of the 25 transects below 1500 m elevation and on none of the two transects at 1680 m. On 22 June 1995, I encountered two pairs *in copula* on the Willow Mountain transect on a lingering snow-bank during light snowfall at 2432 m on the north side of the mountain. Pairs *in copula* were found during overcast conditions, often with light snowfall or rain ($n = 18$), or in shade ($n = 8$), at temperatures near or above freezing (Figures 2 and 3).

The occurrence of pairs *in copula* on transects when *B. californicus* was encountered was significantly related to ambient temperature near the snow surface: $1.5 \pm 1.8^\circ\text{C}$ when mating pairs were present (range -0.5 to 5.5°C , $n = 13$) and $-0.6 \pm 2.1^\circ\text{C}$ when mating pairs were absent (range -5.0 to 3.5°C , $n = 15$; two-sample t -test: $t_{26} = -2.82$, $P < 0.01$). The number of pairs encountered *in copula* (1–4) on trips when *B. californicus* was present ($n = 28$ trips; Figure 2) was also significantly correlated with ambient temperature ($r_s = 0.568$, $P = 0.002$). The correlation with ambient temperature remained significant ($r_s = 0.579$, $P = 0.002$) when adjusted for survey effort, expressed as the number of mating pairs/km traversed (Figure 3).

Boreus californicus either jumped or folded their legs and antennae under the body (i.e., “play dead”) when first disturbed (poked with a pencil tip). Temperatures averaged $1.3 \pm 1.0^\circ\text{C}$ (range 0.5 to 3.5°C , $n = 27$) when the initial response was to jump and $-2.1 \pm 2.7^\circ\text{C}$ (range -5.0 to 3.5°C , $n = 122$) when the initial response was to “play dead” (Wilcoxon rank sums test: $P < 0.001$). Several individuals jumped when first disturbed then folded their legs and antennae under their body after jumping once.

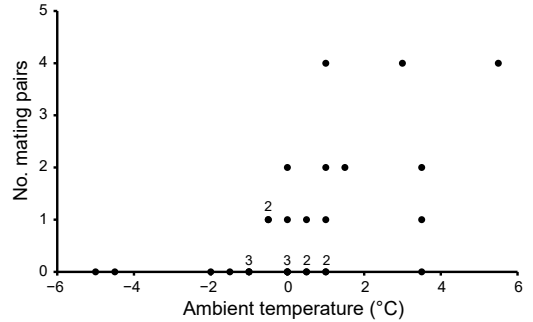


FIGURE 2. Number of mating pairs ($n = 26$) of California Snow Scorpionfly (*Boreus californicus*) on snow in western Montana related to ambient temperature near the snow surface. Points represent survey dates when the species was detected ($n = 28$ surveys). Numbers above some points show the number of surveys sharing that point value.

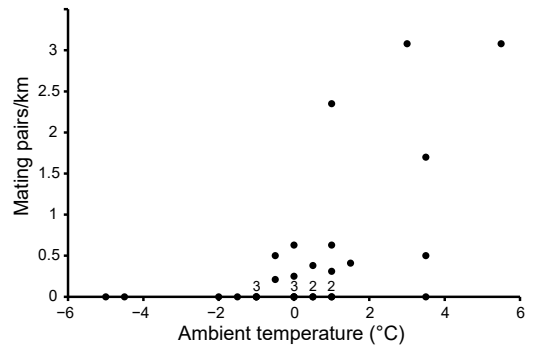


FIGURE 3. Number of mating pairs ($n = 26$) of California Snow Scorpionfly (*Boreus californicus*) on snow/km traversed in western Montana related to ambient temperature near the snow surface. Points represent survey dates when the species was detected ($n = 28$ surveys). Numbers above some points show the number of surveys sharing that point value.

Distances jumped by undisturbed individuals ($n = 21$) varied from 1.0 to 8.0 cm/jump at a rate of 5–7 jumps/min. Jumping was sometimes the response of pairs *in copula* (the male did the jumping while grasping the female to his back with his modified wings; Figure 1), both when disturbed and undisturbed. On 22 June 1995, an undisturbed pair of *B. californicus in copula* at Willow Mountain jumped 10 times in 2 min (temperature 3.5°C), each jump ~ 2.0 cm. Jumping also occurred regularly when undisturbed individuals travelled in a deliberate direction. On 31 December 2000, one male and two female *B. californicus*, above Lolo Pass at 1875 m elevation (temperature 0.5°C), made 60, 70, and 68 jumps in 10 min and covered straight-line distances of 390 cm, 420 cm, and 620 cm, respectively, the last sequence aided by a slight tail wind of 4–5 km/hr.

Discussion

My observations of California Snow Scorpionfly activity on snow expand on the findings of Chapman (1954) from the same region of western Montana. *Boreus californicus* has now been documented on snow in western Montana at elevations <1500 m asl from at least early November to early April—Chapman (1954) reported them in early February to early April in the same general area near Missoula where I encountered them in early November to early March. The period of adult activity at lower elevations in western Montana now closely matches collection dates across the species range as noted in Penny (1977), as well as capture dates of adults in south-central Washington during continuous and systematic pitfall trapping over four years (Looney *et al.* 2019) and where a snow cover was rarely present.

Chapman (1954) failed to detect *B. californicus* above 1220 m elevation on any of his 21 trips in search of snow insects in western Montana, including six trips at 1825–2438 m during the winter of 1952–1953. Note that, on 20 September, he found an unidentified *Boreus*, possibly this species, under a rock at 2255 m in the Mission Mountains (Lake County) in the absence of any snow. I encountered *B. californicus* on snow on several transects up to 1400 m near Missoula, at 1830 m on 6 November 1994 at Ward Mountain, at 1675–1875 m between 24 November to 1 January (1994–1996) at Lolo Pass, at 2432 m on 22 June 1995 at Willow Mountain, and at 2850 m on 6 October 2000 at the summit of Saint Mary Peak. Thus, *B. californicus* has now been found on snow in western Montana over an elevation range of nearly 2000 m, from valley grasslands and mixed conifer forests to mountains cresting above the tree line, with adults active somewhere across this elevation gradient most months of the year except in mid-to late summer (July to late September). What little evidence is available indicates that some adults are present at subalpine and alpine locations later into spring and early summer than at lower elevations and again appear earlier in autumn. The generality of this conclusion for *B. californicus* is hampered by little data from high elevations, but Colorado Snow Scorpionfly (*Boreus coloradensis* Byers) exhibits a similar period of activity on snow (1 October to 27 May) across a similar range of habitats at higher average elevations in Colorado and Utah (Byers 1955; Penny 1977). The pattern fits expectation in relation to the environmental lapse rate (decrease in temperature with an increase in elevation) of $\sim 6^{\circ}\text{C}/\text{km}$ (MacArthur 1972), which results in snow lingering at high elevations later into summer and appearing earlier in autumn. Across the known range of *B. californicus* in western Montana, the lapse rate translates to

an ambient temperature difference of $\sim 12^{\circ}\text{C}$ between valley bottom and mountain top, an important ecological variable affecting the phenology of *B. californicus*, the adults of which are most active at temperatures near freezing.

I found *B. californicus* moving across snow in western Montana when temperatures near the snow surface were as low as -5.0°C , lower than the minimum of -1.5°C reported by Chapman (1954). However, captives kept outdoors in February were able to slowly “crawl” at -5.5°C , and a few were motionless but survived overnight at -12.0°C , indicating an ability of *B. californicus* to withstand temperatures lower than those encountered when they occur on snow of their own volition. However, my newly presented findings and the observations of Chapman (1954) indicate that this species is most active on snow when temperatures are close to freezing, similar to other *Boreus* species studied (Shorthouse 1979; Courtin *et al.* 1984; Hågvar 2001, 2010).

The jumping response to disturbance exhibited by *B. californicus* is most prevalent when temperatures reach or slightly exceed freezing, an observation also made by Chapman (1954). However, I found that “playing dead” (contracting the legs and antennae under the body), also observed by Chapman (1954), is a more common response to disturbance than jumping when temperatures are below freezing. Jumping is an important ability for *B. californicus* as it may allow them to escape potential predators (some jumps reached 8.0 cm) but especially to disperse long distances across the snow. I documented straight-line travel rates for individuals of 390–620 cm in 10 min, which translates to 23.4–37.2 m/hr if sustained. These rates of travel are similar to those reported on snow for *B. brumalis* in Ontario (Shorthouse 1979) and *B. westwoodi* in Norway (Hågvar 2001, 2010); the observed rates, if sustained, convert to ~ 24.0 m/hr and ~ 18.0 – 72.0 m/hr, respectively, although the longest case of directional movement for *B. westwoodi* was 12.2 m in 30 min (24.4 m/hr) at 5.0°C (Hågvar 2001). Males of pairs *in copula* also jumped, but distances and frequency of jumping may be hindered by the presence of the female. An undisturbed pair of *B. californicus in copula* at 3.5°C jumped at a rate ~ 6.0 m/hr. Total distances travelled continuously by *Boreus* on snow before they retreat to subnivean spaces are not known, but Hågvar (2001) reported several cases where individuals were 30–50 m out on snow-covered lakes or bogs, and Shorthouse (1979) found one individual 70 m from shore on a snow-covered lake, locations where retreat from the surface would be unlikely.

Mating activity on snow by *B. californicus* in western Montana is clearly related to temperatures

at or above freezing near the snow surface (Figures 2 and 3), also noted by Chapman (1954) and by Cockle (1908) in British Columbia. However, mating pairs were encountered infrequently, even at temperatures above freezing. Travelling on snow transects, I found a maximum of ~3.0 pairs/km, but more typically ≤ 0.5 pairs/km, which is about what Chapman (1954) reported, i.e., three pairs in 9.6 km or 0.3 pairs/km. Pairs *in copula* occurred on snow throughout much of the period when snow cover was present (early November to late February at lower elevations, to at least late June at higher elevations) and when the temperature near the snow was -0.5°C or warmer, most often in shade or when skies were overcast. Similar conditions were reported for pairs of *B. westwoodi* on snow during November to January in Norway (Hågvar 2001), who suggested that surface activity when overcast may reduce the likelihood of being caught on the snow under a clear sky when air temperature drops rapidly at sunset. Interestingly, Hågvar (2001) observed no copulating animals on snow when present at the two highest densities, where 1–10 m separated individuals under overcast skies at 1.0°C . I made a similar observation on 10 November 1995 with falling snow at -1.0°C . I counted 137 *B. californicus* over 6.4 km, but most were concentrated at five sites in groups of 10–20 animals in 2–4 m² and with no mating pairs, even though both sexes were present in each group. Thus, *B. californicus* seems to be active on snow for reasons other than just mating.

Female *B. californicus* on snow in early and late winter may carry fully developed eggs more often than females in mid-winter, assuming egg development follows the pattern of *B. westwoodi* (Hågvar 2001); perhaps females are less receptive to males at those times. Of the 26 copulating pairs of *B. californicus* found on snow, 76% were encountered in December through February with 58% in February alone, consistent with this possibility. Mating *B. californicus* at the Willow Mountain transect (2432 m) on 22 June 1995 are pertinent in this regard. Two pairs were found *in copula* during light snowfall along with two single females. Mating activity there probably occurs frequently during late spring and early summer, as well as in the absence of snow during autumn and in the subnivean space throughout winter (Hågvar 2001, 2010). Extensive topographic relief allows snow to linger well into summer at high elevations and appear earlier in autumn, along with accompanying colder and favourable temperatures. This undoubtedly influences the timing of reproduction by *B. californicus* across an elevational gradient and produces a phenological shift in mating, or perhaps an expanded mating season, at high elevations, as is evident by my observations in late June on Willow Mountain, the

latest date of the winter active period during which I encountered *B. californicus* on snow, and three females on wind-packed snow above the tree line on 6 October 2000 at the summit of Saint Mary Peak (2849 m), the earliest date I observed the species on snow. Mating probably commences, regardless of elevation or the presence of a snow cover, when ambient temperatures approach freezing.

It is commonly assumed that *Boreus* gains access to snow surfaces by climbing vegetation penetrating the snow or through the air spaces produced around that vegetation and that they retreat to subnivean spaces via the same routes (Shorthouse 1979; Hågvar 2010). Why *Boreus* move to a snow surface (supranivean zone) remains an open question, but it must offer advantages favoured by selection. Possible advantages, proposed by Shorthouse (1979) and Hågvar (2010), are an improved ability to disperse by moving across relatively smooth terrain (perhaps to distribute eggs more widely and reduce inbreeding) and to avoid subnivean invertebrate and vertebrate predators. Little is known regarding predators of *Boreus*, subnivean or otherwise. Subnivean pitfall traps capture few adult *Boreus* (Schmidt and Lockwood 1992; Hågvar and Hågvar 2011), indicating that the space under a snow cover could hinder the ability of boreids, including *B. californicus*, to jump and disperse as effectively as on the surface.

Characteristics of snow cover likely influence the occurrence and abundance of *B. californicus* on snow (Aitchison 2001); thus, better documentation of such characteristics could increase our knowledge of boreid ecology and behaviour associated with their snow-surface activity. Major qualities of snow cover include duration, thickness, hardness, and density (Pruitt 2005). Of special interest is the relation of snow-cover qualities to the critical thickness of snow, the hiemal threshold, where the subnivean space is stabilized at or slightly below 0.0°C and buffered from extreme fluctuations in temperature above the snow cover (Pruitt 1957; Aitchison 2001). The presence and duration of this critical snow thickness (at least 20–30 cm of snow) probably plays an important role in the timing of reproductive activities beneath and on snow by *B. californicus* as related to the broad elevational gradient where the species occurs.

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