

UCLA

UCLA Previously Published Works

Title

Does Long-term Grazing by Pack Stock in Subalpine Wet Meadows Result in Lasting Effects on Arthropod Assemblages?

Permalink

<https://escholarship.org/uc/item/8v77g11d>

Journal

Wetlands, 30(2)

ISSN

0277-5212 1943-6246

Authors

Holmquist, Jeffrey G
Schmidt-Gengenbach, Jutta
Haultain, Sylvia A

Publication Date

2010-03-04

DOI

10.1007/s13157-010-0020-3

Peer reviewed

1 *Wetlands* (2010) 30:252–262 The original publication is available at springerlink.com:
2 <http://springerlink.com/content/c160k3433g6321q7/>
3

4 **DOES LONG-TERM GRAZING BY PACK STOCK IN SUBALPINE WET MEADOWS**
5 **RESULT IN LASTING EFFECTS ON ARTHROPOD ASSEMBLAGES?**

6 Jeffrey G. Holmquist¹, Jutta Schmidt-Gengenbach¹, and Sylvia A. Haultain²

7 ¹*University of California San Diego, White Mountain Research Station, 3000 East. Line Street,*
8 *Bishop, California, USA 93514*

9 *Current: University of California Los Angeles, Institute of the Environment and Sustainability,*
10 *White Mountain Research Center, 3000 East Line Street, Bishop, California, USA 93514*

11 *E-mail: jholmquist@ucla.edu*

12 ²*Sequoia and Kings Canyon National Parks, Three Rivers, California, USA 93271*

13 Submitted 14 June 2009, Revised 9 Sept 2009, Accepted 6 Nov 2009

14 *Abstract:* Pack stock are often used in mountain environments and are grazed in uplands and
15 wetlands, particularly subalpine wet meadows. Effects of pack stock on wetland invertebrates
16 are unknown. Sequoia National Park, (Sierra Nevada, USA), was an ideal location for the study
17 of lasting stock impacts on fauna, because a) there was an 18-year database of stock usage, b)
18 there were meadows with little grazing that could be contrasted with grazed meadows, c) there is
19 a long winter with no stock use, and d) the start of grazing for each meadow is controlled, so we
20 could sample after greenup but just before stock arrived. We could thus address persistent
21 conditions produced by many years of stock use in isolation from any potential short term
22 impacts. We sampled terrestrial arthropods in paired "grazed" and "ungrazed" meadows across
23 the Park and collected associated vegetation data. We found some negative effects of grazing on
24 vegetation structure, but few lasting negative or positive effects of long-term stock grazing on
25 arthropods in these wetlands. Although it appears that pack stock do not cause lasting damage to

1 this arthropod assemblage, the extent of impact at the height of the grazing season remains
2 unknown.

3 *Key Words:* Araneae, baiting, disturbance, Insecta, Sierra Nevada (USA), sweep netting

4

5 INTRODUCTION

6 Pack stock are frequently used on public lands in the Sierra Nevada (USA) and in other
7 mountain environments, and these mules and horses, and occasionally burros and llamas, are
8 often grazed in subalpine wet meadows (McClaran 1989; Spildie et al. 2000; Cole et al. 2004).
9 The timing and locations for grazing are regulated in some areas (McClaran 1989; Moore et al.
10 2000; Spildie et al. 2000), but impacts to vegetation assemblages nevertheless can occur (Weaver
11 and Dale 1978; Olson-Rutz et al. 1996a; Moore et al. 2000; Cole et al. 2004), and recovery is
12 often not rapid (Olson-Rutz et al. 1996b; Spildie et al. 2000).

13 Although direct and indirect effects of outdoor recreation on invertebrates in vegetated
14 assemblages have been demonstrated in a variety of ecosystems (e.g., Duffey 1975; Bayfield
15 1979; Eckrich and Holmquist 2000; Uhrin and Holmquist 2003), we are unaware of any studies
16 on the effects of pack stock grazing on wetland invertebrates, despite the importance of
17 invertebrates to the functional ecology of these habitats (van der Valk 2006; Williams 2006;
18 Batzer and Sharitz 2006). Studies addressing use of grasslands, wetlands, and other vegetated
19 habitats by different large mammals reveal mixed effects on the invertebrate assemblage
20 (González-Megías et al. 2004; Underwood and Fisher 2006). Kruess and Tschardtke (2002)
21 found cattle grazing to affect insects more than the plant assemblage, Bestelmeyer and Wiens
22 (1996) recorded lower ant species richness as a function of cattle and goat grazing, and
23 González-Megías et al. (2004) determined that sheep, goat, and ibex lowered diversity and

1 abundance of arthropods in a Mediterranean mountain environment. Rambo and Faeth (1999)
2 reported that deer, elk, and cattle reduced abundance, but not richness or evenness, of insects in a
3 pine-grassland assemblage. Mysterud et al. (2005) found that sheep grazing in alpine pastures
4 did not affect diversity or abundance of insects, and similarly Heske and Campbell (1991) and
5 Bestelmeyer and Wiens (2001) discovered few differences in ant species richness, abundance, or
6 assemblage structure as a function of livestock grazing. At the other end of the spectrum, Bock
7 et al. (2006) found that grazing of small ranches by horses, cattle, and sheep can increase
8 grasshopper abundances, and Majer and Beeston (1996) found higher ant species richness in
9 more heavily grazed areas. Arthropod diversity can be increased by grazing via indirect effects
10 mediated by shifts in canopy height, structural complexity, and plant diversity (Morris 1990; Olf
11 and Ritchie 1998). Generalization concerning arthropod response to grazing across habitats is
12 difficult due to the complex interactions of many factors (see literature surveys in González-
13 Megías et al. 2004 and Underwood and Fisher 2006). Response of arthropods differs as a
14 function of many variables, including livestock density, differences in grazing behavior,
15 vegetation assemblage, duration of studies, arthropod response variables of interest, and
16 especially duration of disturbance by livestock and the amount of time since last disturbance.
17 Sierra Nevada wetlands were historically not grazed by herbivores larger than mule deer
18 (*Odocoileus hemionus* Rafinesque, see Loomis et al. 1991; Loft et al. 1991; Dull 1999), and
19 larger herbivores with different foraging behavior might be expected to cause shifts in both
20 animal and plant assemblages.

21 If meadows that have been subject to long-term stock disturbance were to be sampled
22 during a period of stock use, it would be difficult to determine if any apparent impacts were a
23 function of long-term use, current use, or a combination thereof. In this study, we address one

1 question regarding potential impacts of pack stock grazing on arthropod assemblages: Does
2 grazing cause lasting effects that persist over time, or do long winters without stock allow an
3 annual recovery of arthropod assemblages from any impacts that occur during summer usage?
4 We do not address effects on wetland arthropod assemblages at the height of the grazing season.
5 Sequoia National Park was an ideal location for this study, because a) there was a detailed, 18-
6 year, meadow-specific database of stock usage, b) there were many meadows with little or no
7 grazing use that could be contrasted with grazed meadows, c) there is a long winter period with
8 no stock use, and d) the opening date for grazing on each meadow is controlled by the Park, so
9 we could sample after greenup but just before stock arrived. Sampling prior to stock arrival
10 allowed us to address lasting effects of many years of stock use in isolation from potentially
11 confounding effects of current use.

12

13

METHODS

14 We compared subalpine wet meadows with and without substantial stock use using a
15 paired design. Generalization from responses of a single group of arthropods can be misleading
16 (Gibson et al. 1992), so we examined effects across all canopy and ground-dwelling arthropod
17 taxa that were collected by sweep nets and baits.

18 Study Area and Sites

19 Sequoia National Park is located in the southern Sierra Nevada mountains of California,
20 USA (Fig. 1). The subalpine meadows that are open to pack stock are usually covered by snow
21 for eight months, as are the 3000+ meter passes that allow access to these wetlands. Stock are
22 not allowed into wetlands prior to snowmelt, and the National Park Service determines opening
23 date for each meadow on the basis of the amount of snowfall for a given year, the timing of

1 snowmelt, and the observed condition of the wetland in a given year. Access to selected
2 wetlands is usually allowed about one month after snowmelt, i.e., individual wetlands are
3 typically opened at various times from mid-June to mid-July. Stock use is intermittent from
4 opening date through August, decreases rapidly after August, and ceases completely when the
5 first substantial snow falls, generally in early November. Most stock use thus occurs over a two-
6 three month period. Stock parties that used our study meadows ranged in size from one to 20
7 animals (\bar{x} = 8.2, SE = 0.68) in the five years preceding the study.

8 Wet meadows are saturated with water much of the year (Williams 2006; Mitsch and
9 Gosselink 2007), and these high diversity oases are common features of the subalpine
10 environment (Körner, 2003). The vegetation assemblages in the subalpine wet meadows
11 managed for stock in Sequoia National Park are often dominated by a reed grass, *Calamagrostis*
12 *muiriana* B.L. Wilson and S. Gray, formerly included in *C. breweri* Thurber, and we therefore
13 focused our study on this assemblage (known as the Shorthair Reedgrass Herbaceous Alliance in
14 the Sequoia/Kings Canyon National Park vegetation classification). Other important taxa include
15 mountain ricegrass *Ptilagrostis kingii* (Bolander) Barkworth, tufted hairgrass *Deschampsia*
16 *cespitosa* (L.) Beauv., various sedges *Carex* spp., rushes *Juncus* spp., shooting star *Dodecatheon*
17 sp. (c.f. *subalpinum* Eastw.), club-moss *Ivesia Ivesia lycopodioides* A. Gray, tundra aster
18 *Oreostemma alpigenum* (Torr. and A. Gray) Greene, dwarf bilberry *Vaccinium caespitosum*
19 Michaux, pussy-toes *Antennaria* spp., and western bistort *Polygonum bistortoides* Pursh.
20 Klikoff (1965), Benedict (1983), and Ratliff (1985) provide good overviews of this assemblage.
21 Assemblages characterized by higher levels of soil moisture, such as fens or wet meadows
22 dominated by *Deschampsia cespitosa* and large sedges (e.g., *Carex utriculata* L. Bailey), are also
23 grazed in the Sierra (Stohlgren et al. 1989).

1 We wished to contrast sites that had a long history of pack stock use with sites that had an
2 equally long history of minimal use. Sequoia National Park has detailed records of pack stock
3 use for many individual wetlands that span the last 18 years, as well as older, less formal records.
4 We used these records to select 10 subalpine wet meadows (Table 1) that a) had been exposed to
5 consistent use by pack stock (henceforth "grazed"), b) could each be paired with a subalpine wet
6 meadow with little or no recent stock use ("ungrazed"), and c) were dominated by reed grass.
7 Note that "grazed" in this context refers to all aspects of stock usage, including trampling, rather
8 than cropping alone. Grazed and ungrazed conditions served as the mensurative treatments
9 (Hurlbert 1984) for this study. We were able to locate pairs that were separated by an average of
10 only 0.96 km (SE= 0.16) and 59 m (SE=14) of elevation and that were in the same watersheds.
11 We emphasized the tight co-location of paired grazed and ungrazed meadows in part to minimize
12 geophysical and botanical differences. We also wished to minimize potential differences as a
13 function of changing weather conditions, and the close proximity of each pair allowed us to
14 sample both sites in rapid succession, before wind speed, air temperature, etc. could change
15 greatly. Although each pair of wet meadows was tightly co-located, meadow blocks were
16 separated by as much as 40 km, and up to two days of backpacking time was required to reach
17 some sites. We thus sampled a relatively large number of blocks across a broad landscape with
18 good replicate dispersion (Hurlbert 1984). We wanted sites to be as close to mid-season
19 condition as possible in terms of the structure of the vegetation and arthropod assemblages, so
20 we waited to sample until one hour to three days before stock reached the wet meadows in June
21 and July of 2008.

22 Each ungrazed or grazed site was sampled using a series of subsamples. We used aerial
23 images of the sites to randomly select two 50 x 50 m subsample locations at each site prior to the

1 field season. After arriving at each site, we established four additional sample locations, each at
2 a randomly determined location within each of the pre-selected 50 x 50 m subsample locations.
3 We used two of these sample locations for some metrics, and four for others (see below).
4 Various metrics for a given ungrazed or grazed site were therefore means or composites of four
5 or eight total measurements.

6 Field and Lab Methodology

7 *Fauna.* We used sweep nets to sample the meadow canopy fauna, and we supplemented
8 these collections with baits targeting ground dwellers, particularly ants. Sweep nets are conical
9 framed nets with a handle (New 1998; Southwood and Henderson 2000) and have a number of
10 advantages for sampling remote areas. These nets are light in weight, easily transportable, do not
11 impact wilderness character, integrate collections over a wide area, collect sparsely distributed
12 species, can be used in habitats that are flooded or saturated with water, and produce samples
13 that require relatively little sorting. Sweep nets have been shown to yield higher numbers of
14 individuals, species, families, and orders, and capture higher levels of diversity than pitfall traps,
15 light traps, or scented traps (Gadagkar et al. 1990). Sweep netting is probably the most widely
16 used method for sampling arthropods in vegetation (Southwood and Henderson 2000), and this
17 technique has been used in other investigations of the effects of grazers on arthropods (Rambo
18 and Faeth 1999; Mysterud et al. 2005).

19 The response variables for each ungrazed or grazed site were means of two 50-sweep
20 samples, with one 50-sweep sample from each of the 50 x 50 m subsample locations. We used a
21 collapsible sweep net with a 30.5 cm aperture and mesh size of 0.5 x 0.75 mm (BioQuip
22 #7112CP). Each of the two 50-sweep samples was in turn a composite of two 25-sweep
23 subsamples from within each 50 x 50 m area. We sampled a total of 400 square meters at each

1 site. Strengths of this approach include the previously noted integration of a large area and
2 sampling of less common taxa, but conversely small scale invertebrate-habitat relationships (e.g.,
3 Crist et al. 1992; With 1994; Wiens et al. 1997) could have been missed. Sweeping was our first
4 activity at each subsample location, because the subsequent work would have been likely to have
5 disturbed fauna. Each sample was transferred to a self-sealing bag, killed with 99% ethyl acetate
6 (Triplehorn and Johnson 2005), and kept as cool as possible until the trailhead was reached and
7 the samples could be transferred to a freezer. All sweep sampling was done by a single worker
8 throughout the project so as to minimize variance.

9 Baiting (Bestelmeyer et al. 2000; Delabie et al. 2000) targets ants and may also collect
10 other taxa (Alonso 2000; Andersen and Majer 2004). Baiting is commonly used to monitor ant
11 assemblages (Bestelmeyer et al. 2000) and has many of the same advantages as sweep nets for
12 sampling remote areas. Our pilot tests of various bait combinations in 50 subalpine wet meadows
13 over several years showed that honey and tuna baits offered the best combination of field
14 practicality and attractiveness to multiple ant taxa. We placed one honey and one tuna bait within
15 each of the two 50 x 50 m subsample locations at each site immediately after sweep netting, each
16 at one of the 25-sweep locations. The baits consisted of ~1 cm² portions of honey or tuna and
17 were placed on green construction paper cards and weighted by rocks. After 30 minutes, ants
18 were removed with forceps and placed in a vial containing 70% ethanol. This method worked
19 more reliably than preserving the entire bait or using an aspirator. The data from the honey and
20 tuna baits at each subsample location were combined, and the data from the two subsample
21 locations were used to generate means for response variables at each ungrazed or grazed site.

1 We sorted sweep samples in the lab, and identified taxa to family, with the exception of
2 mites. Morphospecies counts were made for each sample. We identified ants from the bait
3 samples to species.

4 *Vegetation and Physical Data.* We estimated percent green, standing brown (senescent),
5 and litter cover as well as percent bare ground at the same two locations within each of the
6 subsample locations that were used for sweep and bait samples. All of these metrics were visual
7 cover estimates from a 10 x 10 m plot colocated with the area that was sweep netted. We
8 measured canopy height and litter depth at two randomly selected locations within each area that
9 was sweep netted. Cover estimates for each site were therefore means of four estimates, whereas
10 canopy height and litter depth at each site were means of eight measures.

11 We recorded air temperature (in shade), relative humidity, and wind speed in the center
12 of each 50 x 50 m subsample location using a Kestrel 3000 digital meter. These metrics were
13 thus means of two measurements at each grazed or ungrazed site. Surface soil compaction was
14 coarsely estimated with a Ben Meadows penetrometer at each of the canopy height/litter depth
15 locations, thus yielding eight measurements per site.

16 Analysis

17 We performed 1 x 2 randomized block ANOVAs and ANCOVAs on a variety of faunal,
18 vegetation, and physical metrics using SYSTAT 12. We analyzed a variety of faunal metrics,
19 including order and family population abundances and family and morphospecies richness.
20 Because large collections have more species than small collections, even if drawn from the same
21 assemblage, we also assessed richness with expected number of species and families after scaling
22 to the number of individuals in the sample with the fewest individuals ($E(S_8)$ and $E(F_8)$, Hurlbert
23 1971; Simberloff 1972; Magurran 2004). We analyzed family and morphospecies dominance

1 and used probability of interspecific encounter, i.e., the probability that two species drawn from a
2 sample are of different taxa, as a measure of evenness at both the morphospecies and family
3 level (P.I.E., higher values indicate greater evenness, Hurlbert 1971). Margalef's index (D_{Mg} ,
4 Clifford and Stephenson 1975; Magurran 2004) was used as a diversity measure for both families
5 and morphospecies. We calculated $E(S_8)$, $E(F_8)$, and P.I.E. using the application Diversity.
6 Some metrics demonstrated departures from normality via Lilliefors tests (Lilliefors 1967)
7 and/or showed heteroscedasticity (F_{\max} and Cochran's tests; Cochran 1941; Kirk 1982), but
8 square-root transformations $((y)^{0.5} + (y + 1)^{0.5})$ of proportional data and log transformations (\log
9 $(y + 1)$) of all other data allowed parametric assumptions to be met. Only variables that differ as
10 a function of treatment and that are not likely to be affected by the treatment should be
11 considered for further analysis as covariates (Underwood 1997), and site elevation qualified via
12 these criteria (Table 2). Although elevation differences between grazed-ungazed pairs were
13 small, most grazed sites were slightly lower than their associated ungrazed sites, and it was
14 therefore important to examine elevation as a covariate. We present ANCOVA (general linear
15 model) results for all response variables except air temperature, which was necessary to exclude,
16 because this variable did not meet the assumption of homogeneity of treatment and covariate
17 regression slopes (Sokal and Rohlf 1995; Underwood 1997). Lastly, we constructed rank
18 abundance plots which provide an additional perspective on diversity, richness, and evenness,
19 without collapsing a great deal of information into a single number (Stiling 2001; Magurran
20 2004; Underwood and Fisher 2006).

21 Because this study addressed potential anthropogenic impacts, we wanted good power
22 and tight control over Type II error. Although ecologists tend to emphasize Type I error over
23 Type II error, there is often not an ecological basis for this bias, particularly in situations that

1 involve potential environmental degradation. It is increasingly recognized that both types of
2 error deserve equal scrutiny, and it can be advantageous to set alpha as high or even higher than
3 beta in order to increase power and decrease Type II error (Kendall et al. 1992; Mapstone 1995;
4 Dayton 1998; Field et al. 2004). We used as many replicate ungrazed blocks (10 wet meadow
5 pairs) as possible; we were not able to use more sites because of the limited number of subalpine
6 wet meadows that met our criteria for pairing, so power could not be increased by increasing
7 sample size. Before conducting our field work, we used G*Power (Erdfelder et al. 1996; Faul et
8 al. 2007; Mayr et al. 2007), our known sampling design and sample size, and the standard *a*
9 *priori* estimate for effect size of 0.5, which has been well-established both theoretically and
10 empirically though large meta-analyses (Cohen 1988; Lipsey and Wilson 1993; Bausell and Li
11 2002) to estimate the *a priori* alpha level that would be required in order to have an equivalent
12 beta error. The result was alpha = beta = 0.19, and the associated power (1-beta) was 0.81. Note
13 that this is *not* retrospective power analysis, which is not recommended (Hoenig and Heisy 2001;
14 Nakagawa and Foster 2004). In contrast, the *a priori* beta estimate using these same parameters
15 for a fixed alpha of 0.05 was 0.44 and a power of only 0.56, which would give good protection
16 from Type I error, but poor protection from Type II error and therefore a greater chance of
17 falsely assuming that pack stock have little effect on wet meadow arthropods. We used both
18 alpha = 0.19 and the standard alpha = 0.05 as significance thresholds in order to provide
19 additional perspective for our results.

20

21

RESULTS

22

23

Both sets of meadows had > 80% green vegetation, ~8 cm canopy height, equal soil compaction, and similar percent bare ground, but there were some differences in vegetation

1 structure (Table 2). Grazed meadows had shallower litter depth as well as lower percent litter
2 and brown vegetation cover (ANOVA). Some difference among meadow pairs (block effects)
3 were apparent for these variables as well as for temperature and humidity. Effects were
4 generally lessened when analyzed via ANCOVA, although both litter depth and cover were still
5 different (Table 2) at $\alpha = 0.19$ (see Methods).

6 We collected and identified 2,683 arthropods in the study, representing 11 orders and 81
7 families. Diptera had the greatest family richness (29), followed by Hemiptera (12),
8 Hymenoptera (12), and Coleoptera (10). There were 68 families in the ungrazed samples and 63
9 families in the grazed samples. Rank abundance plots for the two meadow conditions were
10 similar (Figure 2), and both plots fell between log normal and broken stick configurations. There
11 was slightly more abundance at family ranks 7 through 20 on the grazed plots and slightly more
12 abundance at ranks 20-43 on the ungrazed plots.

13 Sweep assemblage metrics for ungrazed and grazed meadows were almost identical when
14 assessed via ANOVA or ANCOVA (Table 3). There was also little evidence of block effects at
15 the assemblage level. The overall assemblage was dominated by Diptera and Hemiptera at the
16 order level (Table 4). Three of the four most abundant families (and 7 of the top 10) were
17 dipterans; anthomyiid flies had the highest overall family abundance, followed by cicadellid
18 leafhoppers, ephydrid shore flies, and chloropid grass flies. Ungrazed and grazed plots had the
19 same six most abundant families, although the rank order differed. Only Diptera and Hemiptera
20 were found in all samples; at the family level, chloropids, muscid house flies, and anthomyiids
21 were found in almost all samples (Table 4). Coleoptera was the only group that differed in
22 abundance between ungrazed and grazed meadows when assessed with ANOVA, indicating
23 more beetles on ungrazed sites, although beetles were relatively uncommon in the assemblage.

1 ANCOVAs that included elevation as a covariate similarly did not reveal grazed-ungrazed
2 differences for abundant taxa, but did show larger numbers of Orthoptera, fungus gnats
3 (Sciaridae), and spiders (Araneae) on grazed sites. Approximately one-third of the population
4 variables had significant block effects, the strongest of which were for Orthoptera, Sciaridae,
5 Anthomyiidae, and Araneae (Table 4).

6 Relatively few taxa and individuals were collected on the bait cards (Table 4). The ant
7 (Formicidae) catch was dominated by *Myrmica discontinua* Weber, but we also collected small
8 numbers of *Formica lasioides* Emery, *F. neorufibarbis* Emery, *F. aserva* Forel, *F. canadensis*
9 Santschi, and *Camponotus vicinus* Mayr, as well as Acari (mites). Species richness was identical
10 in grazed and ungrazed meadows, but total ant abundance was twice as high on grazed as on
11 ungrazed sites ($p = 0.14$, ANCOVA, Table 4). ANCOVAs also showed significant block effects
12 for ant abundance and species richness. No significant differences were apparent via ANOVA.

13

14

DISCUSSION

15 Some changes in coarse vegetation structure persisted from previous years of stock use to
16 the start of the new grazing season, despite the annual winter respite from stock use. There was
17 significantly less litter depth and cover on our grazed sites, and reductions in litter have also been
18 observed as a result of cattle and sheep grazing (King and Hutchinson 1983; Andresen et al.
19 1990; Bromham et al. 1999). We observed less standing, senescent (brown) vegetation at the
20 grazed sites, and this effect was probably due to breakage and grazing of vegetation at the end of
21 the previous year. Although bare ground was nominally more extensive on our grazed sites, this
22 difference was not significant, in contrast with findings from past manipulations of pack stock
23 use (Moore et al. 2000; Spildie et al. 2000; Cole et al. 2004). We also found no evidence of

1 lasting impacts on canopy height, in contrast to several other studies of livestock effects
2 (Andresen et al. 1990; Kruess and Tschardtke 2002; Hartley et al. 2003), and this result is
3 important, because canopy height is often a positive predictor of insect diversity and abundance
4 (Haysom and Coulson 1998; Kruess and Tschardtke 2002). Experimental clipping (Stohlgren et
5 al. 1989) indicates that wetter vegetation assemblages may be more susceptible to livestock
6 impact than the *Calamagrostis* dominated assemblage.

7 We found relatively few negative or positive effects of long-term pack stock grazing on
8 the arthropod assemblages in these subalpine wet meadows, but we addressed only persisting
9 multi-year effects rather than the immediate effects that may occur at the height of stock usage.
10 Hatfield and LeBuhn (2007) found sheep grazing to negatively affect bumble bee assemblages in
11 the Sierra Nevada but similarly found these effects to not carry over to a subsequent year. Our
12 one significant faunal contrast via ANOVA showed beetles to have a negative response to
13 grazing, whereas ANCOVA showed positive effects on four taxa, including ants. Studies of
14 livestock effects on arthropods have variously found positive, negative, mixed, or no effect
15 across the entire assemblage (see Introduction); other efforts report differential responses among
16 arthropod taxa. Herbivores (Andresen et al. 1990; Gibson et al. 1992) and leafhoppers in
17 particular, have been found to be more affected by livestock than other taxa (Morris and Lakhani
18 1979; Morris and Rispin 1987; but see Kruess and Tschardtke 2002). Although invertebrates
19 have been shown to be notoriously sensitive to subtle vegetation differences in many
20 environments (e.g., Wiens et al. 1997; Holmquist 1998; McAbendroth et al. 2005), there were
21 apparently few indirect effects on arthropods driven by litter losses in the grazed meadows. Ants
22 might represent an exception. This group showed a significant positive relationship to grazing,
23 albeit at a higher alpha level and only via ANCOVA after adjusting for elevation. Ants have

1 been shown to have positive responses to livestock grazing in some other habitats (e.g., Majer
2 and Beeston 1996; Bromham et al. 1999; Underwood and Fisher 2006), and these increases can
3 be driven by litter losses (Bromham et al. 1999) similar to those observed in our study.

4 Were there really few effects on fauna? The almost complete lack of significant negative
5 effects on fauna as tested by ANOVA across 12 assemblage and 21 population metrics, not only
6 at $\alpha = 0.05$ but at the high α of 0.19 and associated high power of 0.81, provides no
7 indication of an overall negative grazing effect on fauna. The rank abundance plots were also
8 consistent with this conclusion. Analysis by ANCOVA also did not suggest negative effects on
9 faunal assemblage metrics or populations, or positive effects on assemblage metrics, but did
10 suggest positive effects in four of 21 tested faunal populations (orthopterans, fungus gnats,
11 spiders, and ants). These positive effects may be in fact be present, and other work has shown
12 both orthopterans (Bock et al. 2006) and ants (Underwood and Fisher 2006) to be positively
13 affected by grazing in some habitats. It is also possible that, given the small elevation
14 differences between grazed and ungrazed treatments, the statistical significance of elevation may
15 exceed the associated ecological significance. The presence of significant block effects for about
16 one-third of the faunal population, physical, and vegetation metrics indicates that there were
17 some differences among habitats and that there was sufficient power in the design to detect
18 extensive treatment differences if such differences were present. Although negative effects were
19 generally not observed at the family level, it is possible that some individual species were
20 reduced in abundance or absent on the grazed sites.

21 Why were there no negative effects on fauna? Negative livestock effects on fauna have
22 been demonstrated in a number of environments (e.g., Bestelmeyer and Wiens 1996; González-
23 Megías et al. 2004), and Kruess and Tschardtke (2002) found insects to be more sensitive than

1 plants to cattle grazing. Although many studies of grazing effects on arthropods have used
2 spatial comparisons, several authors have shown arthropod population densities, biomass,
3 species richness, and/or diversity to increase when stock pressure ceases (Andresen et al 1990
4 and references therein; Hatfield and LeBuhn 2007). Sequoia National Park, however, has a
5 particularly rigorous stock management program and strives to limit pack stock impacts by
6 controlling opening dates for individual wetlands on the basis of wet meadow condition, assessed
7 via plant assemblage structure and phenological development, as well as estimates of soil
8 moisture determined by the nature of the preceding winter. Although we found some stock
9 impacts on dead vegetation structure, the low levels of stock usage maintained by Sequoia
10 National Park (mean of 18.5 stock nights/ha/yr) were apparently below the threshold for impact
11 to the arthropod assemblage, at least as assessed at the start of the growing season before stock
12 arrived. Cole et al. (2004) note that meadow vegetation can be maintained in good condition
13 with low levels of stock use, but even moderate use often results in impacts. Park Service
14 regulation of meadow opening dates and stock densities, arthropod dispersal capabilities
15 (Hatfield and LeBuhn 2007), concentration of grazing in *Calamagrostis* dominated meadows,
16 short grazing seasons, long winter recovery periods, and our pre-grazing sampling likely
17 combined to limit impacts and/or our detection thereof. There might be different results in Sierra
18 meadows with wetter conditions (e.g., Stohlgren et al. 1989), a longer grazing season, or less
19 regulation. As an example of one impact pathway that was absent in our wetlands, Andresen et
20 al. (1990) found cattle to reduce canopy height with an associated loss of canopy arthropods. In
21 our Sequoia wet meadows, stock were excluded from grazing areas in the spring and a full
22 canopy developed. We sampled before stock arrived and thus before the canopy could potentially
23 be newly degraded. Our results indicate little long-term stock damage to the arthropod

1 assemblage, and this finding is encouraging, but our results do not address potential impacts at
2 mid-season.

3 If there were no lasting negative effects on fauna, does that mean that any mid-season
4 impacts are inconsequential? No. The many studies recording livestock impacts to epigeal
5 arthropods report results obtained during or immediately after grazing (Kruess and Tscharrntke
6 2002; see Introduction). Our limited mid-season pilot sampling also suggests that pack stock
7 may reduce arthropod diversity and abundance in these subalpine wet meadows. Removal of
8 canopy in the middle of the growing season is more deleterious to the arthropod assemblage than
9 removal during early season (Duffey et al. 1974), and Baines et al. (1998) showed that one mid-
10 season canopy removal had greater negative effect on spider species richness and abundance
11 than two removals in spring and fall. Univoltine species can be affected by mid-season canopy
12 removal more than multivoltine species (Morris 1979), but multivoltine taxa could also have
13 brood size reduced or eliminated during peak stock use periods. Flowering in these subalpine
14 wetlands occurs during stock usage, and removal of flowers can negatively affect butterflies
15 (Feber et al. 1996), and other nectivores (Vickery et al. 2001; Hatfield and LeBuhn 2007), which
16 in turn may reduce pollinator availability to plants. These subalpine wetlands may be "reset"
17 over the long winter and spring, but it is possible that pack stock reduce mid-season productivity
18 and diversity of these wetlands, and such losses could cascade into vertebrate (Vickery et al.
19 2001) and/or upland assemblages. Although it appears that pack stock do not cause lasting
20 damage to the wet meadow arthropod assemblage, the question as to impacts at the height of the
21 grazing season remains unanswered, and we will not have a full understanding of the role of
22 pack stock in these wetlands until this issue is addressed.

23

ACKNOWLEDGEMENTS

1
2 We thank Lyra Pierotti, Chelsea Clifford, Jean Dillingham, Derham Giuliani, and Peter
3 Norquist for cheerfully sorting samples and Eric Frenzel for helping compile historical stock use
4 data. Philip Ward kindly confirmed ant species identifications. We benefited from discussion
5 with Harold Werner, Leigh Ann Starcevich, Liz Ballenger, Peggy Moore, David Graber, Jennifer
6 Jones, David Cooper, Eric Berlow, and Linda Mutch, and from the support of WMRS faculty
7 and staff, especially Vikki DeVries, Barbara Fager, Frank Powell, Daniel Pritchett, Elizabeth
8 Sally, John Smiley, and Denise Waterbury. The paper was improved by comments from Darold
9 Batzer, Scott Martens, Peggy Moore, Steve Ostoja, John Smiley, and anonymous reviewers.
10 This work was funded by the National Park Service (J8R07080005 and J8R07070006). Much of
11 the groundwork for this project was supported by the National Park Service (H8R07010001) and
12 National Science Foundation (0139633 and 0139633-Supplement). All Park Service support was
13 funded through the Great Basin Cooperative Ecosystems Studies Unit, and Angie Evenden
14 expertly assisted with this process.
15

References

- 1
2 Alonso LE (2009) Ants as indicators of diversity. In: Agosti D, Majer JD, Alonso LE, Schultz
3 TR (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian
4 Institution, Washington, DC, pp 80–88
- 5 Andersen AN, Majer JD (2004) Ants show the way down under: invertebrates as bioindicators in
6 land management. *Frontiers in Ecology and the Environment* 2:291–298
- 7 Andresen H, Bakker JP, Brongers M, Heydemann B, Irmeler U (1990) Long-term changes of salt
8 marsh communities by cattle grazing. *Vegetatio* 89:137–148
- 9 Baines M, Hambler C, Johnson PJ, Macdonald DW, Smith H (1998.) The effects of arable field
10 margin management on the abundance and species richness of Araneae. *Ecography* 21:74–86
- 11 Batzer DP, Sharitz RR (eds) (2006) Ecology of freshwater and estuarine wetlands. University of
12 California, Berkeley
- 13 Bausell RB, Li YF (2002) Power analysis for experimental research. Cambridge University,
14 Cambridge
- 15 Bayfield N (1979) Some effects of trampling on *Molophilus ater* (Meigen) (Diptera, Tipulidae).
16 *Biological Conservation* 16:219–232
- 17 Benedict NB (1983) Plant associations of subalpine meadows, Sequoia National Park,
18 California. *Arctic and Alpine Research* 15:383–396
- 19 Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WL Jr, Delabie JHC, Silvestre R
20 (2000) Field techniques for the study of ground-dwelling ants: an overview, description, and
21 evaluation. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: standard methods for
22 measuring and monitoring biodiversity. Smithsonian Institution, Washington, DC, pp 122–
23 144

- 1 Bestelmeyer BT, Wiens JA (1996) The effects of land use on the structure of ground-foraging
2 ant communities in the Argentine Chaco. *Ecological Applications* 6:1225–1240
- 3 Bestelmeyer BT, Wiens JA (2001) Ant biodiversity in semiarid landscape mosaics: the
4 consequences of grazing vs. natural heterogeneity. *Ecological Applications* 11:1123–1140
- 5 Bock CE, Jones ZF, Bock JH (2006) Grasshopper abundance in an Arizona rangeland
6 undergoing exurban development. *Rangeland Ecological Management* 59:640–647
- 7 Bromham L, Cardillo M, Bennett AF, Elgar MA (1999) Effects of stock grazing on the ground
8 invertebrate fauna of woodland remnants. *Australian Journal of Ecology* 24:199–207
- 9 Clifford HT, Stephenson W (1975) *An introduction to numerical classification*. Academic Press,
10 London
- 11 Cochran WG (1941) The distribution of the largest of a set of estimated variances as a fraction of
12 their total. *Annals of Eugenics* 11:47–52
- 13 Cohen J (1988) *Statistical power analysis for the behavioral sciences*, 2nd edn. Lawrence
14 Erlbaum, Hillsdale, NJ
- 15 Cole DN, van Wagtenonk JW, McClaran MP, Moore PE, McDougald NK (2004) Response of
16 mountain meadows to grazing by recreational pack stock. *Journal of Range Management*
17 57:153–160
- 18 Crist TO, Guertin DS, Wiens JA, Milne BT (1992) Animal movement in heterogeneous
19 landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology*
20 6:536–544
- 21 Dayton PK (1998) Ecology: reversal of the burden of proof in fisheries management. *Science*
22 279:821–822

- 1 Delabie JHC, Fisher BL, Majer JD, Wright IW (2000) Sampling effort and choice of methods.
2 In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) *Ants: standard methods for measuring*
3 *and monitoring biodiversity*. Smithsonian Institution, Washington, DC, pp 145–154
- 4 Duffey E (1975) The effects of human trampling on the fauna of grassland litter. *Biological*
5 *Conservation* 7:255–274
- 6 Duffey E, Morris MG, Sheail J, Ward LK, Wells DA, Wells TCE (1974) *Grassland ecology and*
7 *wildlife management*. Chapman & Hall, London
- 8 Dull RA (1999) Palynological evidence for 19th century grazing–induced vegetation change in
9 the southern Sierra Nevada, California, U.S.A. *Journal of Biogeography* 26:899–912
- 10 Eckrich CE, Holmquist JG (2000) Trampling in a seagrass assemblage: direct effects, response
11 of associated fauna, and the role of substrate characteristics. *Marine Ecology Progress Series*
12 201:199–209
- 13 Erdfelder E, Faul F, Buchner A (1996.) GPOWER: a general power analysis program. *Behavior*
14 *Research Methods, Instruments, and Computers* 28:1–11
- 15 Faul F, Erdfelder E, Lang AG, Buchner A (2007) G*Power 3: a flexible statistical power
16 analysis program for the social, behavioral, and biomedical sciences. *Behavior Research*
17 *Methods* 39:175–191
- 18 Feber RE, Smith H, Macdonald DW (1996) The effects of management of uncropped edges of
19 arable fields on butterfly abundance. *Journal of Applied Ecology* 33:1191–1205
- 20 Field SA, Tyre AJ, Jonzén N, Rhodes JR, Possingham HP (2004) Minimizing the cost of
21 environmental management decisions by optimizing statistical thresholds. *Ecology Letters*
22 7:669–675

- 1 Gadagkar R, Chandrashekara K, Nair P (1990) Insect species diversity in the tropics, sampling
2 methods and a case study. *Journal of the Bombay Natural History Society* 87:337–353
- 3 Gibson CWD, Brown VK, Losito L, McGavin GC (1992) The response of invertebrate
4 assemblies to grazing. *Ecography* 15:166–176
- 5 González–Megías A, Gómez JM, Sánchez–Piñero F (2004) Effects of ungulates on epigeal
6 arthropods in Sierra Nevada National Park (southeast Spain). *Biodiversity and Conservation*
7 13:733–752
- 8 Hartley SE, Gardner SM, Mitchell RJ (2003) Indirect effects of grazing and nutrient addition on
9 the Hemipteran community of heather moorlands. *Journal of Applied Ecology* 40:793–803
- 10 Hatfield RG, LeBuhn G (2007) Patch and landscape factors shape community assemblage of
11 bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biological*
12 *Conservation* 139:150–158
- 13 Haysom KA, Coulson JC (1998) The Lepidoptera fauna associated with *Calluna vulgaris*:
14 effects of plant architecture on abundance and diversity. *Ecological Entomology* 23:377–385
- 15 Heske EJ, Campbell M (1991) Effects of an 11–year livestock enclosure on rodent and ant
16 numbers in the Chihuahuan desert, southeastern Arizona. *The Southwestern Naturalist* 36:89–
17 93
- 18 Hoenig JM, Heisey DM (2001) The abuse of power: the persuasive fallacy of power calculations
19 for data analysis. *The American Statistician* 55:1–6
- 20 Holmquist JG (1998) Permeability of patch boundaries to benthic invertebrates: influences of
21 boundary contrast, light level, and faunal density and mobility. *Oikos* 81:558–566
- 22 Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters.
23 *Ecology* 52:577–586

- 1 Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological*
2 *Monographs* 54:187–211
- 3 Kendall KC, Metzgar LH, Patterson DA, Steele BM (1992) Power of sign surveys to monitor
4 population trends. *Ecological Applications* 2:422–430
- 5 King KL, Hutchinson KJ (1983) The effects of sheep grazing on invertebrate numbers and
6 biomass in unfertilized natural pastures of the New England Tablelands (NSW). *Australian*
7 *Journal of Ecology* 8:245–255
- 8 Kirk RE (1982) *Experimental design: procedures for the behavioral sciences*, 2nd edn.
9 Brooks/Cole, Monterey, CA
- 10 Klikoff LG (1965) Microenvironmental influence on vegetational pattern near timberline in the
11 Central Sierra Nevada. *Ecological Monographs* 35:187–211
- 12 Körner C (2003) *Alpine plant life*, 2nd edn. Springer-Verlag, Berlin
- 13 Kruess A, Tschardt T (2002) Contrasting responses of plant and insect diversity to variation in
14 grazing intensity. *Biological Conservation* 106:293–302
- 15 Lilliefors HW (1967) On the Kolmogorov–Smirnov test for normality with mean and variance
16 unknown. *Journal of the American Statistical Association* 64:399–402
- 17 Lipsey MW, Wilson DB (1993) Educational and behavioral treatment: confirmation from meta-
18 analysis. *American Psychologist* 48:1181–1209
- 19 Loft ER, Menke JW, Kie JG (1991) Habitat shifts by mule deer: the influence of cattle grazing.
20 *The Journal of Wildlife Management* 55:16–26
- 21 Loomis JB, Loft ER, Updike DR, Kie JG (1991) Cattle–deer interactions in the Sierra Nevada: a
22 bioeconomic approach. *Journal of Range Management* 44:395–399

- 1 Majer JD, Beeston G (1996) The biodiversity integrity index: an illustration using ants in
2 Western Australia. *Conservation Biology* 10:65–73
- 3 Magurran AE (2004) *Measuring biological diversity*. Blackwell, Malden, MA
- 4 Mapstone BD (1995) Scalable decision rules for environmental impact studies: effect size, Type
5 I, and Type II errors. *Ecological Applications* 5:401–410
- 6 Mayr S, Buchner A, Erdfelder E, Faul F (2007) A short tutorial of *GPower*. *Tutorials in*
7 *Quantitative Methods for Psychology* 3:51–59
- 8 McAbendroth L, Ramsay PM, Foggo A, Rundle SD, Bilton DT (2005) Does macrophyte fractal
9 complexity drive invertebrate diversity, biomass, and body size distributions? *Oikos* 111:279–
10 290
- 11 McClaran MP (1989) Recreational pack stock management in Sequoia and Kings Canyon
12 National Parks. *Rangelands* 11:3–8
- 13 Mitsch WJ, Gosselink JG (2007) *Wetlands*, 4th edn. Wiley, New York
- 14 Moore PE, Cole DN, van Wagendonk JW, McClaran MP, McDougald NK (2000) Meadow
15 response to pack stock grazing in the Yosemite wilderness: integrating research and
16 management. *USDA Forest Service Proceedings RMRS–P–15* 5:160–164
- 17 Morris MG (1979) Responses of grassland invertebrates to management by cutting. II.
18 Heteroptera. *Journal of Applied Ecology* 16:417–432
- 19 Morris MG (1990) The effects of management on the invertebrate community of calcareous
20 grassland. In: Hillier SH, Walton DWH, Wells DA (eds) *Calcareous grasslands—ecology and*
21 *management*. Bluntisham Books, Huntingdon, pp 128–133
- 22 Morris MG, Lakhani KH (1979) Responses of grassland invertebrates to management by cutting.
23 *Journal of Applied Ecology* 16:77–98

- 1 Morris MG, Rispin WE (1987) Abundance and diversity of the coleopterous fauna of a
2 calcareous grassland under different cutting regimes. *Journal of Applied Ecology* 24:451–456
- 3 Mysterud A, Hansen LO, Peters C, Austrheim G (2005) The short-term effect of sheep grazing
4 on selected invertebrates (Diptera and Hemiptera) relative to other environmental factors in an
5 alpine ecosystem. *Journal of Zoology, London* 266:411–418
- 6 Nakagawa S, Foster TM (2004) The case against retrospective statistical power analyses with an
7 introduction to power analysis. *Acta Ethologica* 7:103–108
- 8 New TR (1998) *Invertebrate surveys for conservation*. Oxford University, New York
- 9 Olf H, Ritchie M (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology*
10 *and Evolution* 13:261–265
- 11 Olson–Rutz KM, Marlow CB, Hansen K, Gagnon LC, Rossi RJ (1996a) Packhorse grazing
12 behavior and immediate impact on a timberline meadow. *Journal of Range Management*
13 49:546–550
- 14 Olson–Rutz KM, Marlow CB, Hansen K, Gagnon LC, Rossi RJ (1996b) Recovery of a high
15 elevation plant community after packhorse grazing. *Journal of Range Management* 49:541–
16 545
- 17 Rambo JL, Faeth SH (1999) Effect of vertebrate grazing on plant and insect community
18 structure. *Conservation Biology* 13:1047–1054
- 19 Ratliff RD (1985) *Meadows in the Sierra Nevada of California: state of knowledge*. U.S. Dept.
20 of Agriculture, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA,
21 General Technical Report PSW–84
- 22 Simberloff D (1972) Properties of the rarefaction diversity measurement. *American Naturalist*
23 106:414–418

- 1 Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W. H. Freeman, New York
- 2 Southwood TRE, Henderson PA (2000) Ecological methods. Blackwell, Malden, MA
- 3 Spildie DR, Cole DN, Walker SC (2000) Effectiveness of a confinement strategy in reducing
4 pack stock impacts at campsites in the Selway–Bitterroot Wilderness, Idaho. USDA Forest
5 Service Proceedings RMRS–P–15 5:199–208
- 6 Stiling PD (2001) Ecology, 4th edn. Prentice–Hall, Upper Saddle River, NJ
- 7 Stohlgren TJ, DeBenedetti SH, Parsons DJ (1989) Effects of herbage removal on productivity of
8 selected high–Sierra meadow community types. Environmental Management 13:485–491
- 9 Triplehorn CA, Johnson NF (2005) Borror and DeLong’s introduction to the study of insects, 7th
10 edn. Thomson Brooks/Cole, Belmont, CA
- 11 Uhrin AV, Holmquist JG (2003) Effects of propeller scarring on macrofaunal use of the seagrass
12 *Thalassia testudinum*. Marine Ecology Progress Series 250:61–70
- 13 Underwood AJ (1997) Experiments in ecology. Cambridge University, Cambridge
- 14 Underwood EC, Fisher BL (2006) The role of ants in conservation monitoring: if, when, and
15 how. Biological Conservation 132:166–182
- 16 van der Valk AG (2006) The biology of freshwater wetlands. Oxford University, New York
- 17 Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001)
18 The management of lowland neutral grasslands in Britain: effects of agricultural practices on
19 birds and their food. Journal of Applied Ecology 38:647–664
- 20 Weaver T, Dale D (1978) Trampling effects of hikers, motorcycles, and horses in meadows and
21 forests. Journal of Applied Ecology 15:451–457
- 22 Wiens JA, Schooley RL, Weeks RD Jr (1997) Patchy landscapes and animal movements: do
23 beetles percolate? Oikos 78:257–264

- 1 With KA (1994) Ontogenetic shifts in how grasshoppers interact with landscape structure: an
- 2 analysis of movement patterns. *Functional Ecology* 8:477–485
- 3 Williams DD (2006) *The biology of temporary waters*. Oxford University, New York
- 4
- 5

1 Table 1. Site characteristics and usage patterns of grazed meadows over the past 18 years and over the past five years. All sites were wet meadows, regardless
 2 of place names. Each site was paired with a nearby ungrazed site (Figure 1).

Site	Elevation (m)	Hectares	1990-2007			2003-2007		
			Total stock nights	Mean stock nights/year	Mean stock nights/ha/yr	Total stock nights	Mean stock nights/year	Mean stock nights/ha/yr
Hockett Pasture	2595	3.6	2590	144	39.5	408	82	22.4
South Fork Mdw	2587	4.5	3465	193	43.4	746	149	33.5
South Fork Pasture	2600	4.5	1387	77	17.3	195	39	8.8
Penned-Up Mdw	3242	5.3	621	35	6.6	199	40	7.6
Nathan's Mdw	3061	5.9	1883	105	17.9	342	68	11.7
Lower Rock Ck Crossing	2893	25.5	2263	126	4.9	969	194	7.6
Lower Crabtree Mdw	3169	11.7	2042	113	9.6	585	117	10.0
Upper Crabtree Mdw	3192	17.0	2984	166	9.8	689	138	8.1
Tyndall Creek Mdw	3201	11.3	3352	186	16.4	711	142	12.6
Middle Rattlesnake Cyn	2907	5.3	1892	105	20.0	614	123	23.3
Mean	2945	9.5	2248	125	18.5	546	109	14.5
Std. Error	85	2.3	280	16	4.2	80	16	2.8

3

1 Table 2. Means, standard errors, and results of 1 x 2 randomized block ANOVAs (n= 20; df= 1,9) and ANCOVAs with elevation as a
 2 covariate (df= 1,9,1) for vegetation and physical metrics. No ANCOVA for air temperature due to heterogeneity of treatment and
 3 covariate slopes.

	Ungrazed		Grazed		ANOVA		ANCOVA	
	Mean	SE	Mean	SE	Block	Treatment	Block	Treatment
Elevation (m)	3013.9	90.5	2954.1	85.6	<0.01**	<0.01**	NA	
Canopy height (cm)	8.9	0.9	8.5	0.9	0.19	0.73	0.32	0.44
Litter depth (cm)	1.9	0.2	0.8	0.2	0.14*	<0.01**	0.18*	0.08*
Litter cover (%)	4.6	0.8	2.4	1.0	0.09*	0.02**	0.10*	0.12*
Bare ground (%)	7.8	2.9	12.6	3.7	0.91	0.33	0.95	0.55
Brown cover (%)	6.4	1.7	2.3	0.7	0.16*	0.03**	0.21	0.26
Green cover (%)	81.2	4.0	82.7	3.8	0.84	0.82	0.91	0.90
Wind speed (km/hr)	6.3	0.6	5.7	0.6	0.67	0.50	0.58	0.23
Air temperature (°C)	20.2	0.8	20.0	1.0	<0.01**	0.64	NA	
Humidity (%)	32.1	2.8	33.7	1.7	0.11*	0.39	0.20	0.72
Soil compaction (kg/cm ²)	1.5	0.1	1.5	0.2	0.75	0.98	0.83	0.67

4 *P< 0.19 (see Methods); **P< 0.05.

1 Table 3. Means, standard errors, and results of 1 x 2 randomized block ANOVAs (n= 20; df= 1,9) and ANCOVAs with elevation as a
 2 covariate (df= 1,9,1) for assemblage-level faunal metrics. All metrics are based on 50-sweep samples.

	Ungrazed		Grazed		ANOVA		ANCOVA	
	Mean	SE	Mean	SE	Block	Treatment	Block	Treatment
Total individuals	67.6	15.98	66.6	14.60	0.28	0.90	0.32	0.73
Family richness	13.6	1.91	13.4	1.50	0.61	0.91	0.65	0.61
Species richness	18.3	2.87	18.2	2.20	0.55	0.83	0.63	0.78
Expected no. of families $E(F_8)$	4.8	0.33	4.8	0.15	0.26	0.62	0.25	0.58
Expected no. of species $E(S_8)$	5.3	0.39	5.5	0.24	0.12*	0.45	0.17*	0.77
% Family dominance	40.1	4.72	37.1	2.63	0.23	0.62	0.23	0.59
% Species dominance	35.8	5.48	30.1	3.66	0.26	0.39	0.34	0.85
Hurlbert's PIE (family)	0.8	0.04	0.8	0.02	0.35	0.45	0.32	0.67
Hurlbert's PIE (species)	0.8	0.05	0.8	0.02	0.27	0.36	0.28	0.73
Margalef's family diversity	3.2	0.36	3.0	0.22	0.43	0.75	0.56	0.53
Margalef's species diversity	4.3	0.56	4.3	0.36	0.41	0.86	0.53	0.78
% Predators	11.3	2.04	12.0	2.31	0.12*	0.82	0.15*	0.69

*P < 0.19 (see Methods); **P < 0.05.

3
4

1 Table 4. Means, standard errors, frequencies, and results of 1 x 2 randomized block ANOVAs (n= 20; df= 1,9) and ANCOVAs with
 2 elevation as a covariate (df= 1,9,1) on abundances of orders and the ten most abundant families in sweep samples (top) and on bait
 3 metrics (below). Sweep metrics are based on 50-sweep samples, and all bait metrics are per one aggregate hour of bait deployment
 4 using one honey and one tuna bait. Plecoptera and Psocoptera were too rare to test.

	Ungrazed			Grazed			ANOVA		ANCOVA	
	Mean	SE	Frequency	Mean	SE	Frequency	Block	Treatment	Block	Treatment
<u>Sweeps</u>										
Orthoptera	0.45	0.29	0.40	1.20	0.76	0.40	0.04**	0.31	0.12*	0.11*
Plecoptera	0.05	0.05	0.10	0.00	0.00	0.00	NA		NA	
Hemiptera	18.70	6.16	1.00	15.55	4.12	1.00	0.11*	0.97	0.24	0.88
Cicadellidae	9.10	3.97	1.00	9.70	3.97	0.70	0.27	0.87	0.75	0.32
Delphacidae	7.25	4.83	0.80	4.40	1.31	0.90	0.68	0.77	0.52	0.20
Thysanoptera	0.20	0.11	0.30	0.10	0.07	0.20	0.81	0.54	0.90	0.83
Psocoptera	0.00	0.00	0.00	0.05	0.05	0.10	NA		NA	
Coleoptera	1.05	0.23	0.80	0.40	0.12	0.60	0.95	0.10*	0.91	0.80
Hymenoptera	2.90	0.66	0.90	3.60	1.34	1.00	0.17*	0.76	0.16*	0.39
Ichneumonidae	0.90	0.34	0.70	1.70	1.00	0.70	0.07*	0.49	0.07*	0.58
Lepidoptera	0.15	0.08	0.30	0.30	0.20	0.30	0.82	0.65	0.52	0.28
Diptera	43.20	14.38	1.00	41.95	10.20	1.00	0.42	0.93	0.37	0.42
Culicidae	1.40	0.97	0.50	1.85	1.37	0.50	0.05*	0.85	0.49	0.54

Sciaridae	1.15	0.43	0.60	1.55	1.09	0.50	0.11*	0.72	<0.01**	<0.01**
Empididae	1.50	1.28	0.50	1.15	0.49	0.50	0.22	0.64	0.21	0.29
Anthomyiidae	7.35	2.94	1.00	11.70	5.42	0.90	<0.01**	0.50	<0.01**	0.57
Muscidae	6.55	2.25	0.90	6.80	1.68	1.00	0.83	0.49	0.54	0.28
Chloropidae	6.10	1.75	0.90	10.20	3.26	1.00	0.91	0.38	0.96	0.53
Ephydriidae	12.90	11.52	0.90	4.15	1.94	0.60	0.26	0.94	0.39	0.72
Araneae	0.85	0.30	0.70	1.05	0.73	0.50	0.07*	0.69	0.01**	0.03**
Acari	0.15	0.11	0.20	0.30	0.25	0.20	0.39	0.70	0.54	0.78
<hr/>										
Baits										
<i>Myrmica discontinua</i>	1.55	0.93	0.60	3.40	1.81	0.30	0.61	0.75	0.30	0.20
Formicidae	1.95	0.95	0.70	4.05	1.82	0.50	0.44	0.58	0.12*	0.14*
Ant species richness	0.55	0.19		0.55	0.20		0.34	0.90	0.11*	0.81
Acari	0.25	0.13	0.30	0.80	0.64	0.30	0.37	0.55	0.46	0.22

1 *P < 0.19 (see Methods); **P < 0.05.

1 FIGURES

2 **Fig. 1** Sequoia National Park in the Sierra Nevada mountains in California, USA. Black circles
3 represent grazed meadows paired with meadows with minimal stock use (white circles). Sites
4 are separated slightly for clarity

5

6 **Fig. 2** Rank abundance plot for families comparing ungrazed and grazed wet meadows based on
7 total abundances for study

8

9

10

11

12

13

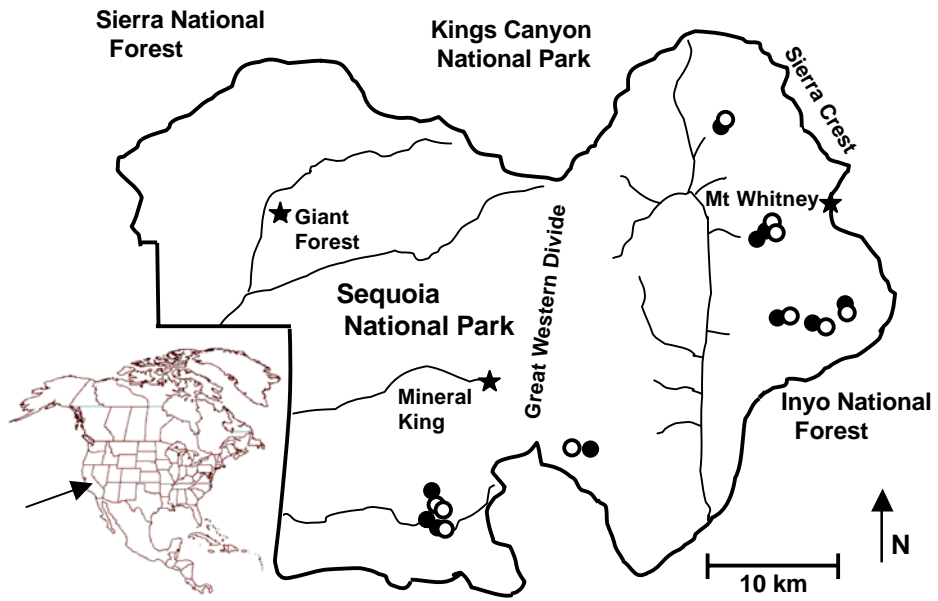


Figure 1

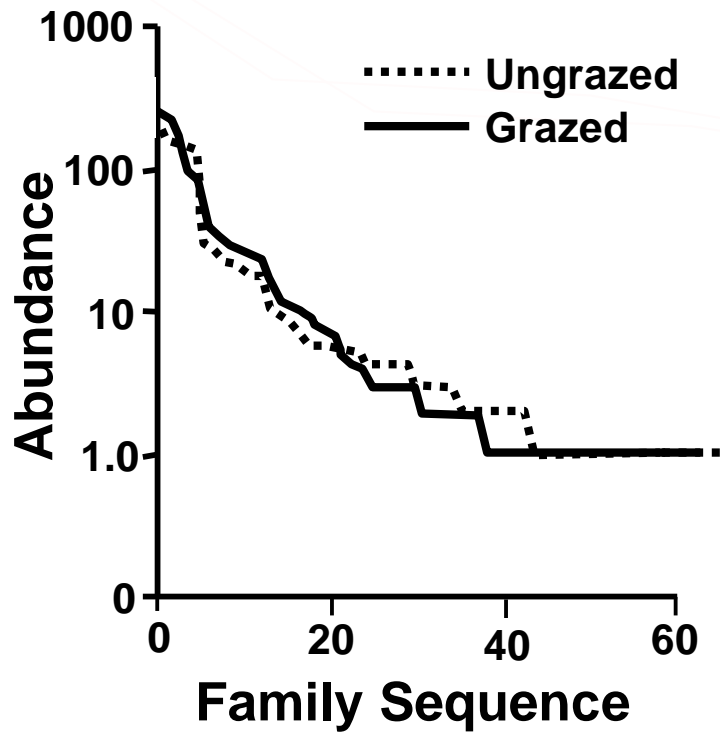


Figure 2