

SPECIES FACT SHEET

Scientific Name: *Somatochlora franklini* (Selys 1878)

Common Name: Delicate Emerald

Phylum: Arthropoda

Class: Insecta

Order: Odonata

Suborder: Anisoptera

Family: Corduliidae (emeralds)

Conservation Status:

Global Status (2004): G5

Rounded Global Status: G5 - Secure

National Status (United States): N3N4

National Status (Canada): N5

State Statuses: Alaska (SNR), Maine (S5), Michigan (SNR), Minnesota (SNR),
New Hampshire (SNR), New York (SNR), Vermont (S2), **Washington (SNR)**,
Wisconsin (S2S3).
(NatureServe 2008).

Technical Description:

Adult: Characteristic of the Corduliidae, the eyes are contiguous and the anal loop of the hindwing is distinctive (somewhat foot-shaped, but with little development of the toe). *Somatochlora* is distinguished from the other genera in this family by the metallic, dark-green abdomen and the pointed (as opposed to forked) inferior anal appendage at the tip of the male abdomen. *Somatochlora franklini* is a very slender emerald with a dark brown triangle at each hindwing base. The face is black with yellow on the sides. The male thorax is metallic green mixed with some brown; the female thorax is brown mixed with green. The thorax of both sexes lacks spots or lines. The male abdomen is black with dull brown spots on the sides of segments 1 and 2, and a dull yellow ring at end of segment 2; the female abdomen has dull orange dorsolateral spots on segment 3. Female eyes stay reddish for much of life, then become green. The body length of this species is 44-54 mm (1.7-2.1 in.) (Paulson 2008, *pers. comm.*).

The very slender abdomen, coupled with the brown mark on the base of the hindwing, helps distinguish this species. The two other species with a brown wing mark (*S. whitehousei*, *S. septentrionalis*) have much shorter abdomens and very different male and female appendages. Other similar species (*S. semicircularis*, *S. kennedyi*, *S. forcipitata*, *S. brevicincta*) lack the brown wing mark and have less slender abdomens, although it should be noted that the wing spot is not extremely obvious in the field (Paulson 2008, *pers. comm.*). Examination of male and female appendages may be necessary for conclusive identification. Male cerci appear forcep-like from above, and resemble a simple

slightly droopy and pointed finger from the side. The female subgenital plate is the length of segment 9, and does not project (Paulson 2008, *pers. comm.*).

Immature: Larvae in this family are generally stout and hairy. *Somatochlora* in the Pacific Northwest can be identified to genus as follows: prementum and palpal lobes cup-shaped (as opposed to flat), palpal lobe with small, regular teeth (as opposed to large, irregular teeth), head without erect, frontal horn, ventral surface of prementum with a basal, median groove, dorsal hook absent on abdominal segment 2, and sides of thorax uniformly colored without dark longitudinal stripe (Tennessen 2007). Species identification is difficult for a non-expert, but see Bright (2005).

Life History:

Adult flight period in Washington is 30 Jul- 24 Aug (Paulson 2007). Males fly back and forth at waist height, with frequent hovering, patrolling the aquatic habitat for females (Bryan 2008, Paulson 2008, *pers. comm.*). Females oviposit by tapping the abdomen onto wet moss or water in tiny pools (Paulson 2008, *pers. comm.*). Adults perch by hanging, either vertically or obliquely, from vegetation. Like all odonates, the majority of the life cycle is spent as aquatic larvae. The larvae of this species are sprawlers, living on the surface of floating leaves or fine sediment (Merritt *et al.* 2008), where they “sit-and-wait” to ambush and engulf their prey (Packauskas 2005).

Range, Distribution, and Abundance:

Global Range: Widely distributed across Canada and northeastern United States (Abbott 2007); most likely to be encountered in sphagnum bogs and very shallow well-vegetated waters in mountainous regions (Bryan 2008).

Washington: Known from one site in Pend Oreille Co.: a patterned sedge fen in Bunchgrass Meadows at 1524 m (5000 ft.) elevation (Paulson 2007).

Oregon: This species has not been found and is not expected in Oregon.

Federal land: Documented from Bunchgrass Meadows on the Colville National Forest (Sullivan Lake Ranger District). Bunchgrass Meadows is now an official Research Natural Area.

Abundance estimations are not known for this species.

Habitat Associations:

This species is found in sedge- and moss-filled fens, at the foot of hillsides below seepage or in wide-open meadows. It is not usually encountered near open water. Adult males fly through stretches of tall grasses, sedges, and shrubs (Paulson 2008, *pers. comm.*).

Bunchgrass Meadows, the only known habitat for this species in Washington, is a high elevation patterned sedge fen. Other highly specific habitat types have been documented in this genus. For example, the endangered *S. hineana* (Hine's Emerald), currently known only from the midwestern United States, favors small seeps draining calcareous escarpments through heavily vegetated wetlands (Bright 2005).

Threats:

Although this species is widely distributed across Canada and considered globally secure, it is unranked or considered imperiled in most states (secure in Maine). Bunchgrass Meadows, the one known site for this species in Washington, is a unique and interesting site for Odonata. It is also the only known Washington site for another *Somatochlora* species (*S. whitehousei*), and home to a population of *Coenagrion interrogatum*, a narrow-wing damselfly which is quite rare and local in the state (Paulson 2008, *pers. comm.*). This site contains no non-native vascular plant species and is noticeably unique in terms of both animal and plant diversity (Ahlenlager 2008). It requires serious conservation efforts, and has recently gained federal protection as an official Research Natural Area (RNA) (USDA Forest Service 2008, Ahlenlager 2008, *pers. comm.*). The main goal of an RNA is to provide opportunities for non-manipulative and non-destructive research in ecosystems that are free from human impact and influenced only by natural processes. Current management of the Bunchgrass RNA includes prohibiting grazing, logging and mining, discouraging recreational use (horseback riding and berry picking are permitted), and reducing travel throughout the site.

Like other members of its genus, habitat disturbance and alteration are the greatest immediate threats to this species (Packauskas 2007). Specific activities that alter fen-habitat in Washington include peat mining, wetland grazing, manipulation of water levels, recreation, recreational development, and management of aquatic vegetation (Fleckenstein 2006). Although the population at Bunchgrass Meadows is now largely shielded from these threats (USDA Forest Service 2008), other potential populations in the area may not be. Insect and disease control (still allowed in Bunchgrass Meadows) may also threaten this species. Livestock grazing is not permitted within the Bunchgrass Meadows, although the LeClerc grazing allotment is adjacent to the RNA, and could potentially impact the hydrology of the site.

Climate-related changes in habitat suitability may threaten southernmost populations and shift the species' distribution northward. Projected changes in this region include increased frequency and severity of seasonal droughts and flooding, reduced snowpack to feed river flow, increased siltation, and increased air and water temperatures (Field *et al.* 2007), all of which could impact this species and its habitat unfavorably. Moreover, since many aspects of odonate survival (e.g. development, phenology, immune function,

pigmentation, and behavior) are sensitive to changes in temperature, global climate change is predicted to have serious consequences on this taxon (Hassall and Thompson 2008).

It is not known if disease and predation are serious threats to this species, but small populations are generally at greater risk of extirpation as a result of normal population fluctuations due to predation, disease, natural disasters, and other stochastic events.

Conservation Considerations:

Inventory: Survey for new sites near the known site at Bunchgrass Meadows, and elsewhere in northeast Washington. The species may occur in upland bog/fen habitat along the northern Washington border, a region that has not yet been surveyed for odonates (Paulson 2008, *pers. comm.*), and is in critical need of inventory. The Washington record is one of the southernmost extensions of this species' global distribution. Since global climate change is expected to threaten southern populations, continued surveys and abundance estimations at Bunchgrass Meadows and surrounding areas would be valuable in evaluating distribution shifts, population declines, and other climate-driven effects.

Management: Manage habitat-disturbing activities to minimize impacts to sedge meadow, fen, and bog-habitat. The following should be considered for management of bog/fen habitat (Sargent and Carter 1999):

- Protect mineral-rich ground-water sources from pollution.
- Avoid destruction of existing hydrology (e.g. diverting, damming, or altering water flow).
- Avoid disturbance of plant community (e.g. grazing or harvesting peat or sphagnum).
- Do not use fertilizers in or near wetland area, since such pollution can drastically change plant communities, often in favor of invasive species.
- Create a buffer zone at least 91 m (100 yards) around the wetland (This can be done by planting shrubs/grasses, or by keeping the area free of disturbance, including roads and trails).

As wetlands throughout Washington are being increasingly impacted by human activities, continued preservation of Bunchgrass Meadows and its ecologically valuable species is critical. However, insecticides and herbicides intended to protect the uniqueness of the native biota should not be used without serious consideration of their sublethal and lethal effects on other sensitive taxa in the community.

Prepared by: Sarah Foltz
Xerces Society for Invertebrate Conservation

Date: October 2008

**Edited by: Celeste Mazzacano, Sarina Jepsen & Scott Hoffman Black
Xerces Society for Invertebrate Conservation**

Date: October 2008

ATTACHMENTS:

- (1) References**
- (2) List of pertinent or knowledgeable contacts**
- (3) Maps of Global Range/Conservation Status, OR/WA Distribution, and Collection Locality at the Bunchgrass Meadows Site.**
- (4) Photographs of Adult (lateral and dorsal view), Emerging Adult, and Larva (dorsal view)**
- (5) Odonata (Anisoptera) Survey Protocol**

ATTACHMENT 1: References:

Abbott, J.C. 2007. "*Somatochlora franklini*" OdonataCentral: An online resource for the distribution and identification of Odonata. 2007. *Texas Natural Science Center, The University of Texas at Austin* 3 Oct. 2008
<<http://www.odonatacentral.org/>>.

Ahlenslager, K. 2008. Email exchange with Sarah Foltz regarding the establishment of Bunchgrass Meadows as a Research Natural Area.

Bright, E. 2005. "Notes on the Michigan species of *Somatochlora*." *Odonata Larvae of Michigan*. 7 July 2005. University of Michigan- Museum of Zoology. 7 Oct. 2008
<<http://insects.ummz.lsa.umich.edu/michodo/test/Somatoch.htm>>.

Bryan, N. 2008. "Delicate Emerald, *Somatochlora franklini*" *Talk About Wildlife*. 24 Oct. 2008 <<http://talkaboutwildlife.ca/profile/?s=747>>.

Field, C.B., Mortsch, L.D., Brklacich, M., Forbes, D.L., Kovacs, P., Patz, J.A., Running, S.W. and M.J. Scott. 2007. Chapter 14: North America. In: *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E., eds.). Cambridge University Press, Cambridge, UK. Available at: www.ipcc.ch/pdf/assessment-report/ar4/wg2/ar4-wg2-chapter14.pdf.

Fleckenstein, J. 2006. "*Coenagrion interrogatum* Species Fact Sheet." *Interagency Special Status / Sensitive Species Program (ISSSSP)*. Jan. 2006. OR-WA Forest Service / Bureau of Land Management. 15 Oct. 2008

<<http://www.fs.fed.us/r6/sfpnw/issssp/species-index/fauna-invertebrates.shtml>>.

Hassall, C. and D.J. Thompson. 2008. The effects of environmental warming on Odonata: a review. *International Journal of Odonatology* 11(2): 131-153.

NatureServe. 2008. "*Somatochlora franklini*." *NatureServe Explorer: An online encyclopedia of life [web application]*. Feb. 2008. Version 7.0. NatureServe, Arlington, Virginia. 6 Oct. 2008 <<http://www.natureserve.org/explorer/>>

Packauskas, R.J. "Hudsonian Emerald Dragonfly (*Somatochlora hudsonica*): a technical conservation assessment." 24 Aug. 2007. *USDA Forest Service, Rocky Mountain Region*. 16 Oct. 2008

<<http://www.fs.fed.us/r2/projects/scp/assessments/hudsonianemeralddragonfly.pdf>>

Paulson, D. 2008. E-mail exchange with Sarah Foltz, including content from his upcoming book, *Dragonflies and Damselflies of the West*, to be published by Princeton University Press, Spring 2009.

Paulson, D. 2007. "Washington Odonata." *Slater Museum of Natural History*. Oct. 2007. University of Puget Sound. 6 Oct. 2008

<<http://www.ups.edu/x7041.xml>>.

Sargent, M.S and Carter, K.S., ed. 1999. Managing Michigan Wildlife: A Landowners Guide. Michigan United Conservation Clubs, East Lansing, MI. 297pp.

Tennessen, K. 2007. *Odonata Larvae of the Pacific Northwest: An Identification Manual*. Created for use in a taxonomic workshop sponsored by the Xerces Society and held at Evergreen State College, Olympia, Washington, March 16-18, 2007.

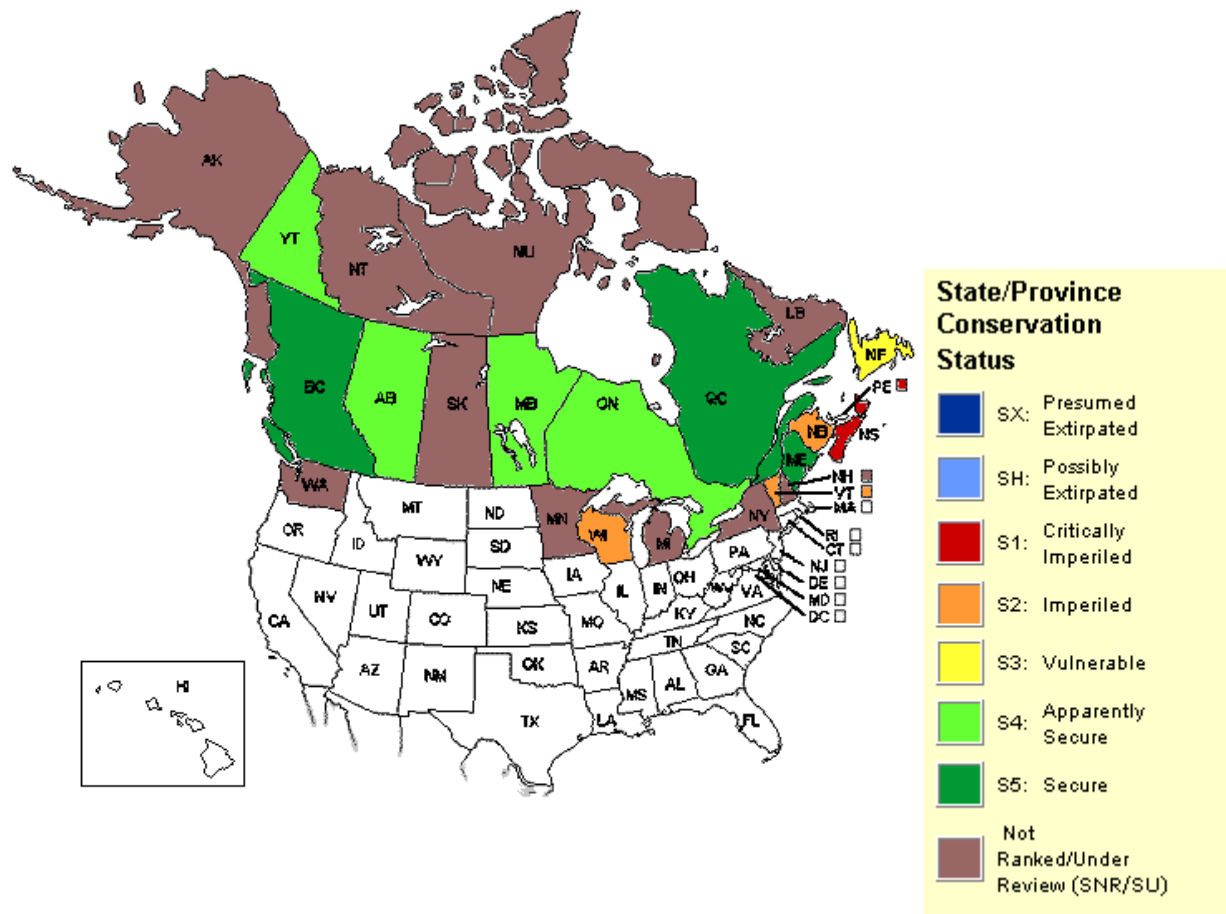
USDA Forest Service 2008. Environmental Assessment. Bunchgrass Meadows Research Natural Area Establishment and Forest Plan Amendment. 27 Oct. 2008

<<http://gis.fs.fed.us/r6/colville/projects/nepa/so/bunchgrass/20080708-final-bunchgrass-rna-ea.pdf>>.

ATTACHMENT 2: List of pertinent, knowledgeable contacts:

Dennis Paulson
Steve Valley
Ken Tennessen
John Abbott

ATTACHMENT 3: Maps of Global Range/Conservation Status, OR/WA Distribution, and Collection Locality at the Bunchgrass Meadows Site.



North American State/Province Conservation Status of *Somatochlora franklini*. Map prepared by NatureServe (2008).

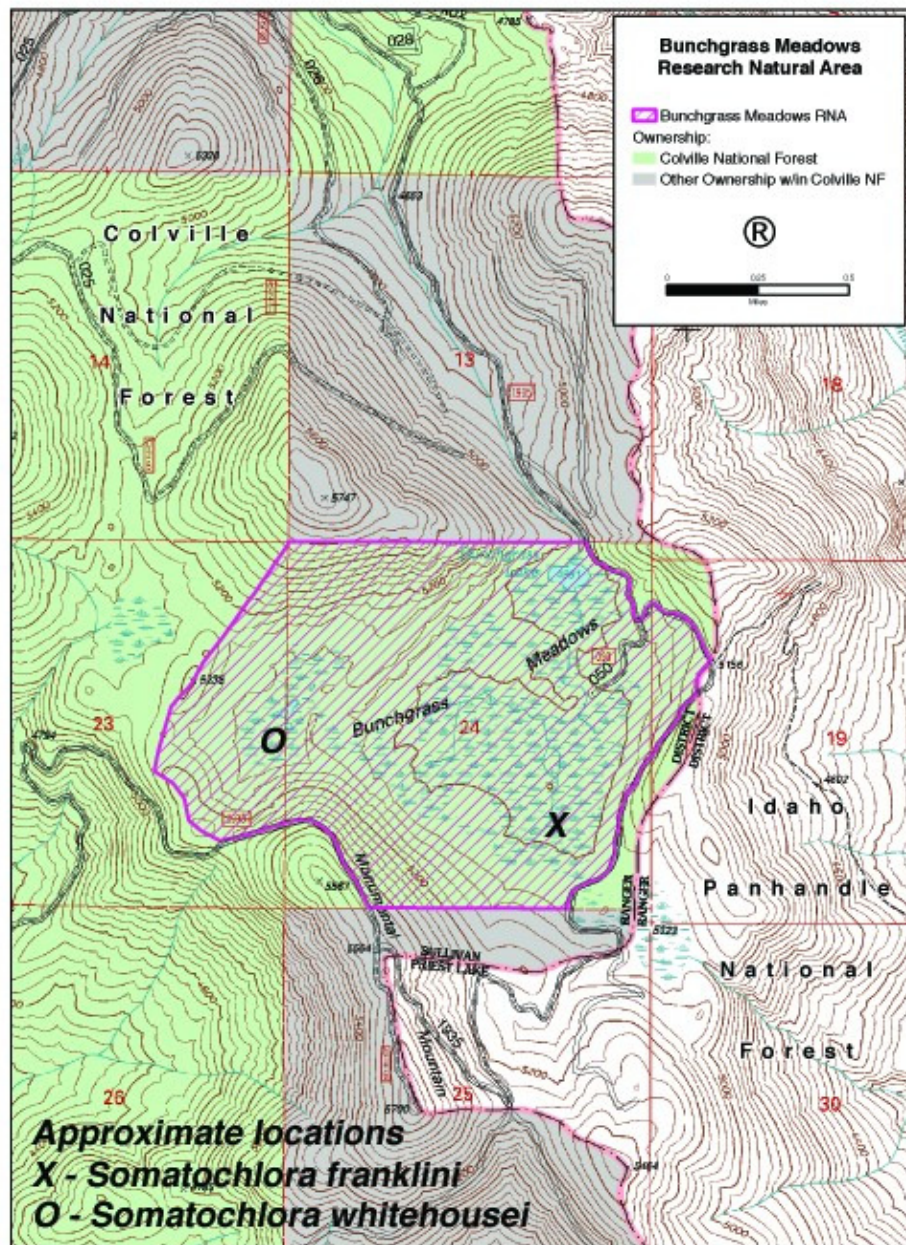
Odonata

• *Somatochlora franklini*

- National Forest
- Bureau of Land Management
- National Park



Records of *Somatochlora franklini* in Washington and Oregon, relative to BLM and USFS land. BLM District boundaries are shown in black, and Resource Area boundaries are shown in grey.



Specific location at the Bunchgrass Meadows site where *Somatochlora franklini* was found. Note, also, the location of congeneric *S. whitehousei*. Map provided by USDA (2008). Collection location provided by Dennis Paulson.

**ATTACHMENT 4: Photographs of adult (dorsal and lateral views),
emerging adult, and larva (dorsal view):**



Mozilla Firefox.Ink

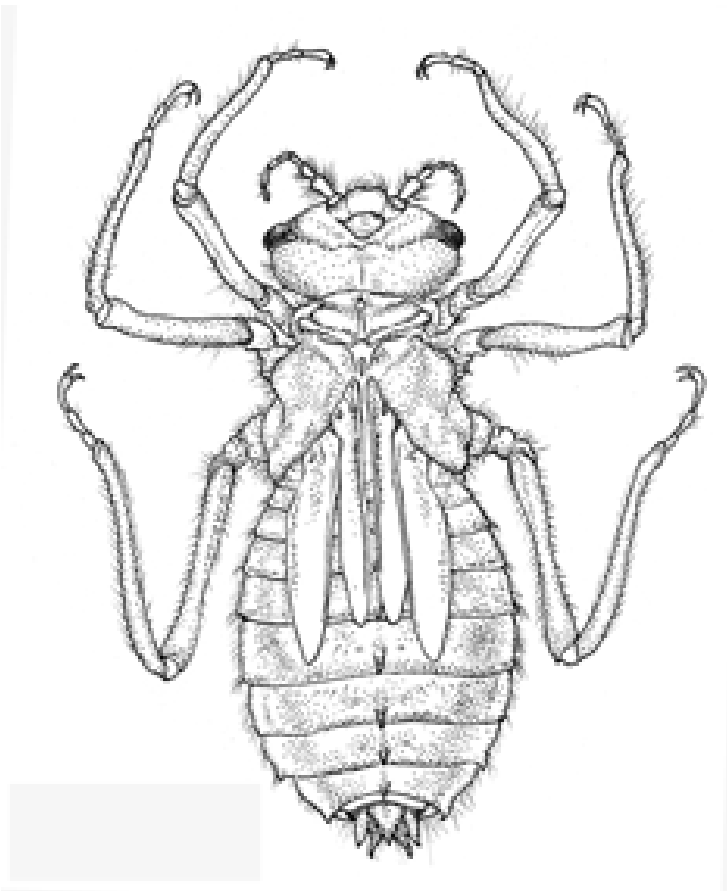
Somatochlora franklini adult male. Photograph by Denis Doucet, Atlantic Canada Conservation Data Centre.



Somatochlora franklini adult male. Photograph (digital scan in life) by Dennis Paulson.



Congeneric *Somatochlora kennedyi* emerging. Photograph by Denis Doucet, Atlantic Canada Conservation Data Centre.



Congeneric *Somatochlora hineana* larva. Photograph of *S. franklini* larva not available at this time. Illustration by Susan Fawcett.

ATTACHMENT 5: Odonata (Anisoptera) Survey Protocol:

Survey Protocol

Where:

Adult odonates can be found feeding in range of terrestrial habitats, but are most effectively sampled at the aquatic habitat where they mate and oviposit. Ponds, streams, rivers, lake shores, marshes, bogs, and fens support a range of odonate diversity. Some species (e.g. *Gomphus kurilis*) frequent a variety of habitats, while others (e.g. *Leucorrhinia borealis*) have highly specific preferences with regard to substrate, vegetation, and water quality. For species-specific habitat information, see the section at the end of this protocol.

When:

Adults are surveyed in summer, during the often-short window of their documented flight period. Adult odonates are most active in warm temperatures, and usually begin to fly at the aquatic habitat with the morning sun. Depending on the species, males arrive as early as 9 am and leave as late as 6 pm. Females tend to arrive several hours later, after the males have

established their mating territories (Campanella 1975). In the high temperatures of the late afternoon, some species seek shade in trees and vegetation.

Although larvae are present all summer, it is preferable to sample later in the season (i.e. just prior to and during the early part of adult emergence), when a higher proportion of the more easily identified late larval instars will be found.

Adult Surveys:

Use a long-handled, open-mesh aerial net, light enough to be swung rapidly. Triplehorn and Johnson (2005) recommend a 300-380 mm diameter net with a handle at least 1 m long.

Approach the site quietly, observing the environment and natural behaviors occurring prior to sampling. Note the number of different species present, and what their flight patterns are. This will help in predicting the movement of target species, and in evaluating whether the site has been surveyed “exhaustively” (i.e. all species observed at the site have been collected or photodocumented). Since dragonflies are wary of humans and readily leave an area when disturbed, it is important to be as discreet in your movements as possible, at all times.

Watch vegetation, logs, tree-trunks, and large, flat rocks for perched individuals, particularly those in the Gomphidae and Libellulidae families. Since dragonflies are powerful fliers and notoriously challenging to catch, try to quietly photo-document specimens prior to attempting to capture. Use a camera with good zoom or macrolens, and focus on the aspects of the body that are the most critical to species determination (i.e. dorsum of abdomen, abdominal terminalia (genitalia), pleural thoracic markings, wing markings, eyes and face). For helpful tips, see the article “Photographing Dragonflies” (Nikula 1997) available at: <http://www.odeneews.org/PhotoArticle.htm> (last accessed: 25 Oct. 2008).

When stalking perched individuals, approach slowly from behind, covering your legs and feet with vegetation, if possible (dragonflies see movement below them better than movement at their level). When chasing, swing from behind, and be prepared to pursue the insect. A good method is to stand to the side of a dragonfly’s flight path, and swing out as it passes. After capture, quickly flip the top of the net bag over to close the mouth and prevent the insect from escaping. Once netted, most insects tend to fly upward, so hold the mouth of the net downward and reach in from below when retrieving the specimen. Collected specimens should be placed on ice in a cooler long enough to slow their movement (a few minutes), and then set on a log or stone and comprehensively photographed until the subject starts to stir. Specimens to be preserved should be placed alive, wings folded together, in glassine or paper envelopes, as they lose color rapidly once killed. Record the eye color and

locality/collection data on the envelope, including longitude and latitude if possible.

Acetone, which helps retain bright colors, is recommended for killing odonates. Glassine envelopes with the lower corner clipped and the specimen inside should be soaked in acetone for 24 hours (2 to 4 hours for damselflies) and then removed, drained, and air-dried. The resulting specimens are extremely brittle, and can be stored in envelopes, pinned with wings spread, or pinned sideways to conserve space. Mating pairs in tandem or copula should be indicated and stored together, if possible. Collection labels should include the following information: date, time of day, collector, detailed locality (including water-body, geographical coordinates, mileage from named location, elevation, etc.), and detailed habitat/behavior (e.g. "perched on log near sandy lake shore"). Complete determination labels include the species name, sex (if known), determiner name, and date determined.

Relative abundance surveys can be achieved by timed watches at designated stations around a site. We recommend between 5 and 10 stations per site, each covering one square meter of habitat, and each monitored for 10 to 15 minutes. Stations should be selected in areas with the highest odonate usage, and spread out as evenly as possible throughout the site. During and one minute prior to the monitoring period, observers should remain very still, moving only their eyes and writing hand. Recorded information should include start and end times, weather, species, sex, and behavior (e.g. male-male interaction, pair in tandem). Observations occurring near, but outside of, the designated station should be included but noted as such.

Catch and marked-release methods can help evaluate population sizes, species life-span, and migration between sites. This strategy (most appropriate if several sites are being surveyed repeatedly throughout a season) involves gently numbering the wing with a fine-tip permanent marker before release.

Larval Surveys:

When surveying for larvae, wear waders, and use care to avoid disrupting the stream banks, vegetation, and habitat. Depending on the habitat, a variety of nets can be useful. D-frame nets are the most versatile, as they can be used in both lotic and lentic habitats. Kick-nets are only useful when sampling stream riffles, and small aquarium nets are most effective in small pools. If desired, relative abundance between sites or years can be estimated by standardizing sampling area or sampling time. When the use of a D-frame net is not feasible (e.g. in areas that have very dense vegetation, little standing water, and/or deep sediment), an alternative sampling device, such as a stovepipe sampler, can be used. This cylindrical enclosure trap (~34 cm in diameter and 60 cm in height) is quickly forced down through the water/vegetation and firmly positioned in the bottom substrate. Material and organisms are then removed by hand using small dip nets (Turner and Trexler 1997).

Net contents are usually dumped or rinsed into shallow white trays to search for larvae more easily, as they are quite cryptic and can be difficult to see if they are not moving. White ice-cube trays may also aid in field sorting. Voucher collection should be limited to late instar larvae, which can be most readily identified. If necessary, early instars can be reared to later stages or adulthood in screened buckets/aquaria with tall grasses added for emergence material. However, since the rearing process often takes many trials to perfect, it is only recommended if knowledge of species' presence-absence status at a particular site is critical, and few-to-no late instars or adults are found.

Voucher specimens can be either (1) preserved on-site in sample vials filled with 80% ethanol, or (2) brought back from the field in wet moss/paper-towels, killed in boiling water, cooled to room temperature, and transferred to 80% ethanol. Although the latter method is more time intensive, it is recommended for maximum preservation of internal anatomy (Triplehorn and Johnson 2005). Live specimens should be separated by size during sorting to reduce cannibalism/predation.

Although easily overlooked, larval exuviae left on rocks, sticks, or vegetation on which the adult emerged are valuable for species documentation. These cast-off exoskeletons of the final larval instar can be identified to species using larval traits, and offer a unique, conservation-sensitive sampling method for odonates (Foster and Soluk 2004). Since exuviae indicate the presence of successful breeding populations at a particular locale, their habitat data can be very informative, and should be documented with as much care as that of larvae and adults.

Species-specific survey details:

Somatochlora franklini

This species is not found (or expected) in Oregon, and is known in Washington from only one site (Bunchgrass Meadows, Pend Oreille Co.). The species may also occur in upland bog/fen habitat along the northern Washington border, a region that has not yet been surveyed for odonates (Paulson 2008, *pers. comm.*), and is in critical need of inventory. The Washington record is one of the southernmost extensions of this species' global distribution. Since global climate change is expected to threaten southern populations, continued surveys and abundance estimations at Bunchgrass Meadows and surrounding areas would be valuable in evaluating distribution shifts, population declines, and other climate-driven effects.

Sites should be surveyed at midday, between 30 Jul- 24 Aug. Approach sites quietly, watching for ovipositing females and males patrolling the aquatic habitat for mates (Bryan 2008). Males fly back and forth at waist height, with frequent hovering; females oviposit by tapping the abdomen onto wet moss or water in tiny pools (Paulson 2008, *pers. comm.*). Members of this family are relatively elusive, spending a considerable amount of time in high altitude flight

(3-10 meters), and often perching high in the canopy, out of the range of camera or net (Nikula 2007). Adults perch by hanging, either vertically or obliquely, from sticks or vegetation. The larvae of this species are sprawlers, living on the surface of floating leaves or fine sediment (Merritt *et al.* 2008), where they “sit-and-wait” to ambush and engulf their prey (Packauskas 2005).

While researchers are visiting sites and collecting adults and exuviae, detailed habitat data should also be acquired, including substrate type, water source, water velocity, and presence/use of canopy cover (Packauskas 2007).

References (Survey Protocol Only):

Bryan, N. 2008. “Whitehouse's Emerald, *Somatochlora whitehousei*” *Talk About Wildlife*. 24 Oct. 2008 <<http://talkaboutwildlife.ca/profile/?s=754>>.

Campanella, P.J. 1975. The evolution of mating systems in temperate zone dragonflies (Odonata: Anisoptera) II: *Libellula luctuosa* (Burmeister). *Behaviour* 54: 278-310.

Foster, S.E. and D.S. Soluk. 2004. Evaluating exuvia collection as a management tool for the federally endangered Hine's emerald dragonfly, *Somatochlora hineana* Willaimson (Odonata: Cordulidae). *Biological Conservation* 118: 15-20.

Merritt, R.W., Cummins, K.W., and M.B. Berg. 2008. An introduction to the aquatic insects of North America. Fourth Edition. Kendall/Hunt Publishing Co., Dubuque, Iowa. 1158pp.

Nikula, B. 1997. “Photographing Dragonflies” 13 September 1997 *Ode News*. 22 Oct. 2006 <<http://www.odenews.org/PhotoArticle.htm>>.

Packauskas, R.J. “Hudsonian Emerald Dragonfly (*Somatochlora hudsonica*): a technical conservation assessment.” 24 Aug. 2007. *USDA Forest Service, Rocky Mountain Region*. 16 Oct. 2008
<<http://www.fs.fed.us/r2/projects/scp/assessments/hudsonianemeralddragonfly.pdf>>

Paulson, D. 2008. Personal communication. E-mail exchange with Sarah Foltz regarding Pacific Northwest odonates.

Triplehorn, C. and N. Johnson. 2005. Introduction to the Study of Insects. Thomson Brooks/Cole, Belmont, CA. 864pp.

Turner, A.M. and J.C. Trexler. 1997. Sampling Aquatic Invertebrates from Marshes: Evaluating the Options. *Journal of the North American Benthological Society* 16(3): 694-709.