Observations on adult *Somatochlora sahlbergi* – a species at risk due to regional climate change? (Odonata: Corduliidae)

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Abstract

Behavioural and autecological observations on adults of *Somatochlora sahlbergi* from northern Finland are presented with hitherto unpublished new aspects of imaginal behaviour. A new interpretation and evaluation of possible threats to its survival is considered in the light of new insights into the chorology and habitat preferences of the species. Threats to the restricted Fennoscandian population, chiefly resulting from the rapidly changing ecological conditions in its subarctic ecosystem, triggered by current trends in regional climate change, are outlined.

Zusammenfassung

Beobachtungen an Imagines von *Somatochlora sahlbergi* – ist die Art durch Änderungen des regionalen Klimaregimes gefährdet? (Odonata: Corduliidae) – Bisher unbekannte Fakten zum Verhalten der Imagines von *S. sahlbergi* werden vorgestellt. Vor dem Hintergrund jüngster Erkenntnisse zur Chorologie und zur Habitatbindung der Art wird die Bedeutung des durch die anhaltende Änderungen des regionalen Klimaregimes rapide voranschreitenden ökologischen Wandels der subarktischen Ökosysteme Fennoskandiens neu interpretiert, woraus sich begründete Gefährdungsszenarien für die Art ergeben.

Introduction

Somatochlora sahlbergi occupies an exceptional position within the Odonata in many respects. As the only tundral faunal element of the order it has a Beringian

distribution and is the only corduliid found in both Eurasia and North America (LOHMANN 1992; CANNINGS & CANNINGS 1985, 1997; WILDERMUTH 2008: 432; SCHRÖTER 2011, 2012). However, the enormous size of its range is in striking contrast to the species' general scarceness, impressively emphasising its enigmatic nature (Tab. 2). In Europe *S. sahlbergi* has been recorded in Finland, Norway, Sweden and Russia. According to current knowledge, in Fennoscandia it is strictly confined to the dry and cold palsa mire zone of discontinuous permafrost north of 67°N and is thus distributed further north than any other European species (DIJKSTRA 2006; WILDERMUTH 2008: 432 f.; SCHRÖTER 2011).

After the first European records of S. sahlbergi on the Kola Peninsula (VALLE 1915, 1931), until the 1980s only scattered additional records of single individuals have been reported from few localities in Finland (HÄMÄLÄINEN 1967, 1984; SAHLÉN 1987). Since the 1990s, however, both number of sites and individuals recorded have significantly increased due to intensified research, including the first records of adults from Norway (PEDERSEN 1992) and Sweden (SAHLÉN 1994). Ecology and distribution of *S. sahlbergi* in Europe has been summed up by WILDERMUTH (2008: 428 ff.). A comprehensive review of the worldwide distribution and ecology of the species has been outlined by SCHRÖTER (2011). Due to its restricted distribution, remoteness of habitats and general unobtrusiveness only a few odonatologists ever had the opportunity to study adult behaviour and autecology of *S. sahlbergi* in Europe in its natural environment. Only rarely have more than a handful of adult S. sahlbergi been encountered on one day, and most records refer only to brief anecdotal observations of single individuals (SCHRÖTER 2011). Thus, the behaviour and ecology of adults of *S. sahlbergi* in Europe is only sketchily known (WILDERMUTH 2008: 432). Based on the hitherto most substantiated data on S. sahlbergi from Fennoscandia, this study aims to extend our knowledge in this regard, providing new aspects of ethology, autecology and habitat affinity of the species. The risks for the species that are based on shifts of ecological conditions caused by a change of regional climate are discussed.

Study region and sampled habitats

The study area was situated on a fjell high plateau in open tundra in the very north of Finland, in the Utsjoki municipality (70°03'13"N, 27°52'49"E), at 195 m a.s.l. The area was characterised by a complex of palsa mire lakes and pools of various size. Palsa mires are restricted to permafrost soil and are characterised by the name-giving palsas, i.e., upright growing peat hummocks with a frozen core. In Finland, palsa mires are restricted to the driest and coldest area north of 68°N in the lee of the Scandinavian mountains (EUROLA et al. 1984; SEPPÄLÄ 2006; LAITINEN et al. 2007). With the exception of a few elevated patches with scattered Mountain Birch *Betula pubescens* ssp. *czerepanovii*, the study area was entirely treeless. Drier sections between the lakes and pools were densely overgrown by knee-high, bushy *Betula nana*. Small patches of bushy *Salix glauca* and *S. lappo*-

num in a depression on the slopes of the high plateau were the only other woody plants present. The area showed a typical mosaic of lakes, pools and interspersed dry sections with palsas in smooth transition to wet patches of *Sphagnum* (sect. *Acutifolia*) carpets, graminoid tundra vegetation and littoral vegetation around the lakes.

The sampled habitat consisted of three mire lakes, all rather deep and in the immediate vicinity east of Lake Skáidejávri (Fig. 1). The lakes' diameters were approximately 280, 105 and 75 m, respectively. All three lakes had rather steep banks predominantly vegetated by *Carex rostrata, C. lasiocarpa, C. limosa, Eriophorum russeolum, E. angustifolium* and *Menyanthes trifoliata*. The water surface was partly covered by a quaking bog of several square metres. Aquatic vegetation was absent with the exception of single small shoots of floating *Utricularia intermedia* within *Carex* stands. The lakes were partly lined with palsas, up to one metre high, which were densely overgrown by *Rubus chamaemorus, Empetrum nigrum hermaphroditum* and *Dicranum elongatum*. Characteristic plants of the surroundings were mainly representatives of typical regional tundra vegetation



Figure 1: Overall view of the study site, a palsa mire complex east of Lake Skáidejávri on a fjell high plateau south of Nuorgam, Utsjoki municipality, Finland (11-vii-2010). – Abbildung 1: Übersicht über das Untersuchungsgebiet, ein Palsamoor östlich des Skáidejávri-Sees auf dem Fjellhochplateau südlich Nuorgam, Gemeinde Utsjoki, Finnland (11.07.2010). Photo: J. Arlt like Betula nana, Salix herbacaea, S. glauca, S. lapponum, Bartsia alpina, Pedicularis lapponica, Antennaria dioica, Carex lapponica, C. lachenalli, C. magellanica, C. nigra juncella, C. vaginata, C. bigelowii, Trichophorum cespitosum, Andromeda polifolia, Vaccinium microcarpum, Sorbus suecicus, Trientalis europaea and Lycopodium annotinum alpestre.

Material and Methods

Dragonflies were recorded by Sami Karjalainen (SK) and Matti Hämäläinen (MH) during visits on 23 and 24-vii-2009 and by Thomas Schneider (TS) and Elias Schneider (ES) during a stay in the region between 22-vii-2011 and 28-vii-2011. Data referring to the flora and mire typology were obtained by Asmus Schröter (AS) during field trips in 2006 and 2010. Botanical nomenclature corresponds to that used by HÄMET-AHTI et al. (1998) and the classification and nomenclature of mosses follows FRAHM et al. (2004). Climate data from the period 1950-2000 at our study site in Finland (70°03'13.07"N, 27°52'49.48"E) and the comparative habitat in Sweden (68°28'00"N, 20°53'54"E) was taken from HIJMANS et al. (2005) at a spatial resolution of 2.5 arcminutes. For proper identification a few specimens of *Somatochlora sahlbergi* of both sexes were collected and numerous photos were taken by TS, ES, MH and SK.



Figure 2: Overgrown palsas (peat hummocks with frozen core) at the edge of one of the three sampled mire lakes providing wind shelter for perching adults of *S. sahlbergi.* Near Nuorgam, Utsjoki municipality, Finland (24-vii-2009). –

Abbildung 2: Uferbereich von einem der drei untersuchten Moorseen mit überwachsenen Palsas (Torfhügel mit Eiskern), in deren Windschatten sich die Imagines von *S. sahlbergi* auf den Boden setzen. Bei Nuorgam, Gemeinde Utsjoki, Finnland (24.07.2009). Photo: MH

Results

Abundance

At least 22 individuals of *Somatoschlora sahlbergi* (13 $3, 9 \,^{\circ}$) were observed. During visits on 23-vii-2009 and 24-vii-2009 SK and MH encountered 15 adults of *S. sahlbergi*: 2 3 and 4 $^{\circ}$ between 16:00 and 18:00 on 23-vii-2009 and 5 3 5 $^{\circ}$ on 24-vii-2009 between 12:00 and 15:00 EEST. TS and ES encountered 1 3 on 26-vii-2011 between 15:00-15:15 and 5 $_{3}^{\circ}$ on 27-vii-2011 between about 14:00 and 16:00 EEST.

Diel activity pattern

According to our observations the flight activity of *S. sahlbergi* was restricted to sunny conditions and temperatures of at least 20°C (TS, ES, SK, MH). In accordance to the preference of the warmest parts of the day the diurnal peak of flight activity was in the afternoon (TS, ES, SK, MH).

Behaviour: patrolling of males and perching

Male *S. sahlbergi* were observed patrolling above the water near the shoreline only during sunny, cloudless weather. As soon as clouds covered the sun, *S. sahlbergi* vanished from the water, but reappeared to continue patrolling flights when the sky brightened again (SK, MH, TS, ES). Increasing windspeed caused a typical positioning of the body's longitudinal axis towards the wind and a targeted search for wind shaded areas behind the nearby palsas (SK, MH).

Males patrolled about 0.5-1 m off shore and about 0.7-1.5 m above the water (TS, ES). Increasing cloud cover caused an immediate decrease in flight activity with subsequent perching on the ground or low vegetation (SK, MH, TS, ES). The males patrolled along stretches of about 30-50 m shoreline. However, patrolling was frequently interrupted by contests with conspecific males or males of *S. metallica* (TS, ES).

Sometimes the flight style suddenly changed without any recognisable reason and continued in a zigzag manner in the direction of the centre of the lake or in the direction of a neighbouring lake, thus the individuals were rapidly lost to sight (TS, ES).

Twice, a male of *S. sahlbergi* was observed flying swiftly along shore from one pond to another, apparently searching for sunny and wind-sheltered stretches. At such a favourable stretch of about 200 m in length five males of *S. sahlbergi* were observed patrolling synchronically for about 40 minutes (TS, ES). One male was subsequently observed dipping into the water three times from a height of 1.5-2 m (SK, MH). Both sexes were observed to fly systematically low in the wind shelter of the palsas (Fig. 2) (SK, MH, TS, ES). Several individuals were observed perching flat on the ground in a style typical of gomphids (SK, MH). While perching they were strikingly approachable and showed a reduced tendency to fly away; therefore several specimens could be photographed from a very close distance (SK, MH).

Species community

During our study period the following dragonfly species were found to co-occur with *S. sahlbergi* at our study site: *Coenagrion johanssoni, Aeshna caerulea, A. juncea, Somatochlora alpestris, S. arctica, S. metallica* and *Leucorrhinia rubicunda*. Whilst in 2009 only a single individual of *S. metallica* was encountered (SK, MH), only two years later this species was strikingly abundant, with an estimated total of more than 100 individuals present, much exceeding the number of individuals of any other species (TS, ES).

Interspecific concurrence

Aggressive interactions between patrolling males of the numerous *S. metallica* and the few *S. sahlbergi* were observed on several occasions (TS, ES). Such interactions led to fighting flights high above the lake or to wild chases over adjacent peat land, both combatants swiftly disappearing from the observer's view. Mutually aggressive interaction of *S. sahlbergi* with other syntopically occurring species was not observed (TS, ES, SK, MH).



Figure 3: Male of *S. sahlbergi* perching on the ground seeking shelter against wind behind a palsa. Near Nuorgam, Utsjoki municipality, Finland (24-vii-2009). – Abbildung 3: Männchen von S. *sahlbergi* im Windschutz eines Palsas am Boden sitzend. Bei Nuorgam, Gemeinde Utsjoki, Finnland (24.07.2009). Photo: SK

Identification in the field

It was quite easy to distinguish the abundant *S. metallica* from the scarce *S. sahlbergi* in the field. Due to significant differences in size and overall colouration, males of *S. sahlbergi* look smaller and darker than *S. metallica*, and the abdomen of *S. sahlbergi* is distinctly less shiny green. Moreover, even the pale yellow-grey-ish ring between the abdominal segments 2 and 3 in *S. sahlbergi* was frequently recognized during low patrol flights at the water's edge (TS, ES, SK, MH).

Discussion

Behaviour: patrolling and perching

The patrol stretches of *Somatochlora sahlbergi* are amongst the longest observed in the Corduliidae and nearly as long as those reported for *Macromia splendens* (WILDERMUTH 2008: 226). Observations concerning males patrolling a territory along the shoreline have been previously published from Finland, Sweden and Russia (VALLE 1931; HARITONOV 1975; HÄMÄLÄINEN 1967; SAHLÉN 1994; DUBA-TOLOV et al. 2004; BILLQVIST 2011). Observations on the sudden interruption of patrol flights of males due to increasingly overcast weather have been previously reported from Sweden by BILLQVIST (2011), who observed a male slowly touching down «like a glider» to perch close to the ground on low vegetation.

The behaviour of several individuals, observed perching flat on the ground in a style typical of gomphids, is untypical for a corduliid and resulted from the lack of proper vertical structures to protect themselves from cold wind (Fig. 1). Due to their reduced escape reaction while perching on the ground, they can remain easily overlooked (SAHLÉN 1994; SANDHALL 2000:167; SK, MH). Therefore, any random survey in potentially suitable habitats for *S. sahlbergi* performed during cloudy weather periods may remain fruitless and lead to misleading conclusions regarding the occurrence of the species in that area. A second reason for the sudden virtual disappearance of patrolling males during intermittent cloudiness might be a specific behaviour, in order to search quickly for a favourable sunny zone nearby, or to approach the next wind-sheltered palsa (TS, ES). Such behaviour has a certain similarity to the scan-flight strategy described for *Somatochlora arctica* by WILDERMUTH (2003).

This strategy could be one of the reasons why *S. sahlbergi* is mainly encountered as single individuals and only during optimal weather conditions. As temperature conditions frequently vary due to a swiftly changing mixture of sunny and cloudy spells, male *S. sahlbergi* are probably very mobile within their habitat, scanning the area for microclimatically optimal places for perching, patrolling and encountering females. Dipping activity shown by some of the observed male *S. sahlbergi* has frequently been observed in other corduliids (WILDERMUTH 2008: 171), and has mostly been explained as evaporative cooling (UBUKATA 1975; LEIPELT et al. 2001).

Species community

With the notable exception of the high abundance of *S. metallica* and records of *C. johanssoni*, the species encountered at the sampled habitat largely corresponded to communities expectable for mire lakes in the palsa mire zone of Finland (HÄMÄLÄINEN 1984). The records of *C. johanssoni*, however, represent only the second case of syntopic occurrence of *S. sahlbergi* with a zygopteran in Europe (SCHRÖTER 2011).

The sampled habitat as meta-population

The majority of the national total of 45 adults of *S. sahlbergi* hitherto recorded in Finland has been encountered at the palsa mire lakes in our study area. Together with populations of comparable abundance described from Russia (VALLE 1938) and Sweden (SAHLÉN 1994), this particular population is one of the strongest currently known in Europe (Tab. 1). However, with regard to the exceptionally poor number of records of *S. sahlbergi* in both Europe and worldwide, (SCHRÖTER 2011: 7) it has to be taken into account that in the case of *S. sahlbergi* timescales work differently; generally established standards of statistics and data evaluation, which are followed in the case of "ordinary" species, can hardly be applied to *S. sahlbergi*. Virtually nothing is known about its population dynamics and density in Fennoscandia or elsewhere (SCHRÖTER 2011: 21). However, with regard to continuity and abundance the presented population justifiably could be considered a stem habitat ("Stammhabitat") sensu KNAUS & WILDERMUTH (2002), probably playing a major role for the species in the region.

Interspecific competition with Somatochlora metallica

Based on the current data, our knowledge and understanding of the local system of interspecific competition and niche differentiation at habitats of S. sahlbergi tends towards zero. In consequence, the role of the eurythermic S. metallica is difficult to assess (SCHRÖTER 2011). In Finland S. metallica is distributed throughout the country; however, the centre of occurrence of this species is clearly located in forested areas in the southern half of the country (VALTONEN 1980; HÄMÄLÄINEN 1984; KARJALAINEN 2010; AS). At latitudes comparable to our study area in Utsjoki, especially at lakes in bare open tundra exposed to the wind, this species is very local, and usually only single individuals are encountered. Therefore, the great abundance of *S. metallica* in 2011 at our study site appeared even more surprising, since the area is rather well explored and such high numbers have not been encountered earlier; at most only single adults or single exuviae have been recorded (P. Pynnönen, J. Koskinen, T. Brockhaus, J. Arlt pers.comm.; MH, SK, AS). A similar picture of very low S. metallica abundance at another site of *S. sahlbergi* at Kevo is delineated by BUTLER (1992), who found single larvae of S. metallica only. Moreover, S. metallica has never been recorded at the well known site of *S. sahlbergi* around Dávvajávri, Sweden (SAHLÉN 1994; M. Billqvist, J. Arlt pers. comm.; AS). The same applies to three sites in adjacent Norway at the southern coast of Varanger Fjord (PEDERSEN 1992; HOLUŠA 2009; Table 1: Minimum number of European records of adults of *Somatochlora sahlbergi* up to 2012 by country and sex. – Tabelle 1: Mindestanzahl europäischer Nachweise von Imagines von *Somatochlora sahlbergi* bis zum Jahr 2012.

Country	Males	Females	Sources
Russia	29	4	VALLE (1931)
Finland	33	12	Sahlén (1987); натікка.ғі (2012); this study
Norway	3	1	Holuša (2009); hatikka.fi (2012)
Sweden	12	4	Sahlén (1994) Billqvist (2011) hatikka.fi (2012)
total	77	21	

SCHRÖTER 2011). Thus, abundance and dominance of *S. metallica* at water bodies of bare open tundra at 70°N, as in 2011 at our study site, can be considered very unusual from a Fennoscandian perspective, and obviously this is a new phenomenon in the region.

According to CORBET (1999: 337), intensity of interspecific interactions in adult dragonflies is correlated with similarity of body size and therefore especially high in congeneric species. As *S. alpestris* seemed to be surprisingly rare and occurs only in small numbers at the sampled habitat, *S. metallica* almost certainly played the key role as antagonist for *S. sahlbergi*. This assumption was impressively supported by our observations of aggressive inferences of male *S. metallica* with *S. sahlbergi*. As the largest member of the genus (WILDERMUTH 2006, 2008: 411), *S. metallica* is probably physically superior to *S. sahlbergi*. Hence, quite apart from the observed aggressive interactions, the large number of *S. metallica* adults alone must have a strong impact on the considerably smaller population of *S. sahlbergi*.

A comparison of climatic key parameters of the studied region with another European core population at Lake Dávvajávri, Sweden (68°28'14"N 20°56'51"E) revealed a remarkable difference and may therefore contribute to the explanation of the surprising pattern of occurrence of *S. metallica*. The mean annual temperature at the sampled habitat in Finland is more than two degrees higher than at the Swedish site, which means a considerably less severe climate (Tab. 2). On a worldwide scale, the climate of the sampled habitat is amongst the warmest of all known *S. sahlbergi* sites (SCHRÖTER 2011). Moreover, the temperature range is strikingly smaller, which corresponds to a comparably less pronounced subarctic, i.e. more moderate, climate due to lower altitude of the site and the specific local oreographic conditions. By contrast, the Swedish population at the palsa mires around Lake Dávvajávri is situated in a basin surrounded by gently sloping fjell ridges that provide wind shelter. In turn, in this basin cold air aggregates, gen

erating a stagnant 'lake' of cold air (J. Arlt, AS unpubl.). This mire area could be considered a palsa mire in exemplary expression with palsa formations up to 4 m high (SAHLÉN 1994; SCHRÖTER 2011), indicating a local climate close to the optimum for the development of palsa mires (LUOTO et al. 2004; SEPPÄLÄ 2006; SCHRÖTER 2011). The sampled habitat, in contrast, is a wind exposed terrain on top of an open treeless plateau, where no cold air accumulates. Thus, differences in climatic key parameters between the sampled habitat and the Swedish site at Dávvajávri might define just the range for the occurrence of eurythermal species like *S. metallica*. Hence, the relatively moderate climate at the study region might explain the occurrence of the species at the sampled habitat and in turn the lack at Dávvajávri in Sweden with more pronounced subarctic continental climate. This assumption was supported by unexpected records of *Coenagrion johanssoni* at the sampled habitat, a species that has not been recorded at Dávvajávri to date.

Diel activity pattern

Among all members of the local species community, S. sahlbergi turned out to be the least resistant to cool, windy weather and cloud cover. Full flight activity appeared to be restricted to sunny conditions and temperatures of $\geq 20^{\circ}$ C. The restriction of the daily flight period to relatively high temperatures was considerably more pronounced than in the other co-occurring flier-type species (TS, ES, MH, SK). In contrast, S. metallica, Aeshna caerulea and A. juncea were on the wing even during cloudy weather when the air temperature temporarily declined to 16°C (TS, ES, AS). Other authors previously emphasised the species' striking dependence on weather; according to SANDHALL (2003:167), S. sahlbergi tended to fly in a considerably less vital and slower manner during cooler days, reaching the same level of flight power as its congeners only during particularly sunny days. Observations by SAHLÉN (1994), obtained at the Swedish Lake Dávvajávri during an extraordinary warm and sunny summer with day temperatures over 25°C, provided evidence of considerably more powerful flight by patrolling male *S. sahlbergi* compared to previous observations under less optimal temperature conditions at Kevo in Finland (SAHLÉN 1987).

Similar data reported from other countries support our observations on the comparatively low temperature threshold of flight activity of these species. *Aeshna juncea* is widely known for its ability to be active under quite cool conditions. In mires of the Black Forest, Germany, the threshold value for the flight activity of male *A. juncea* was only 15°C. Once males were on the wing, flight activity was maintained even when the temperature fell below 12°C (STERNBERG 1990, 1996). *Somatochlora alpestris* has been recorded patrolling at a temperature of only 9°C in the Black Forest (STERNBERG 2000a) and the Swiss Alps (WILDERMUTH 2008: 165). Several other authors emphasize the shade tolerance of *S. metallica* (STERN-BERG 2000b) and even a facultative crepuscular behaviour (WILDERMUTH 2008: 208, AS own obs.), indicating a strong tolerance of cloudy weather conditions. Table 2. Comparison of climatic key factors and altitude between our study site of *Somatochlora sahlbergi* near Nuorgam, Utsjoki municipality, Finland, and the Swedish core site at Dávvajávri (68°28′0″N 20°53′54″E). – Tabelle 1. **Vergleich der klimatischen Schlüsselfakto**ren und Höhenlagen zwischen unserem Fundort von *Somatochlora sahlbergi* bei Norgam, Gemeinde Utsjoki, Finnland, und dem schwedischen Fundort am Dávvajávri (68°28′0″N 20°53′54″E). Ø T_{an} annual mean temperature, mittlere Jahrestemperatur; Ø T_{max} w maximal mean temperature of the warmest month, durchschnittliches Temperaturmaximum des wärmsten Monats, Ø T_{max} c minimal mean temperature of the coldest month, durchschnittliches Temperaturminimum des kältesten Monats.

Locality	Ø T _{an} [°C]	Ø T _{max} w [°C]	Ø T _{max} c [°C]	Altitude [m a.s.l.]
Nuorgam, Finland	0	14.4	-13.5	195
Dávvajávri, Sweden	-2.4	15.4	-18.6	548

Thus, unlike *Aeshna caerulea, A. juncea* and its three local congeners, *S. sahlbergi* is obviously a highly specialised species with a specific pattern of flight activity, which are probably archaic ecological features taken over from the species' putative centre of origin, Beringia, with its dry climate (MATTHEWS 1982; CANNINGS & CANNINGS 1985, 1997; SCHRÖTER 2011, 2012).

Somatochlora sahlbergi in Fennoscandia – a stenoecious species in a rapidly changing subarctic environment

Due to scanty available data, most authors who have considered the threats to European dragonfly species have refrained from assigning *S. sahlbergi* to any certain level of risk, but have nevertheless sketched out potential threats because of its limited range (VAN TOL & VERDONK 1988; SAHLÉN et al. 2004; WILDERMUTH 2008: 298). In the IUCN Red List of Threatened Species (IUCN 2011) the species is classified as «Data deficient», in the Finnish Red List as «Least concern» (VALTONEN 2010), in the Swedish Red List as «Near threatened» (GÄRDENFORS 2010) and in the Norwegian Red List as «Vulnerable» (KJÆRSTAD et al. 2010). Moreover, OLSVIK & DOLMEN (1992) without further specification considered Norwegian *S. sahlbergi* to be negatively affected by airborne pollution from adjacent Russia. However, due to a chronic lack of specific facts on almost all aspects of *S. sahlbergi*, all these considerations must be regarded as speculative and abstract.

However, recent progress in ecological understanding of *S. sahlbergi* (SCHRÖTER 2011, 2012) opened up new perspectives for the interpretation of our data on behaviour and ecology of adults, providing new evidence for specific threats at least on a regional scale. In the following, the threats to this particular regional population are discussed and tentatively attributed to a change of regional climate with specific reference to the investigated habitat. For practical reasons, three major issues of threats are discussed separately but should not detract from the fact

that these are closely linked in a chain of coincident and complex interactions of climatic and ecological parameters:

(1) Damage to mountain birch forest. – Within the European range of *S. sahlbergi*, the arctic birch, *Betula pubescens* ssp. *czerepanovii*, is the dominating tree species except for regional bushy *Salix* species. It is typical for the ecotone between the zone of boreal coniferous forest and the alpine areas, and defines the character of large parts of the subarctic landscape. The most important natural disturbance factor for these forests is the periodic outbreak of the two geometrid moth species *Epirrita autumnata* and *Operophtera brumata* (JEPSEN et al. 2008). In the past these outbreaks used to occur at an interval of about ten years. They constitute a well-known case of cyclic population dynamics (RUOHOMÄKI et al. 2000; MJAASETH et al. 2005). The outbreaks result in complete defoliation of the birch, leaving tree skeletons over hundreds of square kilometres (AS; J. Arlt pers. comm.). Normally, affected birch forests recover during the years between outbreaks. The occurrence of both geometrids and periodical outbreaks are determined by climate. Scientific documentation of outbreaks dates back to the 1860s, providing a profound understanding of these phenomena (TENOW 1972).

During recent decades, however, as a result of the climate change many insect species of the temperate zone have successfully expanded their distribution area in Fennoscandia northwards. This applies also to the two moths, E. autumnata and O. brumata. According to JEPSEN et al. (2008), O. brumata has spread massively north- and eastwards in the last 15 years and therefore the former core outbreak area has considerably extended. Likewise, E. autumnata has penetrated into formerly colder and more continental regions. In the same period a significant increase in both mean annual and minimum winter temperatures has been measured, especially in the continental parts of Fennoscandia. Accelerated development, increasing outbreak frequencies and increasing effective length of outbreaks have also been recognised (JEPSEN et al. 2008; HAGEN et al. 2008). The situation is also exacerbated by the fact that in most areas that have formerly been frequented only by *E. autumnata*, the outbreaks of *O. brumata* lagged only two years behind those of *E. autumnata*. Such alternation is fatal for the birch forest, as it multiplies the numbers of outbreaks that had formerly been caused by *E. autumnata* in a 10-year interval only. Thus, birch trees currently have less time to recover, which results in a large-scale forest dieback. According to HOGSTAD (1997) and TENOW et al. (2007), some areas suffered outbreaks, initially by E. autumnata and subsequently by O. brumata, for five to six consecutive years.

With reference to the sampled habitat it is noteworthy that *O. brumata* has reached the study region only in 2000 (JEPSEN et al. 2008). Due to several massive outbreaks of both moths between 2003 and 2010, the few scattered stands of mountain birch have been seriously damaged (AS; J. Arlt unpubl.). With the exception of a few scattered, small patches with tree skeletons, the surroundings appeared to be practically treeless (Fig. 1).

In adjacent Sweden, patches of mountain birch have been recognised as perching places for *S. sahlbergi* (SAHLÉN 1994; SANDHALL 2000:167; BILLQVIST 2011), and undoubtedly they have a role as potential shelters against wind, for copulation and for roosting. Due to its position, our Finnish study habitat is very windy. The continuous loss of birch stands inevitably results in a change of the microand meso-climate to the detriment of weather sensitive *S. sahlbergi*. In turn, this change benefits concurring species with a broader activity pattern concerning weather and temperature, like *S. metallica*.

(2) Vanishing palsa mires. – The growth of palsas is based on a complex interaction between edaphic, climatic and vegetation prerequisites (SEPPÄLÄ 1988, 2006; HOOFGARD et al. 2003). Due to their high species diversity, palsa mires are listed as priority habitat type of Community importance in Annex I of the Habitats Directive (EUROPEAN COMMISSION 2007). Besides S. sahlbergi, several other arthropods are considered to be bound to the specifically dry and cold climate conditions of this type of mire. Due to regional climatic warming, palsa mires are rapidly degrading throughout their European range. In Finland, for instance, the area initially covered by palsa mires has already declined by two thirds (LUOTO et al. 2004a, b; FRONZEK et al. 2006, 2010; KARLGÅRD 2008). One reason for the ongoing erosion of palsa mires is the higher precipitation in both summer (rain) and winter (snow) due to increase of temperature and moist air masses, which results in transition of palsa peatland to moss mires with thermokarst pools (SEPÄLLÄ 1990, 1994; ZHANG et al. 1990; LUOTO & SEPPÄLÄ 2003; CHAPIN et al. 2007). Even a slight increase of temperature might have a strong impact on the fragile edaphic structures and biotic communities of palsa mires. According to CHAPIN et al. (2007), BOER et al. (1990), KATTSOV et al. (2004) and MCBEAN et al. (2004), the annual precipitation is expected to increase even more in the north. CORBET (1969, 1972) emphasized the increasing importance of microclimate with increasing latitude, and our data show that palsas play a major role for *S. sahlbergi* as windsheltered perching places in the open landscape of the study region (Figs. 2, 3). The close ecological ties of *S. sahlbergi* to palsa mires, as outlined in SCHRÖTER (2011, 2012), have been considered to be primarily based on the specific climate of palsa mires and not on certain plant communities or topographic conditions of the mires themselves. Physical structures of palsa mires might primarily play a role as a proximate factor for *S. sahlbergi* to recognise suitable habitat, whilst the specific dry and cold climatic conditions of palsa mires represent the crucial ultimate factor. However, our particular case of palsas offering wind shelter suggested an even more or less direct causal chain between structural elements of the mire and the living conditions of *S. sahlbergi*.

(3) Increasing cloud cover due to change of precipitation. – Besides indirect impacts of the changing regional precipitation rate, changes in cloud cover during the flight period of *S. sahlbergi* will also most likely affect interspecific competition within the local species community.

With regard to the extraordinary distribution pattern of S. sahlbergi (SCHRÖTER 2011, 2012), the dependency on sunny and cloudless weather might be the primary explanation for the species' range, which is confined to palsa mire areas that are characterised by a typical sunny and dry climate regime. In consequence, the loss of structures providing wind shelter, combined with prolonged periods of cloudy weather during the flight period, might have direct fatal effects on S. sahlbergi. As its time frame of active flight for foraging and mating is reduced, the species' competitive position relative to syntopic species, especially *S. metallica*, is weakened. According to CORBET (1999: 337), interspecific interaction may considerably reduce the time males can spend at the rendezvous site. Interactions of mature adults of syntopic species are usually reduced by differences in the pattern of daily activity or niche differentiation by seasonal segregation. However, this might apply to latitudes with temperate or warm climate, but not to the subarctic with tundra climate, where summers are very short (BERNARD 1995). The evaluation of the phenology of *S. sahlbergi* presented by SCHRÖTER (2011) clearly shows a significant activity peak in the fourth pentade of July, which matches well with the period in which our data have been obtained. Due to the short subarctic summer, the largely coinciding patrol manner of both species along the shoreline and the specific sensitivity of *S. sahlbergi* to warm and sunny weather, it seems impossible that *S. sahlbergi* has any ability to respond to increasing interspecific pressure from *S. metallica* by shifting its spatial, daily or even seasonal flight pattern.

Somatochlora sahlbergi at risk

According to our current biogeographical knowledge, *S. sahlbergi* is a highly stenoecious species invariably confined to permafrost areas with specifically dry climate. This corresponds fully with the palsa mire zone of Fennoscandia (SCHRÖTER 2011, 2012). Although our data, and the considerations based thereon, are just presenting a snapshot of a long causal chain of complex ecological, geographical, climatic and physiological interrelationships, all processes stated above might mutually reinforce their impact on the species during the next decades. Hence, *S. sahlbergi* at the sampled habitat sooner or later runs the risk of entering a vicious circle of a worsening of its living conditions. If our observations of high concurrence pressure by *S. metallica*, the increasing damage to local mountain birch standings and the erosion of palsas in the course of a creeping process of changing regional climate continue, *S. sahlbergi* runs the danger of being replaced stepwise by euryoecious and eurythermal species like *S. metallica*.

Even though other cold stenothermic arboreal tundra species such as *S. alpestris* or *A. caerulea* will sooner or later be under pressure if these processes continue, nevertheless these species are at present common in the North and have considerably less specific habitat requirements and a much higher degree of ecological plasticity (WILDERMUTH 2006; DIJKSTRA 2006; KARJALAINEN 2010; AS, MH, SK). It is likely that these species have the ability – at least to a certain extent – to

respond to increasing mean annual temperatures by moving into higher altitudes of the fjell zone (UBUKATA 2000; OTT 2001). In contrast, the stenoecious *S. sahlbergi* is much less able to adapt to changing ecological conditions, and a shift of its range into higher fjell zones seems impossible due to the precipitation rate alone (SCHRÖTER 2011, 2012). If the current change of local climate in the study area continues, it seems evident that the fate of *S. sahlbergi* at the sampled habitat is sealed. Other metapopulations of *S. sahlbergi* within a more pronounced tundral climate, such as that at Lake Dávvajávri in Sweden (Tab. 2) might withstand somewhat longer, but will finally suffer from the same fatal dynamics. However, further research and time will answer the question whether and to which extent the process as described above might be generalised and thus will apply to the entire restricted Fennoscandian population of *S. sahlbergi*.

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