

**Terrestrial invertebrates:
functional roles in ecosystems and
utility as vital signs in the Sierra Nevada**

by
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A) Background

The vital signs program is designed to monitor key ecosystem components in order to detect shifts in overall system health. Terrestrial invertebrates actually represent most of the ecosystem in terms of species richness, abundance, and trophic web structure, so it is important to monitor this dominant assemblage. Meadow invertebrates are potentially ideal candidates for monitoring, because these animals 1) include representatives of several trophic levels and are important food resources and processors of organic material, 2) represent a “crossroads” for ecological flows, e.g., aquatic-terrestrial, 3) are easy to sample quantitatively, and 4) are sensitive to a variety of stresses and in turn are capable “vectors” for cascading disturbances.

Meadows are expected to be an important element of the ecosystem model, and monitoring of meadow invertebrates would be a powerful complement to ongoing meadow vegetation sampling. For instance, there is often an assumption of relatively linear animal response to vegetation shifts (“If we build it they will come”), but animals respond to many other variables besides vegetation. Sampling fauna directly, in addition to vegetation monitoring, should provide a more complete assessment of the meadow segment of the ecosystem model. This report will describe some of the ecosystem roles, utility as vital signs, and functional responses of invertebrates, or as E.O. Wilson describes them, “the little things that run the world” (Wilson 1987). Some sections will emphasize our research group’s current efforts, in part because relatively little is known about some invertebrate processes in the Sierra and other alpine meadow systems.

B) Importance of invertebrates in ecosystem function

“Why consider conserving insects? . . . In short, they make ecosystems tick. . . . They cannot be ignored” (Samways 1994).

Coleman and Hendrix (2000) argue persuasively that invertebrates are “webmasters” that govern ecosystem function to a degree far out of proportion to their biomass. Invertebrates are critical in decomposition, nutrient cycling, physical processes, and disturbance regimes (Meffe and Carroll 1997). As an example, soil invertebrates modulate the following to varying degrees: soil temperature, moisture, nutrients, plant species composition, soil compaction, mixing, trace gas production, aggregate formation and stability, soil crusting, aeration, runoff, carbon storage, organic matter stabilization, macropores, water transport, and microbial community structure (Anderson 2000, Whitford 2000). Ants can be considered keystone species in seasonally dry ecosystems because of their role in macropore formation alone (Whitford, 2000).

Janzen (1987) considers insects to be the “glue and building blocks” of ecosystems. He outlines three prominent roles: 1) as prey items, with the caveat that vertebrate predators are often surprisingly picky; “Insect species are not merely interchangeable bits of nutrients,” 2) as seed destroyers, and 3) as pollinators.

Insects are also important ecosystem regulators via the action of many species as powerful herbivores. The strength of this regulation is a function of small size, easily amplified biomass via short time to first reproduction, sensitivity to ecosystem condition communicated via airborne chemicals, diversity of niches occupied, and direct and indirect effects on primary production (Schowalter 2000).

Primary productivity is, however, regulated via pathways other than herbivory. Bolger et al. (2000) suggest a triad of determinants of ecosystem productivity: plant biodiversity (e.g., Tilman et al. 1996), mycorrhizae (van der Heijden 1998, Read 1998) and a third, poorly understood influence, invertebrate decomposers.

Although generally minute, most ecological interactions, functions, and flows must pass through various invertebrate taxa. A recent and elegant study by Bailey and Witham (2002) provides a fine example. This work investigated population dynamics of mammals, trees, arthropods, and birds in montane Arizona and showed that this system was controlled by a mixture of top-down and bottom-up effects. For instance, indirect effects of elk on fly populations in turn strongly influenced the balance of the ecosystem. Samways (1994) notes that “conservation action has broadened from local to global concern, from vertebrates to invertebrates, and from isolated vertebrate species to the interactiveness of whole ecosystems.”

C) Role of invertebrates in trophic webs

Invertebrate trophic webs can be staggeringly complex. Sugden (2000) offers one such example from the Sierra Nevada: The Western Sand Wasp, which functions as both a predator and pollinator, preys on the Big Black Horse Fly, which in turn preys on humans and other large mammals. Via such predation, the Bodega Gnat benefits from reduced competition with the Big Black Horse Fly for mammalian blood meals. Eggs of the Big Black Horse Fly are parasitized by a scelionid wasp. Larvae of Edwards' Cuckoo Wasp attack the larvae of the Western Sand Wasp. The Cuckoo Wasp, does not get a free lunch, as it is in turn parasitized by Sacken's Velvet Ant. This food web could be expanded almost indefinitely. There is a perception that tropical food webs are more complex than those of temperate regions, but this is not true (Schoenly et al 1991); Sugden's relatively small extract of a Sierran web indicates the depth of temperate trophic complexity.

Insects dominate many food webs (Schoenly et al 1991), and food chain lengths for insect components of webs range from three to as high as seven. Insect "roles reach beyond occupying merely the critical middle links in ecosystems or the occasional position of top predator in unusual places such as caves" (Schoenly et al 1991). Much trophic complexity can be captured via monitoring invertebrates alone (see vital signs section).

Insects are generally thought of as vertebrate food, and indeed, this is an important function. The Mountain Yellow-Legged Frog preys on both aquatic and terrestrial insects (Mullally 1953, Zwiefel 1955). Terrestrial insects are critical prey (Healy 1985) for numerous bird species, and invertebrate sampling is an integral

component of many bird management programs (Blackburn et al. 1975, Martin and McGinnes 1975, Healy 1985, Jackson et al 1987, Hollifield and Dimmick 1995, Peoples et al. 1996). Invertebrates are also important in many mammal diets, e.g., various invertebrates make up 40% of alpine ground squirrel diet (Valdez and Ceballos 1991).

Nonetheless, insects themselves serve as high-level predators in many more habitats than would be thought (Schoenly et al 1991). There are at least four levels of insect consumers in Sierran alpine meadows (Holmquist, pers. obs.), for instance, herbivorous leaf-hoppers, preyed upon by spiders, which are preyed upon by wasps, which in turn fall prey to other wasps. With further examination, meadow insect webs will probably prove to be at least as complex as Sugden's (2000) example from drier Sierra terrain.

The "stealth" trophic function of invertebrates is decomposition. As an example, millipedes in Big Bend National Park have been found to be key detritivores (Crawford 1976) that make nutrients available to other organisms.

D) Invertebrates as links between habitats

“Mobile link organisms” are critical for tying together resources, propagules (e.g., pollen), and processes (Lundberg and Moberg 2003). Invertebrates are particularly important as linkages at critical interfaces: land/air (litter, soil, plant canopies), root/soil, and land/water (Coleman and Hendrix 2000). As an example of organisms as ecosystem links, Holmquist et al. (1998), found a functional group of invertebrates to facilitate flows among three disparate systems: uplands, stream, and the ocean.

There are several examples of trophic linkages across land/water boundaries in California, and in particular the Sierra. Grasshoppers have been shown to graze river algae (Bastow et al. 2002). The Mountain Yellow-Legged Frog depends in part on terrestrial invertebrates (Mullally 1953, Zwiefel 1955). One of the most striking examples of such a trophic linkage is that of *Desmona bethula* (Erman 1981). This caddisfly larva leaves streams at night to feed on terrestrial plants. One warm summer nights, the caddis will remain out of the water until dawn.

Alpine meadows are a particularly active arena for mobile link organisms. Meadow invertebrates are tightly-bound to neighboring streams, lakes, and ponds. Many aquatic larvae emerge from streams and ponds to spend their adult lives in meadows before returning to the water to deposit eggs. Examples can be drawn from the beetles, Diptera, mayflies, stoneflies, and caddisflies (Arnett 2000). Many organisms that are aquatic as larvae are important pollinators in meadows, and these species are also important prey for vertebrates in these terrestrial habitats.

Our current work in DEPO (contract R8590030067) is showing that there are very strong aquatic/terrestrial linkages *within* meadows. Meadows are flooded in the

first three weeks after snowmelt. During this time, the meadows are pond-like with emergent vegetation or slough-like with slow drainage into the nearby river and streamlets. In the wet phase, meadows are miniatures of Marjorie Stoneman Douglas' (1947) "Rivers of Grass," also known as the Everglades. The meadows are similarly teeming with life, and the mud appears alive with wriggling larvae, up to 1,000 or more per square meter. Our project is demonstrating that the majority of annual insect production in the DEPO meadows occurs in the flooded portions of meadows during this short time period. Many of these insects spend their adult lives in the neighboring dry portions of meadows. However, our work suggests that most of the insects emerging from the wet-phase meadows are transported into nearby upland forests and thus fuel the food webs in these habitats. Meadows are thus a nexus for exchanges with streams and forests as well as aquatic-terrestrial linkages that are internal to the meadow system.

E) Invertebrates and disturbance

Invertebrates are particularly sensitive to disturbance— and some are exquisitely sensitive— because most of these organisms can emigrate as well as suffer mortality *in situ*. In addition, effects are often amplified by rapid reproduction or lack thereof. However, disturbance will often increase diversity in invertebrate assemblages if disturbance levels are similar to, or lower than, natural rates of disturbance (Brown 1997), a finding that is an additional perspective on “intermediate disturbance” (Horn 1975, Connell 1978).

Management practices often affect invertebrate populations in striking fashion. Logging and related activities can devastate insect assemblages (Intachat et al. 1997, 1999). Fire, in contrast, often has positive long-term effects on invertebrate populations (James 1991, Seastedt 2000).

Nitrogen deposition is considered to be a threat to ecosystems and is certainly a concern for SEKI. However, effects can be complex; fertilization experiments have resulted in increases in soil nematodes and microarthropods (Seastedt et al 1988, Blair et al. 2000).

Mining activities have been shown to negatively affect grasshoppers (Andersen et al. 2001). This effect is direct and not mediated by effects on vegetation.

Pesticides, like nitrogen deposition, pose a threat to SEKI invertebrate species because of proximity to the Central Valley. Pesticide impacts on terrestrial invertebrates are well-documented and one of the most damaging ecosystem effects is loss of pollinators (Allen-Wardell et al. 1998). In a worse case scenario, pesticide input in combination with habitat fragmentation can result in a “pollination crisis” (Allen-Wardell

et al. 1998; Lundberg and Moberg 2003) in which an entire functional group of “genetic linkers” are extirpated (Lundberg and Moberg 2003). As an example of how devastating this loss can be, almond framers in California have lost virtually all wild pollinators, necessitating the import of managed honeybees (Watanabe 1994). Harrington et al. (1999) have identified a related problem and have suggested that increases carbon dioxide could cause disastrous offsets in the timing of plant flowering and their pollinator presence. These case studies provide examples of how invertebrates can serve as disturbance vectors, transferring effects to other taxa and locations.

Invertebrates are as vulnerable as plants and vertebrates to exotics; invasive insects can greatly reduce diversity of native invertebrates (Porter and Savagnano 1990, Vinson 1994, New 1995). Parasitoids introduced to Hawaii to control nuisance moths probably extirpated numerous native species (Zimmerman 1948). Exotic ants are likely to have eliminated many other Hawaiian moth species (Gagné and Howarth 1984). The loss of the caterpillars of these species in turn may have led to the extinction of their native predators, such as wasps and contributed to the decline of native bird species (Zimmerman 1948, New 1995). Hymenoptera (ants, wasps, and bees) are generally viewed as the most pernicious arthropod invasives (New 1995). The Argentine ant, the Long-Legged ant and the Big-Headed ant have caused the decline of many native ant and spider species via competition and predation (Gillespie and Reimer 1993, New 1995). *Vespula* wasps introduced in New Zealand compete for honeydew with native insects (Beggs and Wilson 1991).

Moyle and Light (1996a; b) suggest that native species richness is a poor predictor of resistance to exotics and that an intact natural disturbance regime is the

most important factor in limiting establishment of invasive species. While an intact disturbance regime is clearly important, Holmquist et al. (1998) showed an inverse relationship between abundance of exotics and native species richness and that this relationship can be more important than disturbance regime. These results are consistent with a positive relationship between invasion resistance and diversity (e.g., Elton 1958; Case 1991; Ross 1991; Vermeij 1991; Lodge 1993). Predators often prevent establishment of exotics (Lodge 1993), and Courtenay and Stauffer (1990) provide examples of establishment of exotics in the absence of predators.

Excessive take of collectable species such butterflies, although difficult to document, is a world-wide concern (New 1995). Beetles, particularly tiger beetles (Carabidae:Cicindelinae), are also targets. This threat is likely to increase in our Sierra parks.

“Probably some of the strongest effects of fragmentation on ecological processes will turn out to involve the invertebrate community” (Meffe and Carroll 1997); this contention has been supported in the relatively few fragmentation studies in which invertebrates have been the focus. Clearly, habitat patches can be reduced below thresholds needed for population maintenance. A more insidious effect of fragmentation is the creation of “hard” edges, i.e., ecotones of high contrast between habitats (Wiens et al. 1985). Such hard edges can inhibit movement and dispersal patterns and/or reduce population sizes (Holmquist 1998, Strong et al. 2002, Holmquist and Schmidt-Gengenbach 2002, Uhrin and Holmquist 2003), in part because invertebrates are typically very sensitive to changes in microclimate as a result of fragmentation (Klein 1989, Didham et al. 1996, references in Samways 1994).

Population isolation is a common effect (DeVries and den Boer 1990, Frampton et al. 1995, Strong et al 2002). Carabid beetles have been extirpated in habitat fragments (Turin and den Boer 1988); flightless species and other poor dispersers are especially vulnerable (Niimalä et al. 1998, De Vries and den Boer 1990). Some carabids move no more than a few hundred meters in a year (Baars 1979), so isolation via fragmentation is not surprising. Spiders with poor dispersal capabilities can become restricted to only the largest of fragments (Hopkins and Webb 1984). Isolation by hard boundaries is particularly threatening in the context of climate change; animals may simply be unable move to suitable habitat as physical conditions in historical home ranges become untenable (Iverson and Prasad 1998, Noss 2001). Habitat isolation can be so severe that dispersal capability can be lost evolutionarily, as found by Dempster (1976) for butterflies. Losses of invertebrates to fragmentation can vector disturbances to other taxa via loss of pollinators, seed predators, herbivores, and predators (Didham et al. 1996).

Roads represent a special type of hard edge (Haskell 2000, Strong et al. 2002) and can be severe barriers, although effects depend greatly on the species in question (Samways 1994). Dispersal and other movement patterns of beetles and spiders are disrupted by roads (Oxley et al. 1974, Mader 1984, Mader et al. 1990). Roads are barriers as a function of a combination of factors including microhabitat (temperature, humidity, and evaporation level), vehicle emissions, noise, dust, headlight illumination, increased salinity, vegetation cutting and chemical spraying, plant composition, road mortality. Also, road mortality of insects, though taken for granted, can be significant (Samways 1994).

Foot trails in alpine meadows, though nominally less intrusive than roads, can have surprisingly large effects on invertebrates. Fragmentation of meadow plant assemblages by trails is relatively apparent, but effects on mobile fauna are more difficult to discern. Holmquist and Schmidt-Gengenbach (2002) sampled meadow invertebrate fauna in YOSE and DEPO using transects that ran perpendicular to trails in order to assess functional fragmentation of the meadow assemblage. Effects of trails extended further into the surrounding meadow habitat than would have been predicted on the basis of vegetation alone. Invertebrate assemblages in portions of meadows bordering trails had 24% of the abundance of "core" meadow areas across all species. Ants provide a good example of the extension of trail effects into intact meadow vegetation. There was an average of 1.6 ants per square meter in trails, and 5.0, 9.0, and 63.6 ants per square meter in vegetation next to trails, 2 meters from trails, and 5-10 meters from trails, respectively. Abundances on the trails were even lower than expected: there was a mean of only 10.2 invertebrates (of all types) per m² of trail versus 157.5 animals/m² of core meadow habitat. Trails negatively influenced higher trophic levels, including both primary (e.g., leafhoppers) and secondary (e.g., spiders) consumers. Invertebrates were affected over an area that was 20 times greater than that of the removed vegetation. As seen above, meadow invertebrates are tightly-linked to both aquatic and upland forest systems, and impacts to meadow fauna can be expected to cascade into these other habitats. Holmquist and Schmidt-Gengenbach (2002) recommend that footpaths should be planned with the understanding that ecological "footprints" of trails extend well beyond the confines of visible disturbance.

This work will be extended this summer to include assessment of footpaths in alpine meadows as barriers to insect movement.

Human and other trampling of non-trail substrata can also affect invertebrate fauna, although comparatively little is known in comparison to effects on vegetation (Bayfield 1979, Cole 1995a, b). Invertebrates in alpine meadow soil in Austria are negatively influenced by trampling (Meyer 1993). Abundance and species richness of soil fauna have been reduced in other systems due to soil compaction (Chappell et al. 1971; Dózsa-Farkas 1987). Trampling effects on mobile invertebrates in the aquatic environment can also be mediated by substrate modification (Eckrich and Holmquist 2000). Effects of heavy foot traffic on mobile terrestrial invertebrates have seen little attention, and these such impacts are likely to be significant in heavily-used national parks and monuments such as SEKI, YOSE, and DEPO, particularly in high elevation meadows with short growing seasons. A controlled experimental study would be easy to implement.

Snow sports can have impacts on invertebrates that share features with disturbances via trails, roads, and trampling. Meyer (1993) found soil invertebrates to be negatively affected by skiing, ski trail preparation, and snowmobiling. Above-ground, beetles are affected both in terms of assemblage structure and disruption of movement patterns (Strong et al. 2002). Haslett (1988) found fly assemblages in ski areas to shift from a complex group of specialists to domination by generalist species.

Grazing represents a complex suite of component disturbances including trampling, dewatering, soil compaction, incision, plant biomass removal, and alteration of nutrient dynamics; all have the potential to significantly degrade invertebrate

assemblages. Few studies address effects of grazing on invertebrates, and much of this work has been on soil fauna rather than plant-associated animals (Blair et al 2000). Exclosure experiments indicate reduction in soil nematodes in association with grazing (Blair et al 2000). Mowing experiments (Todd 1996) have also lowered abundances of soil nematodes. However, clipping of above-ground biomass can increase below-ground abundances of beetle larvae (Seastedt et al 1986), so overall effect of grazing on below-ground fauna remains unclear. Above-ground effects can be present as well. Meyer and Hans-Dieter (1996) showed that sheep grazing reduces insect species richness in a German salt marsh. Dennis et al. (1997) addressed grazing effects on carabid and staphylinid beetles experimentally using a series of treatments including sheep and cattle grazing of varying intensities in a UK grassland. The authors concluded that adapting grazing strategies to results derived from monitoring this beetle assemblage would allow managers to continue grazing, maximize insect biodiversity, and limit spread of an exotic plant.

With the help of Sylvia Haultain, I have conducted a limited pilot survey of invertebrates on grazed and non-grazed sites near Rock Creek in SEKI. The ungrazed sites had more total invertebrates than the grazed sites. There were more spiders (35 versus 16/sq m), leafhoppers (7 v 1/sq m), and ants (12 v 3/sq m) on the ungrazed sites versus the grazed sites. Most notably, there were 48 snails/sq m versus zero on the grazed sites. There were, however, more mites on the ungrazed sites than the grazed sites (40 v 9/sq m). I suspect that the mites were responding to the dryer conditions on the dewatered grazed plots. Although these results are only from three pairs of sites, the numbers suggest that grazing may be negatively affecting invertebrates of several

trophic levels. The second component of the current cooperative agreement will be the establishment of invertebrate monitoring sites such that both grazing impacts and efficacy of invertebrates as ecosystem vital signs can be assessed.

F) Ecology and natural history of alpine invertebrates

In one of the few thorough inventories of alpine meadow invertebrates, Dethier (1984) found 465 species in the Swiss National Park over a four-year period. Of these, 244 were new records for the Park, and ten species were new to science. Similarly, our current DEPO inventory is yielding high species richness and lack of dominance. Virtually every species collected is a new record for DEPO.

Tolbert et al. (1977) found that spiders, beetles, grasshoppers, and leafhoppers were the most common taxa in Colorado alpine tundra, and that arthropod abundances increased with soil moisture. Our recent results from YOSE are somewhat different: spiders, beetles, and leafhoppers were important faunal components, but ants and mites were the most common taxa, whereas grasshoppers were comparatively rare (Holmquist and Schmidt-Gengenbach 2002). Mites were our most abundant organisms (Acari; 24% of fauna), followed by ants (Hymenoptera; 23%), beetles (Coleoptera; 11%), leafhoppers (Homoptera; 11%), flies (Diptera, 10%), spiders (Araneae, 8%), and substantial numbers of bristletails, "true bugs", grasshoppers, caddisflies, moths, lacewings, and other insects. In our current DEPO survey we similarly collected few grasshoppers. Ants were much less important than in YOSE. The most abundant taxon was Diptera (35% of fauna), followed by leafhoppers (24%), spiders (13%), mites (12%), and beetles (9%), and lesser numbers of ants, true bugs, grasshoppers, Collembola, moths, and other insects. Bristletails were absent from DEPO. Both Tolbert et al. (1977) and Dethier (1984) noted an inordinate number of predators, and our YOSE and DEPO work also shows a relatively "top-heavy" trophic structure. The large number of spiders and other predators may be taking advantage of the many

transient species that emerge from aquatic habitats and pass through meadows on their way to forested uplands. Our work also demonstrates a correlation between soil moisture and arthropod abundance, but this trend is subordinate to elevational and seasonal gradients. For instance, drier meadows in Yosemite Valley had greater abundances than moister Tuolumne meadows.

We are currently conducting the first quantitative survey of invertebrates in flooded alpine meadows, and as noted above, these ephemeral meadow ponds have much higher abundance than neighboring dry portions of the same meadows in DEPO. Dry meadow samples had 163 arthropods/m², whereas ponded areas had twice as many animals with 329 arthropods/m² and some individual samples yielding over 1,000 animals m². There was a much higher level of dominance in the flooded areas as well as a different taxonomic composition: Diptera dominated with 88% of the fauna, followed by Coleoptera with 8%, and lesser numbers of mayflies, spiders, ants, mites, true bugs, and leafhoppers.

Meadows may be virtually isolated habitat islands for some species, because dispersal can be very limited. For example, Baars (1979) found annual movement of some beetles to be less than a few hundred meters, as discussed above. Some Sierra beetles have similarly small ranges (Papp, 1978). Shields (1997) reports relatively little movement by Sierra butterfly populations, although Shapiro (1973) describes significant altitudinal migrations for Sierra butterflies. Because of generally limited dispersal capabilities and/or behavior, even comparatively mobile fauna may be influenced by climate change. Species with narrow temperature tolerances, such as alpine meadow

grasshoppers (Coxwell and Bock 1995), are likely to be affected strongly by climate change.

There may be general altitudinal trends in meadow arthropod abundance and species richness in the Sierra. Low elevation sites had 2.5 times the overall abundance of high elevation sites (227 versus 91 animals/m²) in YOSE (Holmquist and Schmidt-Gengenbach 2002). Devil's Postpile NM, at an intermediate elevation, had intermediate abundances, with 163 arthropods/m². Mites and ants were the most common taxa at low elevation, whereas mites and flies were most common at high elevation. There were altitudinal differences within taxa as well. Mites, ants, leafhoppers, and bristletails were more common at low elevation than at high elevation, whereas the opposite held for flies, beetles, and spiders. Bristletails were absent from high elevation sites. True bugs, Lepidoptera (butterflies, moths, and skippers), Orthoptera (grasshoppers, crickets, and katydids), Neuroptera (lacewings), and Trichoptera (caddisflies) had relatively low abundances and showed few altitudinal trends (Holmquist and Schmidt-Gengenbach 2004). These elevational trends were season dependent, however. During late season there were fewer animals at all elevations (see below), but at this time there were more total animals at high elevation than low elevation (39 versus 9 animals/m²). This trend held across almost all orders and was particularly strong for mites and flies, which had over ten times as many representatives in Tuolumne than Yosemite Valley. This trend may be a function of higher late season soil moisture at higher elevations.

Although faunal abundances were higher at lower elevations in YOSE, species richness showed the opposite trend (Holmquist and Schmidt-Gengenbach 2004). High

elevation sites had about twice the species density as low elevation sites (6.7 species/0.25 m² versus 3.4 species/0.25 m²; 2-way ANOVA, $p = 0.00061$ for altitude, $p = 0.32$ for interaction with season), because low elevation sites had high numbers of a few common ant and mite species, particularly the ant *Solenopsis molesta*. Although ants and mites were also common at altitude, there were many species of flies, beetles, and spiders, and there was thus great evenness at high elevation sites.

Seasonal trends may be even stronger than those for abundance. Total abundances were nine times lower in late season than in early season (32 versus 285 animals/m²) in YOSE (Holmquist and Schmidt-Gengenbach 2002). These trends were present across all orders, although no taxon disappeared completely. Ants, mites, and bristletails lost over 90% of their abundance during the course of each summer (Holmquist and Schmidt-Gengenbach 2004). Spiders were the least affected by season; late season abundances were still 62% of early season abundances. Species richness was also higher in early season than in late season (7.1 species/0.25 m² versus 3.1 species/0.25 m²; 2-way ANOVA, $p = 0.000067$ for season, $p = 0.32$ for interaction with altitude). We are seeing similar trends in DEPO, although the seasonal reductions in fauna are somewhat less than in YOSE. Mean total abundance declined from 220 to 105 animals/m², i.e., by a factor of two instead of nine as in YOSE. Most taxa had seasonal losses, and mean number of beetles fell from 26 to 2 animals/m². However, spiders and ants maintained relatively constant numbers throughout the season, and a few grasshoppers appeared in late season despite being absent in early summer.

G) Invertebrates as vital signs

Numerous ecologists have argued against monitoring managed areas exclusively via plants and vertebrates, and have contended that invertebrates should play an important role as reserve selection criteria and as indicators because of the prominent role that these organisms play in ecosystem function (Refseth 1980, Disney 1986, Usher 1986, Majer 1987, Yen 1987, Eyre and Rushton 1989, Sutton and Collins 1991, Pearson and Cassola 1992, Usher 1992, Kremen et al. 1993, New 1993, Oliver and Beattie 1994). Plant data, though critically important, cannot serve a proxy for invertebrate assemblage health. For instance, Kremen (1992) found little concurrence between plant richness and butterfly richness along old trail and road edges. Similarly, Holmquist and Schmidt-Gengenbach (2004) found many fewer invertebrates in disrupted portions of meadows than in core meadow habitat, despite similar vegetation parameters throughout. Similar results have been reported from aquatic systems, e.g., Eckrich and Holmquist (2000) and Uhrin and Holmquist (2003).

Clark and May (2002), in a recent *Science* article, *Taxonomic bias in conservation research*, demonstrated that vertebrates are grossly over-represented in conservation and management efforts, whereas invertebrates are poorly represented in such programs. Insects are particularly useful as vital signs because of their abundance, species richness, ubiquitous presence, importance in ecosystem function (Holloway 1980, Rosenberg et al. 1986) and are particularly sensitive to disturbance, expressed both by mortality and emigration. As noted above, effects are often amplified by insects' prodigious reproductive potential. Also, the variety of trophic levels represented, even within a given taxon, makes for great indicator sensitivity (Samways

1994). For these reasons, invertebrates will often be better for rapid response “sentinel species” (New 1995) than vegetation surveyed in isolation.

Because of this utility, invertebrates have been used as indicators throughout the world; a few examples follow. Given the diversity present in neotropical forests, it is not surprising that insects have served as indicators in this system (Brown 1997). Europe has a long history of interest in landscape configuration, and moths, ants, and ground beetles (Carabidae) have been used as indicators of land use change (Eyre et al. 1986, Eyre and Luff 1990, Rushton et al. 1990, Ehrhardt and Thomas 1991, Luff and Woiwod 1995). Insects have also been used as indicators in evaluating grazing pressure in Germany (Meyer and Hans-Dieter 1996). In Australia, indicators have included grasshopper diversity in Kakadu National Park (Andersen et al. 2001) and leaf litter invertebrates in Barrine National Park (Jansen 1997). Use of invertebrates as indicators in Africa includes dung beetles in a savanna ecosystem in Tembe Elephant Park, South Africa (McGeoch et al. 2002) and snails in Madagascar (Emberton 1996).

It is not possible or advisable to monitor all species; there are simply too many! There are an estimated 10,000 arthropods species in eastern Sierra alone Sugden (2000). Use of a small subset of invertebrate taxa as indicators is most effective (Greenslade and New 1991, Kremen et al. 1993, Stork 1994).

There are various indicator species analyses available; one approach is determination of “Indicator Value” (Dufrêne and Legendre 1997). This measure combines a species’ abundance with frequency of occurrence in samples. The method is robust in the face of differences in numbers of sites among site groups, differences in

abundance between sites within a site group, and differences in abundances of taxa (McGeoch and Chown 1998). Indicator Value can help determine useful species or higher-level taxa to use as indicators, e.g., Magura et al. (2001), Andersen et al. (2001), and McGeoch et al. (2002). A particularly useful indicator subset are “detector species”—those that can be specifically used to detect subtle shifts in habitat type (McGeoch et al. 2002).

Rigid adherence to mathematically-determined indicators has limitations, however, and indicator choices based on past success, widespread use, and broad applicability may be more useful. Six characteristics that are desirable for insect groups as indicators are outlined by Hellawell (1986) and New (1995):

- 1) Reasonable, but not overwhelming diversity
- 2) Well-known taxonomy
- 3) Easily sampled
- 4) Sufficient abundance for reliable detection of changes in incidence and abundance
- 5) Widespread in the target ecosystem
- 6) A mixture of ecological roles in the taxon and knowledge of these roles

A number of groups have been used with success, such as Diptera and parasitic Hymenoptera (Disney 1986) and ants and termites (Andersen 1990). Ground beetles have been fairly widely used (Stork 1990, Eyre and Luff 1990, Freitag 1979, Pearson and Cassola 1995, New 1995). New (1984, 1987, 1995) suggests multiple indicator groups for terrestrial systems: Collembola (soil and litter, in decomposer food webs), leafhoppers and chrysomelid beetles (herbivores, often host-specific but with different

feeding ecologies), ants (particularly valuable because widespread and have many different trophic interactions), and ground beetles (active predators).

There is also information available on groups that have served as poor indicators. Kremen (1992) found butterflies to be good indicators of heterogeneity derived from topographic gradient, but of only limited use for detecting disturbance, and poor indicators of plant assemblage health. Luepke (1979, as per New 1995) also rejected the following taxa as potential indicators: tardigrades (water bears), nematodes, phytophagous insects, hymenopteran parasites, and centipedes. These non-recommendations are based on various factors including small biomass, poor information base, difficulty collecting, and redundancy with other taxa.

Ants have had great success as indicator groups in terrestrial systems (Greenslade 1978, Andersen 1990). Much of this utility is due to the following characteristics of ants: extremely abundant, high species richness, many specialists, some species occupy high trophic levels, easily sampled, easily identified, and responsive to changing environmental conditions (Majer 1983). Erhardt and Thomas (1991) found ants to be three times more responsive to environmental change than the plants with which they were associated. Use of functional groups and/or genera of ants can be particularly efficient, because these higher-level groups 1) bypass ignorance of species level biology, 2) simplify complex assemblages, 3) provide insights into major processes, 4) allow meaningful comparisons on large geographic scale (Andersen 1990).

We will be assessing potential arthropod vital signs for use in SEKI and YOSE via a small-scale monitoring project this summer and will be making recommendations

for vital signs as part of our final report. In the meantime, I believe that ant populations, at the generic or perhaps species level, are promising vital signs for monitoring ecosystem health in SEKI and YOSE. Additional monitoring of order (e.g., Hymenoptera, Diptera, etc.) and total arthropod assemblage abundances would probably be valuable and efficient as well, particularly for the short wet phase in early season. My contention that ant populations are a leading *a priori* contender as vital signs is based on our sampling to date in YOSE, DEPO, and SEKI and knowledge of the natural history of the group. Per Hellowell's (1986) criteria:

1) Reasonable, but not overwhelming diversity:

Our collections to date include three subfamilies, seven genera, and nine species. Several other species are likely to be collected by an extensive monitoring program.

2) Well-known taxonomy:

We have excellent species-level keys available, and in addition, RR Snelling will be publishing an additional regional key shortly.

3) Easily sampled:

Our vacuum apparatus works very well with ants. Tests with *Formica limata* yielded a 92% capture rate (see sampling methodology, below).

4) Sufficient abundance for reliable detection of changes in incidence and abundance:

Ants were important constituents of our collections. As seen above these abundances appear to respond to a variety of influences.

5) Widespread in the target ecosystem:

We collected ants from YOSE, DEPO, and SEKI, and ants were present in the majority of our samples.

6) A mixture of ecological roles in the taxon; knowledge of these roles:

Wheeler and Wheeler (1986), and others as cited, provide descriptions of a variety of ecological characteristics of the species collected to date (below):

Family Formicidae

Subfamily Formicinae

Camponotus herculeanus

Workers highly polymorphic, live in forest-dominated habitats in stumps, fallen trees, in heartwood of injured trees that are still standing, and soil. Eat dead and living insects, plants (sap and other secretions), seeds, fruit, pollen, nectar, fungi, honey, honeydew, do not eat wood removed from their galleries.

Myrmecocystus sp. (being confirmed)

Certain workers ("repletes") can store plant secretions and nectar in gaster, (adaptation to arid & semi-arid habitats) and will regurgitate to other workers on demand. Larvae are not fed from repletes, but rather on dead insects. Generalized predator-scavenger, rivals the seed-harvesting genera in abundance (Snelling 1976).

Formica

Anatomically unspecialized. Behavior plastic. Nest in soil under stones, or exposed soil surrounded by crater.

Neogagates group

Small colonies of few hundred individuals, nest in the soil under stones or in exposed soil with a crater around entrance. Small, timid, often enslaved by *Formica* in the *sanguinea* group and by *Polyergus*.

Formica limata

Formica neogagates

Will tend Homoptera for honeydew.

Fusca group

Formica neorufibarbis

Lives at high altitude; holds elevational record for Nearctic ant fauna (Gregg 1963). Generally docile. Brood reared quickly (adaptation to short summer). Feeds on honeydew, liquid from plants (mostly flowers), and dead arthropods (Francoeur 1973, Bernstein 1976).

Subfamily Dolichoderinae

Tapinoma sessile

Most common in forest-dominated areas. Common, wide-ranging, versatile, variety of habitats. Lives in soil under stones and other objects, under loose bark of stumps and logs, and in plant cavities. Workers do not exhibit the usual intraspecific hostility between colonies. Feed on secretions of floral nectaries, dead & living insects, sometimes cultivate aphids for honeydew.

Subfamily Myrmicinae

Solenopsis molesta

Monomorphic. Most common & widespread thief ant, nesting in walls separating chambers in nests of larger species, where this species robs food and brooded larvae; sometimes nests under stones, rotting wood, or exposed soil.

Omnivorous or predaceous, feeds on dead & live insects, can be highly granivorous also, workers known to tend mealybugs, plant lice, scale insects (Smith 1965).

Leptothorax crassipilis

Form small colonies in rotten wood, soil, insect galls, and nests of other species, with a preference for pre-formed cavities.

Myrmica sp. (being confirmed)

Montane genus. Prefers damp localities. Nests chiefly under stones, can be in soil or rotten wood. Workers carnivorous, but also feed on honeydew of Homoptera and exudates of plants (Smith 1979).

H) Sampling methodology

Because we are finding the early-season wet phase of alpine meadows to be so productive, I believe that it is important to sample these temporary impoundments in addition to the dry phase conditions that dominate the meadows both spatially and temporally. The D-frame hand net is typically used for sampling shallow temporarily flooded areas; other more methods include core and suction samplers (Merritt and Cummins 1996). I believe that most efficient and quantitative device for sampling still, shallow water with emergent vegetation is the throw trap (Kushlan 1981, Holmquist et al., 1989). A throw trap (or drop trap) is a box lacking a solid top or bottom that is cleared of fauna with a net) and have been shown to be highly efficient, relative to other collecting devices, for quantitatively sampling demersal organisms in vegetated habitats (Kushlan 1981, Freeman et al. 1984, Jacobsen & Kushlan 1987, Rozas & Minello 1997). Throw trapping of well-separated stations is effectively sampling with replacement (Jacobsen & Kushlan 1987), and re-sampling vegetated sites at six month intervals over a period of four years does not cause shifts in measures of vegetation cover or assemblages of mobile fauna (J.G. Holmquist, pers. obs.). Throw traps have been used in a number of habitats including freshwater marshes (Erwin et al. 1985, Jordan et al. 1994), shallow seagrass beds (Holmquist et al. 1989), seagrass several meters below the surface (Holmquist 1997), and flooded Mojave playas (Brostoff et al. submitted), and are currently in use in our DEPO inventory.

I recommend a device and protocol derived from that of Kushlan (1981) and Holmquist et al. (1989). The trap is a 0.5 m x 0.5 m box without a top or bottom and constructed of sheet aluminum. The clearing device is a 0.5 m-wide framed and

handled net (bar seine) with 0.5 mm square mesh. The trap is thrown downwind and then pressed into the sediment. The bar seine is passed repeatedly through the trap for a minimum of ten passes and until three successive passes produce no additional animals.

There are many different methods for sampling terrestrial meadows and grasslands. Techniques include sweep nets (Beall 1935), pitfall traps, pesticide knock-down, Malaise traps, visual counts, mark-release-recapture, attractants, sticky traps, and vacuums (Powell et al. 1996). Pitfall traps have been used fairly frequently, e.g., Meyer and Hans-Dieter (1996) and Nyffeler and Benz (1988) but obviously are not useful for flying species. We do, however, plan to use pitfall traps in conjunction with marking in order to investigate trails as barriers to movement this summer. Malaise traps are useful for taxonomists interested in certain groups, particularly several dipteran families, but are not quantitative and do not sample the majority of insect taxa (Powell et al. 1996). Malaise traps have been used successfully for an initial inventory in SEKI by Kimsey and Cranston (2002). Most of the remaining methods are similarly non-quantitative to varying degrees for sampling a broad spectrum of fauna.

Vacuums with nets inserted in the intake tube generally offer an improvement in efficiency, and this technique has been used in a variety of studies (Richmond and Graham 1969, Summers et al. 1984, Hand 1986, Macleod et al. 1994). Vacuums are more efficient than visual censuses (Arnold et al. 1973) or sweep netting (Dietrick et al. 1960, Callahan et al. 1966, Arnold et al. 1973, Buffington and Redak 1998), especially for ground dwellers (New 1998), because sweep netting underestimates ground-

dwelling invertebrates (Whittaker 1952, Hughes 1955). This increased efficiency incorporates both abundance and spp richness (Buffington and Redak 1998). Vacuums also cause less damage to invertebrates than sweep netting (Callahan et al. 1966) and are particularly efficient at removing animals in litter and lower vegetation (Stewart and Wright 1995). Vacuum sampling has been found to be most efficient when used with some form of enclosure box which is placed prior to suctioning (Henderson and Whittaker 1977, Hower and Ferguson 1972, Harper and Guynn 1998), although enclosures are often not used.

Despite the general efficiency of vacuum sampling, this method has not worked well in capturing rapidly-moving insects (Powell et al. 1996). The operator creates disturbance, and even if an enclosure box is used, flying and other vagile insects will flee the area before the enclosure is placed. Much of the efficiency of throw trapping is a function of the “throwing,” i.e., by tossing the trap from a distance, animals are captured before the field personnel are detected by the fauna. In an effort to create a terrestrial analog to the throw trap, Holmquist and Schmidt-Gengenbach (2002), constructed a 0.5 m² steel quadrat with a conical mesh covering. The mesh cone has an elasticized hole at the apex through which a vacuum intake tube can be inserted. This quadrat is thrown toward the target area from a distance and staked down to form a seal with the substrate. The vacuum intake is then inserted through the mesh aperture for sampling.

We use a Craftsman 320 km/h gasoline vacuum modified with a mesh collecting chamber inserted in the intake tube in conjunction with the netted quadrat. Henderson and Whittaker (1977) and Hossain et al. (1999) found that vacuum sampling is most

efficient if initial vacuum passes are made and then followed by clipping of vegetation and additional vacuuming. After staking the quadrat, we make multiple passes through the vegetation with the vacuum intake from different orientations over a two-minute period. Then the intake is removed, and the vegetation is clipped with electric trimmers inserted through the elasticized aperture of the netted quadrat. The trimmers are then removed and the intake inserted for an additional two minutes of sampling. The intake is then extracted from the quadrat, the integral mesh collecting bag is removed from the intake tube, and the fauna and litter are either transferred to a bag and placed on ice or, if the work is in a remote location, exposed to ethyl acetate for killing purposes. Sorting is done in the lab.

As we sought a method as efficient across a wide range of fauna as throw trapping, we tested the efficiency of the method in two different ways. 1) We released known numbers of both flying and non-flying insects into a previously-placed quadrat in order to test vacuuming efficiency. 2) We assessed the contribution of the thrown netted quadrat by sampling a naturally occurring assemblage with and without the quadrat.

We used crickets, *Acheta domesticus*, and ants, *Formica limata*, as our subject organisms. The animals were released into the quadrats and given a settling period as recommended by Hossain et al. (1999) before sampling using our protocol. Cricket recapture was 100% (SE= 0%, n=4) and ant recapture was 92% (SE= 2.8%, n= 4).

We tested the usefulness of the thrown netted quadrat by completing 14 pairs of net/no-net samples using our netted quadrat and a non-netted quadrat. More fauna were collected in the net samples than in the no-net samples (mean= 125 versus 107

individuals/m²; SE= 35.7 and 42.7, respectively), but this difference was not significant (one-way paired t-test, $p= 0.12$). Differences were greater, and significant, when volant (flying) individuals were considered in isolation (mean net= 54.0 individuals/m², SE= 12.1; mean no-net= 24.4, SE= 6.65; $p=0.00039$). Similarly, total species richness did not differ (mean net= 12.7 species/0.25m², SE= 1.13; mean no-net= 11.4, SE= 1.16; $p=0.10$), but volant species richness was significantly greater in the netted quadrats than in the non-netted quadrats (mean net= 5.86 species/0.25m², SE= 0.417; mean no-net= 4.79, SE= 0.505; $p=0.030$).

The thrown netted quadrat appears to more efficiently capture flying insects and in conjunction with the vacuum results in a technique for sampling alpine meadows that is analogous to the throw trap in quantitative efficiency. These two methods seem ideal for use in an vital signs program emphasizing meadow invertebrates.

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