Odonatologica 31(1): 55-63 *March 1, 2002*

THE IMPACT OF INCIDENTAL SUMMER SNOWFALL ON TWO ALPINE METAPOPULATIONS OF *SOMATOCHLORA ALPESTRIS* (SELYS) (ANISOPTERA: CORDULIIDAE)

H. WILDERMUTH[1] and P. KNAUS[2]
[1]Institute of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich (Corresponding address: Haltbergstrasse 43, CH-8630 Rüti), e-mail: hansruedi@wildermuth.ch
[2]Institute of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich (Present address: Swiss Ornithological Institute, CH-6204 Sempach), e-mail: peter.knaus@vogelwarte.ch

Received May 7, 2001 / Reviewed and Accepted June 1, 2001

In the course of a 2-yr mark-resighting study on *S. alpestris* at 2000 m a.s.l. in the Central Alps of Switzerland snow fell during the beginning of the reproductive period in July 2000. The snow cover was up to 30 cm thick and remained for about 8 days. Only 3% of the individuals marked as tenerals and 4% of those marked as matures before the cold spell were resighted afterwards. In 1998 (a season without snow) the corresponding resighting proportions amounted 10% and 54% respectively. In 2000, at a second study site at 1700-1800 m, 11% of the individuals marked as matures before the cold spell were found again. It is concluded that, unlike the aquatic stages, the imagines of *S. alpestris* are not well adapted to survive cold periods with snowfall lasting more than a few days. Various survival strategies focused on egg and larval development of the sp. are discussed with respect to adaptation to a subarctic climate.

INTRODUCTION

Somatochlora alpestris is a palearctic species ranging from Norway to Hokkaido with a mainly arcto-alpine and to a lesser extent boreo-montane distribution in Europe (MÜLLER, 1988; ASKEW, 1988; STERNBERG, 2000a). In Scandinavia it extends far beyond the Arctic Circle, the northernmost locality of its range being situated at 70°05'N (VALLE, 1952). In Central Europe *S. alpestris* is restricted to mountainous areas among which Alps bear the largest populations. Most imaginal records in Switzerland are from the subalpine zone (WILDERMUTH, 1999). The uppermost breeding sites in the alpine range are found above tree line, i.e. at 2600 m in Austria and at 2440 m a.s.l. in the Swiss Alps (KAPPELLER, 1952; KEIM, 1996; WILDERMUTH, 1999). Together with *Aeshna juncea*, *S. alpestris* is one of the very few odonate species that regularly breeds above the tree line thus encountering maximal mean summer temperatures of 3.5-5.0°C (SCHREIBER, 1977). Obviously the lack of suitable larval habitats due to the cool climate limits their upper vertical distribution. Whereas eggs and larvae have to cope with extreme ecological conditions such as low mean temperatures, freezing and drought (JOHANSSON & NILSSON, 1991; STERNBERG, 1995), adults may sometimes face with unpredictable spells of cold weather during the maturation and reproductive periods. In this respect it may be asked if and how the adults are able to survive a series of successive days with cold rain, snow and frost. One might assume that *S. alpestris* is adapted to inclement weather by special physiological or behavioural device lacking in those species unable to develop in zones with subarctic climate. However, as no data have been available on this problem so far, it was impossible to test this supposition.

During a two-year mark-resighting study in the Central Alps of Switzerland in July 2000, an unusual weather situation with a long cold and wet period offered an unforeseen opportunity to collect quantitative data on the survival of imaginal populations and to compare the findings with those of the preceding year 1998, when the weather followed a standard course. Here we present the results of our observations on two metapopulations of *S. alpestris* that were affected differently by heavy summer snowfall. We show that the adults were unable to survive long spells of inclement weather and discuss how alpine populations compensate for losses by fatal weather events.

STUDY SITES, MATERIAL AND METHODS

This study was carried out in 1998 and 2000 during the emergence and flight season of *S. alpestris*, i.e. from mid June to the end of August, in the subalpine zone of the Swiss Central Alps. Study sites were two localities in the Prättigau Valley ca 22 and 14 km NE of Chur, canton Grisons, Switzerland: (A) Valpun region, 46°57'N, 09°46'E and (B) Furner Berg, 46°56'N, 09°39'E (Fig. 1). The main study site at (A), Bärenseewen, was

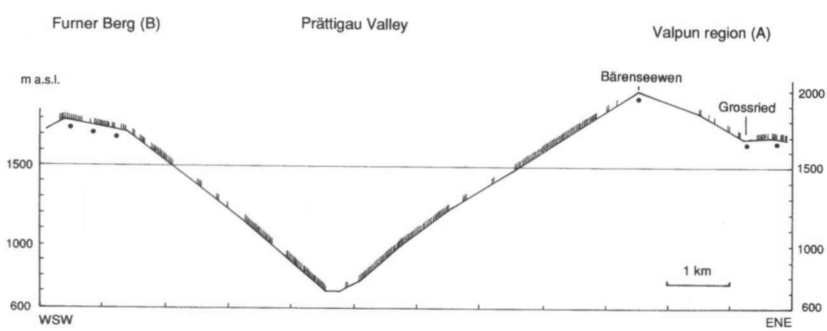

Fig. 1. Cross section of the Prättigau Valley S of Schiers with study sites (A) and (B). Forested and deforested slopes are indicated by vertical bars, breeding sites of *Somatochlora alpestris* by dots.

situated on a longitudinal plateau comprising approximately 10 ha and about 27 small ponds at 1970-2040 m altitude, 100-150 m above the upper limit of the subalpine spruce forest and consisting mainly of treeless alpine pasture interspersed with *Rhododendron ferrugineum*-shrubs. Six additional localities outside the Bärenseewen plateau were regularly checked. They were situated 250-2000 m distant from the main study site, at 1670-1900 m a.s.l. (B) comprised an area of ca 2 km² with a mosaic of pasture, spruce forest, small bogs and approximately 20 ponds of different sizes between 1700 and 1800 m. Stable breeding populations of *S. alpestris* and further alpine species in this region have been known for more than 20 years (SCHIESS & DEMARMELS, 1979; WILDERMUTH, 1986). For additional information on the localities, see KNAUS (1999).

During the emergence period we concentrated on site (A) in both study years, especially on Bärenseewen. In order to assess the size of the imaginal population, at Bärenseewen the F-0 exuviae available were collected exhaustively and regularly at every water body. 674 exuviae were found in 1998 and 254 in 2000 (KNAUS, 2000, and unpublished). All freshly emerged individuals available were marked. Prior to marking tenerals were taken from their support as soon as they had opened the wings and kept in a cage of gauze overnight. The following day the hardened wings were painted with nail varnish (diluted 4:1 with acetone). We used an individual code with large spots and bright colours (yellow, red, blue, green) that allowed identification of the individuals even in flight. In order to facilitate their individual identification in flight different colours on fore and hind wings were applied. 127 (57 ♂, 70 ♀) tenerals were marked in 1998 and 92 (50 ♂, 42 ♀) in 2000 at (A). In addition we marked mature, reproductively active adults. In 1998 at (A) a total of 187 individuals (152 ♂, 35 ♀) were netted at water and released immediately after marking. In 2000, due to inclement weather in mid July, only 23 mature adults (19 ♂, 4 ♀) could be marked at (A). Immediately before and then after the period with bad weather we marked 162 (140 ♂, 22 ♀) adults at locality (B). Resighted individuals were identified by eye or with close-focusing binoculars.

Weather data were obtained from a mobile weather station that was located at the Bärenseewen plateau (A) in 1998. Automatic records of temperature and global irradiation 2 m above ground every 10 min allowed to determine the daily means of both variables (see KNAUS, 1999). The data were compared with those from the two nearest fixed weather stations of Davos (46°49'N, 09°51'E, 1590 m a.s.l.) and Weissfluhjoch (46°50'N, 09°49'E, 2690 m a.s.l., 3.7 km NW of Davos) (SMA, 1998). In 2000, due to the lack of exact weather data for locality (A) and (B), we employed the data of Davos and Weissfluhjoch (SMA, 2000). As the temperatures of these two stations and locality (A) proceeded approximately in parallel in 1998 (cf. Fig. 2), the corresponding course of the temperature for 2000 was reconstructed by interpolation, the mean difference between Davos and locality (A) amounting 2.2°C (n = 92, range 0-4.3°C) (cf. Fig. 2). Further records about general weather from June to August were taken from METEOSCHWEIZ (2000). The local situation concerning snowfall, snow cover, damage to vegetation, and general impact of inclement weather on the insect fauna was assessed by direct observation.

RESULTS

WEATHER DURING EMERGENCE AND FLIGHT PERIOD. – The general weather data for June, July and August 1998 and 2000 are summarized in Table I and the relevant variables during these periods are outlined for every day in Figure 2. In 1998 emergence began on 19 June at locality (A), after a short spell of low air temperature and snowfall, and ceased on 25 July. During the whole emergence and flight period the mean daily air temperature never fell below 0°C. From June to August it remained 1.9°C above the average, while sunshine amounted 115% of the standard. In 2000 June was extraordinarily warm, sunny and dry, this situation extending until the first days of July. The emergence period lasted from 17 June to 7 July. On 8 July a cold snap ensued, lasting extraordinarily long, i.e. until 16 July. From 7-17 July in Davos there was daily rainfall, in total 156 mm. The lower limit of snowfall sank to 1300-1800 m on 11 July. At locality (A) the plateau was covered with a compact layer of snow up to 30 cm thick, lasting 8-9 days. The daily minimum temperature at 2000 m amounted less than 0°C on 8 subsequent days. Snow fell also on locality (B), but the cover was much thinner and remained shorter than at (A), and within the cold spell minimum daily temperatures dropped only on two days below the freezing-point. After a brief spell of dry weather a wet 8 day-period with 140 mm rainfall followed. On the whole, July was cold and wet compared with the average. August was inclement to begin with. Then a long period with warm and sunny weather followed and extended nearly until the end of the month, duration of sunshine and temperature being above the mean.

GENERAL IMPACT OF SNOWFALL ON MACROVEGETATION AND INSECTS. – Little impairment of the vegetation was recorded at locality (A), freezing damage on leaves being very little. However, a very few adult insects were seen after the inclement weather period. Cynthia Fritillary (*Euphydryas cynthia*), conspicuous before the snowfall, was no longer on the wing and all Zygoptera (*Coenagrion puella, C. hastulatum, Enallagma cyathigerum*) had disappeared from the ponds. *Somatochlora alpestris*, *Aeshna juncea* and *Leucorrhinia dubia*, all abundant in 1998, were present in very low numbers, and *Aeshna caerulea*, not uncommon in 1998, was absent.

At locality (B) the damage to vascular plants was conspicuously greater, due to the fact that fewer freezing-tolerant species occur at this altitude. The widespread abundant fern *Athyrium filix-femina* was heavily affected: many leaves had turned brown and were pressed onto the ground. On the other hand, more dragonfly individuals survived than at (A). After the snowfall, *A. juncea* was rather numerous and a few other Anisoptera species (*Aeshna caerulea, Somatochlora alpestris, S. arctica*) were found in small numbers as was usual at almost every suitable water body.

Table I

Weather in June, July and August in 1998 and 2000 according to data of the fixed weather station of Davos 1590 m a.s.l.

Month	Temperature[1] [± °C]		Duration of sunshine[1] [%]		Precipitation[1] [%]		Dull days (mean of daily clouding >80%)		Bright days (mean of daily clouding <20%)	
	1998	2000	1998	2000	1998	2000	1998	2000	1998	2000
June	+1.9	+3.0	118	134	140	54	8	8	2	6
July	+1.6	-1.0	97	91	117	167	10	15	0	2
August	+2.2	+2.3	129	128	77	140	6	9	5	7

[1] SMA, 1998, 2000: deviation from mean of many years.

SEASONAL DEVELOPMENT OF *SOMATOCHLORA ALPESTRIS*. – In 1998, 13 of 127 (10.2%) individuals marked as tenerals were resighted at locality (A), whereas in 2000 only 3 of 92 (3.3%) were encountered again (Tab. II). For the adults marked as matures the corresponding numbers were 100 of 187 (53.5%) in 1998 and 1 of 23 (4.3%) in 2000. At locality (B) 40 of the 162 (24.7%) individuals marked as

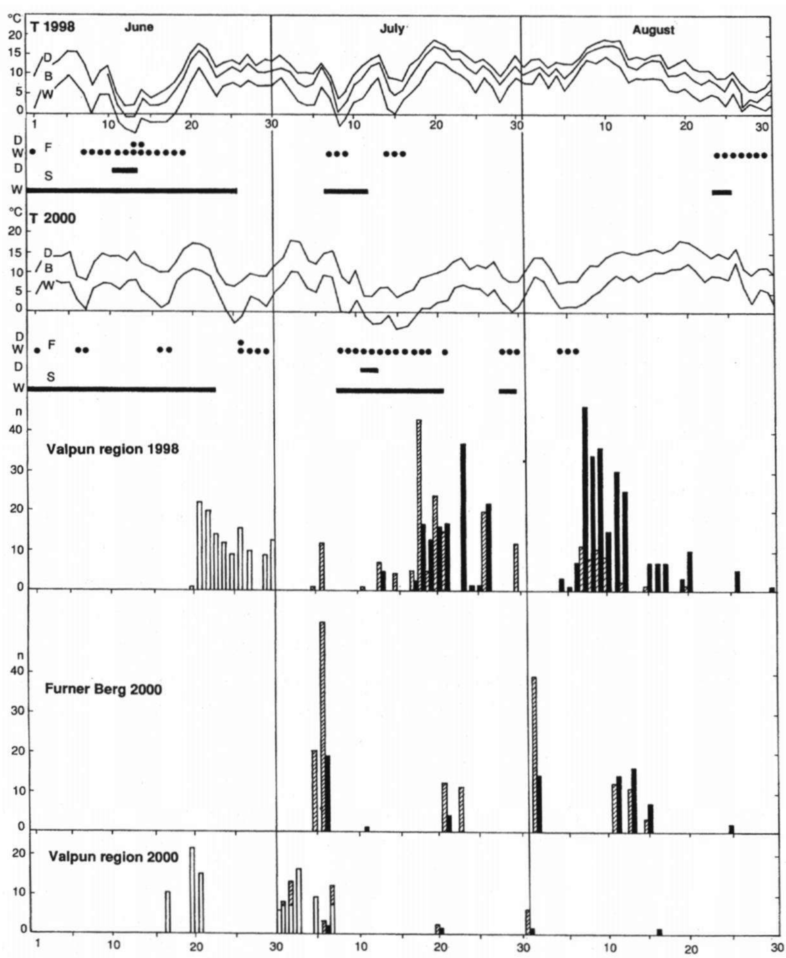

Fig. 2. Number and seasonal distribution of markings and resightings of adult *S. alpestris* at locality (A), Valpun region, and (B), Furner Berg, with corresponding weather data from June to August in 1998 and 2000. White columns: number of individuals (n) marked as tenerals, hatched: individuals marked as matures, black: resightings. Weather data from Davos (D) 1590 m, Bärenseewen (B) at locality (A) 2000 m, and Weissfluhjoch (W) 2690 m. – [F (dots): days with temperatures below 0°C; – S (bars): snow cover; – T: daily mean of air temperature]

mature adults were observed again. The seasonal distribution of markings and resightings is summarized in Figure 2. At (A) all the resighted individuals were marked before the period with snowfall, while at (B) marking occurred partly before (n = 74) and partly after (n = 88) the cold snap. Following this period the resighting rate of the first group was 0.30 (n = 22) and that of the second 0.20 (n = 18).

As the frequency of observation differed between study years and localities, the daily encounter rates with marked individuals including repeated resightings were calculated (cf. Tab. II). With respect to resighted individuals that were marked as matures at (A), the rate of resighting was distinctly lower in 2000 than in 1998 and in 2000 it was lower at (A) than at (B). No difference was found at (A) between 1998 and 2000 with respect to those individuals that were marked as tenerals.

The results of sampling on some selected fine days following the cold period in 2000 showed clear differences in the abundance of *S. alpestris* at the two study sites. On 20 July, only 1 marked individual of *S. alpestris* was resighted and only 2 adults could be netted for marking at locality (A). 11 days later we had 1 resighting and 6 captures of unmarked individuals. On 16 August 16 ponds were sequentially checked for dragonflies during 35 min shortly after solar noon. Altogether 9 individuals of 4 species including 2 males of *S. alpestris* were found. In comparison, at locality (B) we marked 39 adults and resighted 7 different individuals on 1 August 2000, and on 10 August 1998 15 *S. alpestris*-males (among 21 recorded) were marked within 110 min at just one small pond (Grossried) 1.7 km E of the Bärenseewen plateau (A).

Table II

Number of marked and resighted individuals at the study sites (A) and (B): — EM: total number of emerged adults (exuviae); — JM: number of individuals marked as tenerals; — AM: number of individuals marked as matures; — TM: total number of marked individuals; — JR: number of resighted individuals that were marked as tenerals; — AR: number of resighted individuals that were marked as sexually matures; — TR: total number of resighted individuals; — SR: sum of all resightings (including repeated resightings); — [in square brackets]: number of days on which individuals were marked or resighted, respectively; — (in round brackets): number of different individuals resighted per sampling day

locality year	EM	JM	AM	TM	JR	AR	TR	SR
A	674	127	187	314	13;10.2%	100;53.5%	113;36.0%	397
1998		[12]	[16]	[28]	[13]	[27]	[27]	[27]
					(1.0)	(3.7)	(4.2)	(14.7)
A	254	92	23	115	3;3.3%	1;4.3%	4;3.5%	5
2000		[8]	[6]	[11]	[3]	[1]	[4]	[4]
					(1.0)	(1.0)	(1.0)	(1.2)
B	-	-	162	162	-	40;24.7%	40;24.7%	76
2000			[8]	[8]		[8]	[8]	[8]
						(5.0)	(5.0)	(9.5)

DISCUSSION

Although the number of resightings at the two study sites and years cannot exactly be compared because of differences in sampling frequency, annual population size and study season, it is evident that the imaginal population of *S. alpestris* at locality (A) was depressed after the cold spell in July 2000. It was obviously the unusually protracted period with sub-zero temperatures and snowfall that led to the drastic decline in the number of adults. The few individuals that were resighted alive after the snowfall probably did not survive at 2000 m but rather at lower altitude where they found shelter amongst conifer trees. As shown in a mark-resighting study on displacement, adults belonging to the same metapopulation easily move over vertical distances of 400 m in both directions when in search of oviposition and rendez--vous sites (KNAUS, 1999). At locality (B) most of the imaginal population survived the cold spell, due to the fact that the individuals were less exposed to inclement weather than at (A). It is likely that the adults remained beneath branches of spruce trees, i.e. at places where they normally roost, thus being protected to a certain extent against snow and sub-zero temperatures. And what is probably more important, at 1700 m the cold period did not last as long as at 2000 m. LEHMANN (1985) observed in Tyrol (Austria) at 2050 m that *S. alpestris* and other alpine species were still abundant after two cold days with a snow layer of about 10 cm thickness. Based on these findings it may be assumed that *S. alpestris* can survive a few days with snow and minimum daily temperatures of minus 3-4°C, but it is not able to endure protracted periods of frost, unlike the larvae that may survive enclosed in ice or frozen sediment for about 6 months (JOHANSSON & NILSSON, 1991).

Somatochlora arctica, a species that coexists in many places with *S. alpestris* (WILDERMUTH, 1998; STERNBERG, 2000b), was found on a snowfield in Kamchatka (E Siberia), 7 of 40 individuals still alive (REINHARDT, 1994). One male had survived after it had been associated with the frosty substrate overnight for at least 10 hours. However, cold hardiness of *S. arctica* is probably inferior to that of hibernating *Sympecma* imagines (JÖDICKE, 1997) and definitely lower than in many other subarctic insects. It is likely that adults of both *S. arctica* and *S. alpestris* may survive cold snaps. However, they are not adapted to long lasting periods with snowfall and sub-zero temperatures. Moreover, in mountainous areas some individuals of a metapopulation may always survive if they happen to be at lower altitude during a sudden fall in temperature. After the cold spell the loss of individuals is partly compensated for by roving females that come from localities at lower altitude. Therefore we infer that the upper limit of vertical distribution in *S. alpestris* is not caused by incidental snowfall during the flight season, but rather by the absence of suitable habitats due to the cool climate in the suprasubalpine zone (WILDERMUTH, 1999).

We suggest that the survival strategies of *S. alpestris* in zones with subarctic climate focus on the aquatic stage. The most important risks of extinction derive from drought and freezing of the habitat, unsuitable water temperatures and predation, the young larvae thereby being most heavily affected (STERNBERG, 1990). However, the risk of extinction of an individual's offspring by fatal ecological events is spread over space and time. A female will deposit her eggs in water bodies differing in size, depth and other structural variables (KNAUS, 1999). As for time, the duration of embryonic development varies greatly, depending on temperature conditions and the date of oviposition. Furthermore, with progressing season, the proportion of diapause eggs increases from 0 to 37%, probably due to a female's age. Following diapause, most eggs hatch without delay at 16°C, whereas in a smaller fraction this happens only if the temperature exceeds 20°C (STERNBERG, 1995). As demonstrated by STERNBERG (1989) and KNAUS (2000), *S. alpestris* is a spring species sensu CORBET (1962). Because diapause eggs are unusual in spring species, this type of development in *S. alpestris* may be considered an adaptation to the extreme climate in the subalpine and subarctic zones (STERNBERG, 1995). The entire development of this species takes 2 to 5 years comprising 11-13 stadia excluding the prolarva (STERNBERG, 1990). This constitutes another strategy of risk spreading during the aquatic stage, because by such variability in developmental time the reproductively active offspring of an individual may be distributed over several successive years.

ACKNOWLEDGEMENTS

We thank ELISABETH FAYET, STEFAN KOHL, NATHALIE MIL, GUDRUN MOELLER, MARION STAUBER and CHRISTOPH VORBURGER for assistance in the field. KARL SCHROFF (Swiss Federal Institute of Technology, Zürich) placed the mobile weather station at our disposal. CHRISTIAN GEIGER and GUSTI SOLINGER generously made available the house owned by Pro Natura at Stelserberg (Schiers) and the Office for Nature and Landscape Protection of the Grisons (Chur) gave permission to capture and mark dragonflies. PHILIP S. CORBET and KLAUS STERNBERG kindly reviewed an earlier version of the manuscript and provided valuable suggestions.

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