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Journal

Environmental Management, 52(6)

ISSN

0364-152X 1432-1009

Authors

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

Publication Date

2013-09-03

DOI

10.1007/s00267-013-0154-1

Peer reviewed

2013. *Environmental Management* 52: 1474-1486

The final publication is available at Springer via

<http://link.springer.com/article/10.1007/s00267-013-0154-1>

Equine grazing in managed subalpine wetlands:

Effects on arthropods and plant structure as a function of habitat

Jeffrey G. Holmquist^{*}, Jutta Schmidt-Gengenbach, Sylvia A. Haultain

J.G. Holmquist, J. Schmidt-Gengenbach

University of California San Diego, White Mountain Research Station, 3000 East Line
Street, Bishop, California, USA 93514

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

*Corresponding author. Tel.: +1 760 387 1909; fax: +1 760 873 7830

E-mail: jholmquist@ucla.edu

S.A. Haultain

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

Abstract Grazing management necessarily emphasizes the most spatially extensive vegetation assemblages, but landscapes are mosaics, often with more mesic vegetation types embedded within a matrix of drier vegetation. Our primary objective was to contrast effects of equine grazing on both subalpine vegetation structure and associated arthropods in a drier reed grass (*Calamagrostis muiriana*) dominated habitat versus a wetter, more productive sedge habitat (*Carex utriculata*). A second objective was to compare reed grass and sedge as habitats for fauna, irrespective of grazing. All work was done in Sequoia National Park (California, USA), where detailed, long-term records of stock management were available. We sampled paired grazed and control wet meadows that contained both habitats. There were moderate negative effects of grazing on vegetation, and effects were greater in sedge than in reed grass.

Conversely, negative grazing effects on arthropods, albeit limited, were greater in the drier reed grass, possibly due to microhabitat differences. The differing effects on plants and animals as a function of habitat emphasize the importance of considering both flora and fauna, as well as multiple habitat types, when making management decisions. Sedge supported twice the overall arthropod abundance of reed grass as well as greater diversity; hemipteran and dipteran taxa were particularly abundant in sedge. Given the greater grazing effects on sedge vegetation, greater habitat provision for terrestrial arthropods, and value as aquatic arthropod habitat, the wetter sedge assemblage is worthy of additional consideration by managers when planning for grazing and other aspects of land usage.

Keywords: land management, pack stock grazing, subalpine wetland, terrestrial arthropod assemblages, vegetation assemblages, disturbance

Introduction

Grazing disturbance effects can differ across vegetation assemblages, and the nature and strength of such differences vary as a function of environment and the nature of grazing pressure (Ravolainen et al. 2011; Manning et al. 2013). Productive, wetter, and less structurally robust assemblages of plants tend to be more sensitive to grazing (Stohlgren et al. 1989; Cole and Spildie 1998; Bråthen et al. 2007; Sørensen et al. 2009; Jones et al. 2011), but some of these plant assemblages have been shown to tolerate grazing well relative to other vegetation and even respond positively to grazing (Kitti et al. 2009; Deléglise et al. 2011). Differing grazing effects as a function of vegetation type may (Bestelmeyer and Wiens 2001) or may not (Verdú et al. 2007) cascade into the arthropod assemblage, although there has been comparatively little study of grazing effects on invertebrates as a function of vegetation assemblage.

Landscapes are mosaics, often with patches of more mesic vegetation types embedded within the matrix of drier vegetation (Kitti et al. 2009; Deléglise et al. 2011; Holmquist et al. 2011a). Assemblages in these wetter patches may be more easily damaged by grazing, because trampling impacts can be facilitated by moist, less firm substrata (Jensen 1985; Marlow et al. 1987; Willat and Sulistyaningsih 1990; Allen and Marlow 1994; Cole 2004; see also Turner 1987; McClaran 1989; Eckrich and Holmquist 2000). Differing responses as a function of vegetation type (Cole 1995a; b; Cole and Spildie 1998) may be amplified in mountain wetlands as a result of the short growing season, high soil moisture (Nagy and Grabherr 2009) and high level of aquatic-terrestrial connectivity, with many ecological flows passing through the arthropod assemblage (Yi et al. 2006; Epanchin et al. 2010; Holmquist et al. 2011a).

Subalpine wet meadows in Sequoia National Park, in the Sierra Nevada of California, USA, are potentially vulnerable habitats that are opened annually for two- to three-month pulses of equine grazing that begin about one month after the start of the short growing season (McClaran 1989; Holmquist et al. 2010; 2013; see also Kohler et al. 2004). Grazing is primarily by mules and horses that are used to transport people and materials into the backcountry ("pack stock," McClaran 1989; Cole et al. 2004; Newsome et al. 2004). These subalpine grazed wetlands often have a reed grass, *Calamagrostis muiriana* B.L. Wilson and S. Gray (formerly included in *C. breweri* Thurber) as an important component; pack stock have been shown to have only minor to moderate effects on reed grass and the associated arthropod assemblage during the short Park grazing seasons (Holmquist et al. 2010; 2013). Although the reed grass assemblage in these wet meadows is saturated or briefly flooded during snowmelt, the meadows also support patches of vegetation that remain flooded for a month or more following snowmelt and retain higher soil moisture throughout the growing season (Benedict 1983; Stohlgren et al. 1989; Neuman 1996; Loheide et al. 2009; Roche et al. 2012). These wetter habitats support a virtual monoculture of the rhizomatous sedge *Carex utriculata* L. Bailey (Benedict 1983; Allen and Marlow 1994; Neuman 1996), which provides a structurally distinct habitat: a taller canopy (up to 70 cm vs. ~9 cm, Holmquist et al. 2010; 2013), broader blades (2-12 mm vs. 1 mm, Botti and Sydoriak 2001), up to twice the productivity of reed grass (Stohlgren et al. 1989), lower shoot density, and higher soil silt content (400 vs. 2900 shoots/m², 60 vs. 10% silt, Holmquist and Schmidt-Gengenbach unpublished). Stock graze both sedge and reed grass habitats intensively (Ballenger et al. 2012 unpublished report). We hypothesized that there would be more grazing effects in the wetter sedge assemblage than in

the drier reed grass assemblage and that there would in turn be more grazing impact on arthropods in sedge than in reed grass.

Arthropod assemblages have been shown to vary as a function of both plant species and structure in a variety of vegetated habitats (Lawton 1983; Stoner and Lewis 1985; Holmquist 1997; Dennis et al. 1998; Morris 2000; Reid and Hochuli 2007), and faunal movements and assemblage structure are influenced by habitat context as well (Wiens et al. 1985; Holmquist 1998). Although the reed grass-dominated vegetation assemblage has greater plant taxonomic and structural diversity (Benedict 1983; Neuman 1996; Holmquist et al. 2010; see also Dennis et al. 1998), the tall canopy of the sedge monoculture creates a larger volume of habitat, and canopy height can be a positive predictor of faunal diversity and abundance in Sierran wetlands (Holmquist et al. 2011a).

Our primary objective was to compare effects of stock on terrestrial arthropods and vegetation structure in reed grass versus sedge habitats. Interaction terms that would indicate differences in control-grazed response slope as a function of habitat were of particular interest. Inclusion of arthropods, in addition to primary producers, allowed us to examine the response of a large portion of total assemblage complexity (Marty 2005; Cardoso et al. 2011; Pocock et al. 2012). A second objective was to determine whether the less dense, but productive and tall, sedge habitats support a higher diversity and abundance of arthropods than reed grass, irrespective of grazing.

Methods

Design overview

We examined vegetation influence on pack stock effects with a 2x2x2 blocked factorial design (Treatment: Control, Grazed; Vegetation: Reed grass, Sedge; Year: 2010, 2011) using paired control and grazed subalpine wet meadows. There are meadows in Sequoia National Park that have been closed to grazing for ~25 years, and we were able to locate six meadows that had both reed grass and sedge habitats and that could be paired with nearby grazed meadows that also had both vegetation types (Fig. 1). Meadows senesce by late September (Stohlgren et al. 1989) with accompanying sharp declines in arthropod diversity and abundance (Holmquist et al. 2013). We sampled meadows just before vegetation senescence and thus after the majority of grazing for a given season. By making use of long-term management manipulations of grazing pressure, this design was effectively a large-scale and long-term experiment that allowed us to explore the grazing effects that are occurring in these meadows under current management (see also Bestelmeyer and Wiens 2001; Bråthen et al. 2007). Any differences in response to grazing between the two vegetation assemblages were likely to be a function of differences in morphology, soils, and palatability between the two vegetation assemblages, and fauna would be expected to be affected primarily via indirect effects. The results were thus indicative of overall effects of grazing exposure when stock are released into meadows with access to both habitat types.

Study area and meadows

The National Park Service (NPS) controls stock access to these subalpine wetlands, and stock are generally not permitted in meadows until at least one month after snowmelt

(McClaran 1989). Intermittent stock use of the meadows lasts from two to three months, depending on snow year. This study included a subset of the reed grass-dominated grazed meadows used in previous studies of pack stock effects (Holmquist et al. 2010; 2013): Hockett, South Fork Pasture, Penned-up, Nathan's, Rock Creek Crossing, and Lower Crabtree, each coupled with a control meadow. Sampling at the end of the growing season incorporated both multi-decadal and annual effects of grazing relative to the long-closed control meadows (Holmquist et al. 2013). The grazed meadows were exposed to a mean of 16.0 (SE = 5.2) stock nights/ha/year over the last 20 years; mean stock nights/ha were higher in 2010 (22.2, SE = 9.1) than in 2011 (8.3, SE = 3.5). The two meadows of each pair were separated by a mean of only 755 m (SE = 191), but meadow pairs were separated by up to 40 km (Fig. 1). Reed grass- and sedge-dominated assemblages accounted for 42% (SE = 6.3) and 40% (SE = 5.4), respectively, of the wetland area in the study meadows (data from Neuman 1990 unpublished report; pers. obs.). The remainder of the area was composed of other relatively dry assemblages that were more similar to reed grass than sedge, i.e., various drier habitat assemblages represented 60% of the total. There were no differences in proportions of reed grass in grazed versus ungrazed meadows (t-test: $p = 0.61$), and there were similarly no differences for sedge ($p = 0.40$). Distances between centroids of sampled reed grass and sedge habitats within individual meadows averaged only 31 m (SE= 4.7); distances did not differ as a function of grazing treatment ($p = 0.39$). Cropping and equine manure were visible in both vegetation types in grazed meadows. We sampled meadows approximately one week before vegetation senescence at the end of the 2010 and 2011 growing seasons. Early season sampling was not possible, because the sedges are completely flooded before stock arrive, and sedge habitats are more aquatic than terrestrial at that time. There were different antecedent

conditions for the two years, because there was more snowfall in 2011 than 2010 (131 and 89 cm snow water equivalent, respectively, at Hockett Meadow). Each meadow opening date is determined by the NPS after evaluation of soil saturation (sufficiently dry, McClaran 1989) and vegetation characteristics (sufficiently well-developed), so we sampled under similar phenological conditions in 2010 and 2011, despite the differing snow years. Sampling in 2010 concluded in early September, whereas 2011 sampling extended to the end of September. We used two randomly-selected subsample locations at each grazed or control meadow, and there were two additional randomly-selected subsamples nested within each of the first pair of subsamples for some vegetation and physical measurements. Subsamples were averaged such that there was one value for each grazed or control replicate for each year for a given metric. There were new random locations for subsamples each year, and thus Year was incorporated as an additional factor instead of using repeated measures. Holmquist et al. (2010; 2013) provide additional details on grazing management, vegetation, and study meadows.

Faunal methodology

We made 50 standard sweep net sweeps (New 1998; Southwood and Henderson 2000) at each study meadow, evenly divided between the two subsampling locations. The net had a 30.5 cm aperture and mesh size of 0.5 x 0.75 mm. We did the sweeping before collecting vegetation data at each meadow in order to minimize disturbance (additional faunal sampling details in Holmquist et al. 2010; 2013).

Faunal samples were identified to family (see also Fahrig and Jonsen 1998; Koricheva et al. 2000), and then morphospecies counts were made for each sample (Kremen et al. 1993; Oliver and Beattie 1996; Gerlach et al. in press). This study was particularly broad in that we

examined responses across all arthropod families (see also Fahrig and Jonsen 1998; Koricheva et al. 2000; Pocock et al. 2012).

Vegetation and Physical Data

Vegetation structural parameters are effective tools for detection of stock effects on vegetation assemblages, to the extent that such measures have been used as proxies for grazing intensity or manipulated as independent variables to represent grazing (Hendricks et al. 2005; Elliot and Henry 2011; Jones et al. 2011). We measured percent bare ground, percent green, standing brown (senescent), and litter cover using a point-intercept transect centered and randomly oriented in each subsample location. We measured canopy height, litter depth, and soil strength (Ben Meadows pocket penetrometer) at two random locations within each subsample. We used a Kestrel 3000 meter to record average wind speed and air temperature at a point midway between the two subsamples.

Analysis

Univariate analyses of the 2x2x2 blocked factorial were done with ANCOVAs (df = 1,1,1,5; SYSTAT 12), comparing the influences of grazing, vegetation, year, and associated interactions on arthropods and vegetation structure. Response variables included abundances by taxon, richness, dominance, percentages of predators and herbivores, percentages of more- and less-motile fauna, expected number of species (which compensates for differing abundance; $E(S_{18})$, Hurlbert 1971; Magurran 2004), and evenness (probability of interspecific encounter, P.I.E., Hurlbert 1971). We calculated $E(S_{18})$ and P.I.E. using the application Diversity. Some measures were divided by canopy height to compensate for differing habitat volumes represented

by the two vegetation types. Proportional variables were square-root transformed $((y)^{0.5} + (y + 1)^{0.5})$ and others were log transformed $(\log(y + 1))$. Control meadows were significantly higher than grazed meadows, although the differential was small (mean difference = 59.8 m, SE = 13; Holmquist et al. 2010), so we used elevation as a covariate (Underwood 1997; see also Wettstein and Schmid 1999). Calculation of the general linear model included substitutions for missing cells. We estimated power for ANCOVAs a priori (Bausell and Li 2002) using G*Power (Mayr et al. 2007). We calculated the alpha level that would be required in order to have an equivalent beta error (Kendall et al. 1992; Mapstone 1995; Erdfelder et al. 1996; Dayton 1998; Reynolds et al. 2011): alpha = beta = 0.16, and the associated power (1-beta) was 0.84. We present both alpha = 0.16 and the standard alpha (= 0.05) as significance thresholds to provide additional perspective for our results, with the particular goal of avoiding Type II error given the potential impact to these wetlands should we incorrectly reach a conclusion of "no effect." We also constructed rank abundance plots, compared distributions with Kolmogorov-Smirnov two-sample tests (Magurran 2004), and assessed trends across variables with two-tailed sign tests.

Multivariate analyses for fauna included comparisons as a function of study factors using multi-response permutation procedures (MRPP) as well as analyses of dispersion using PERMDISP2 software developed by MJ Anderson (see also Anderson 2001; Ratkowsky 2008). Response and explanatory matrices contained all meadows; the response matrix included families that were collected in three or more samples (57 families; McCune and Grace 2002; Peck 2010; but see Poos and Jackson 2012). The response matrix was relativized by maximum abundance for each family; the final response matrix had a coefficient of variation of 51%, and 66% of the cells contained zeros. The explanatory matrix included coding variables for Treatment and Vegetation. We used the Sørensen distance measure for all analyses and rank-

transformed the distance matrix prior to the MRPP analyses. We examined differences among groups with MRPP using the a priori coding variables from the explanatory matrix (Treatment and Vegetation combinations). In order to assess the relative influence of non-study factors, we then ran a second MRPP using a new group membership variable that used the four highest level groups resulting from a hierarchical, polythetic, agglomerative cluster analysis (group average linkage). The permutational dispersion analysis was based on 9,999 permutations.

Results

Vegetation and Physical

Grazing, vegetation type, and study year were significant influences on several response variables; there were a number of significant interaction terms, and block effects were present for most parameters (Table 1). Only three individual variables showed overall significant effects of grazing (less litter depth and cover, greater soil compaction), but the directional trend across all metrics, vegetation types, and years was strong ($P < 0.0001$; two-tailed sign test). Significant differences as a function of vegetation assemblage included taller canopy height in sedge and greater green cover and soil strength in the reed grass assemblage. Five variables differed significantly between the two years of the study (canopy height, litter depth, bare ground, green cover, brown cover; Table 1). There were four Treatment x Vegetation interactions: canopy height, litter depth, bare ground, and green cover. All interactions indicated greater grazing impact in sedge than in reed grass, although proportional changes for canopy height were similar for the two vegetation assemblages. There were also several significant interactions that demonstrated an influence of Year on both Treatment and Vegetation trends (Table 1); trends for these variables were stronger in 2010 than in 2011.

Litter depth was greater in sedge in 2010, but was greater in reed grass in 2011, whereas soil strength was greater in reed grass than sedge in both years, but more strongly so in 2011. Atmospheric metrics had no significant differences across study variables, with the exception of a block effect for temperature.

Fauna

Diptera and Hemiptera dominated control and grazed meadows in both vegetation types. Ephydriidae, Anthomyiidae, Muscidae (all Diptera), Cicadellidae, and Aphididae (Hemiptera) were the most abundant of the 80 families collected (Online Resource 1). Family richness was greatest for Diptera (34), Hemiptera (12), and Hymenoptera (12). Seventy-one percent of the families were present in three or more samples.

The lack of significant Treatment differences for any faunal assemblage-level metric stood in contrast to the vegetation results, but there were more significant faunal differences for Vegetation and Year factors (Table 2) than were observed for vegetation structure responses (Table 1). There was no significant Treatment trend across metrics ($p = 0.15$), and there was only a single Treatment x Year interaction (% predators). There were no Treatment x Vegetation interactions. Sedge supported twice the total abundance of reed grass as well as greater family and morphospecies richness, but expected number of species was lower in sedge than reed grass after compensation for differing canopy height. The weak directional trend across all metrics ($p = 0.080$; two-tailed sign test) indicating higher diversity in sedge became strongly significant if considered on a per-area basis only ($p = 0.0008$), i.e., if the metrics that compensated for differing canopy height were not considered. All rank-abundance plots most closely approximated a log normal distribution (Fig. 2). The grazed rank-abundance

distribution had less evenness than the control distribution in reed grass ($p = 0.020$, Kolmogorov-Smirnov two-sample test), whereas the two distributions were not different in sedge ($p = 0.42$). There was also less evenness in reed grass than in sedge, irrespective of grazing (Fig. 2; $p = 0.017$). The many significant Year contrasts indicated higher diversity in 2011. Vegetation x Year interactions indicated that the differences by Vegetation were stronger in 2010 than 2011. In contrast to the vegetation results, there was only a single block effect (PIE; Table 2).

Individual orders and dominant taxa also showed a large number of significant responses to Vegetation and Year, and there was a relatively greater response to Treatment than observed for assemblage metrics (Table 3). Cicadellid leafhoppers and dolichopodid flies were less abundant on grazed than control plots, whereas the inverse held for Orthoptera and Coleoptera. There was a strong overall trend of lower abundance on grazed meadows across the common taxa in Table 3 ($p = 0.0020$; two-tailed sign test), but not when all families were considered ($p = 0.59$; Online Resource 1). A single Treatment x Vegetation interaction was present: fewer agromyzid flies in grazed than control reed grass, but more in grazed than control sedge. There was, however, a strong trend across abundant taxa (Table 3) of lower abundances in grazed reed grass relative to control reed grass ($p < 0.0001$), whereas this trend was absent in sedge ($p = 0.31$). This trend was not present in either assemblage when rare taxa were included (reed grass, $p = 0.43$; sedge, $p = 0.99$; Online Resource 1). There were five Treatment x Year interactions, but there was not consistent directionality. The significant Vegetation contrasts involved a number of hemipteran and dipteran taxa and indicated greater abundances in sedge (Table 3); chloropid flies were the single exception. There was a strong trend of greater abundances in sedge across the taxa in both Table 3 ($p = 0.0003$) and across all

families ($p = 0.0008$; Online Resource 1; see also MRPP results below). Twenty families were found only in sedge, whereas only eight families were collected exclusively in reed grass, and most of the latter taxa were represented by a small number of individuals (Online Resource 1). Half of the Table 3 taxa had Vegetation x Year interactions, and most were the result of higher sedge abundances in 2010 but higher reed grass abundances in 2011. There were also many strong Year effects; in general, hemipteran taxa had greater abundances in 2011, but most of the other taxa with significant Year effects had greater abundances in 2010 (Table 3). Block effects were present, but these spatial differences were not associated with particular groups.

The initial MRPP randomization test ($p = 0.013$) suggested that there were distinct compositional differences among the main study factors, but the low effect size ($A = 0.056$) also indicated that there was a great deal of variance within each of these factors. Two pairwise comparisons were significant: control reed grass vs. control sedge ($p = 0.0050$) and grazed reed grass vs. control sedge ($p = 0.0004$), and there was also a weaker contrast between grazed and control reed grass ($p = 0.13$). The subsequent MRPP that used the group membership variable from the cluster analysis had a lower p-value (< 0.0001) and higher A ($= 0.25$); further, all pairwise comparisons were significant ($p \leq 0.014$) indicating that factors other than vegetation type and grazing exposure were likely important influences as well. Dispersion analyses were not significant. Overall dispersion results were consistent, whether derived from deviations from centroids or from spatial medians (each in turn from both ANOVA tables and permutation of residuals); p-values ranged from 0.59 to 0.74. No pairwise dispersion comparisons were significant among any combination of factors ($0.18 < p < 0.85$). The significant MRPP results in combination with the non-significant dispersion results suggest that assemblage structure did differ as a function of study factors rather than in variability/dispersion alone.

Discussion

There were negative grazing effects on vegetation, and as hypothesized these effects were greater in sedge than in reed grass habitats. Although some tall montane sedges are relatively unaffected by grazing (Allen and Marlow 1994; McIlroy and Allen-Diaz 2012), our findings better align with results obtained by Clary (1995) and Sørensen et al. (2009) who found high elevation and/or high latitude sedges to demonstrate more grazing effects than other vegetation. Stohlgren et al. (1989), also working in Sequoia and using experimental clipping, determined that assemblages dominated in part by sedge were more affected than assemblages dominated in part by reed grass. Reed grass forms a dense root mat (Botti and Sydoriak 2001), which, in combination with a shoot density six times greater than sedge, should confer some protection from trampling via higher shear strength (Morrocco and Ballantyne 2008; Monz et al. 2010). The greater effects of grazing on sedge relative to reed grass in our study were likely also driven in part by soil moisture (Jensen 1985; Marlow et al. 1987; Allen and Marlow 1994), which is two to fourteen times greater in sedge than in reed grass in the Sierra (Neuman 1996; Holmquist and Schmidt-Gengenbach unpublished). Higher soil moisture and silt content may have contributed to the observed lower soil strength in sedge, which, coupled with a morphology that may be more easily penetrated, probably influences the observed patterns of hoof punching: conservatively twice as deep in sedge as in reed grass (Neuman 1996). Differential resistance *per se* of the plant assemblages was beyond the scope of this study and is a candidate for future study (see also Cole 1995b; Rejmánková 1999).

We had hypothesized greater grazing impact on arthropod assemblages in sedge than in reed grass, but the effects on arthropods in reed grass, albeit limited, were equal to or greater than in sedge, despite the greater effects of grazing on sedge vegetation structure. Evidence for

greater grazing influence on reed grass fauna included a strong trend of lower abundances across common taxa in grazed reed grass versus no trend in sedge, significantly different rank-abundance distributions for grazed versus control reed grass, in contrast to the lack of difference for sedge, as well as weaker trends apparent from MRPP. The unexpected differences between the faunal responses in reed grass versus sedge may have been due to the larger volume of habitat (per unit area) provided by the latter as a result of the taller canopy. Minor alterations of vegetation structure in sedge would still leave the majority of habitat intact, and levels of grazing pressure were clearly below any threshold for cascading effects on fauna. In contrast, similar changes to reed grass structure could have a proportionally larger effect with commensurate indirect effects on the associated arthropod assemblage. Thus the most important "interaction" detected in the study was the greater grazing effect on vegetation structure in sedge but greater effect on fauna in reed grass. The differing effects on plants and animals as a function of habitat emphasize the importance of considering both flora and fauna in management decisions (see also Kruess and Tscharrntke 2002). Overall effects on fauna were nonetheless relatively minor, thus aligning with earlier findings from studies addressing different questions in this managed environment (Holmquist et al. 2010; 2013). Mitigating factors may include relatively low stock use, late openings during study years, movement of fauna among habitats, and sampling grain (Holmquist et al. 2013, submitted).

Taxon-specific grazing effects were split; some taxa, such as cicadellid leafhoppers, were less abundant in grazed meadows, whereas others, such as acridid grasshoppers, were more abundant. Herbivores, particularly leafhoppers, are tightly tied to the vegetation canopy (Andresen et al. 1990; Gibson et al. 1992), and this group can in turn be susceptible to impacts from grazing (Morris 1979; Holmquist et al. 2013; but see Kruess and Tscharrntke 2002).

There is thus the possibility of negative feedback (Bormann & Likens 1979; Heinselman 1981; Clark 1989) in terms of effects on vegetation, such that an increase in vertebrate grazing effects may be somewhat mitigated by concomitant release from leafhopper herbivory. Conversely, the positive relationship of another group of herbivores—grasshoppers—to grazing is consistent with other grazing studies in these meadows (Holmquist et al. 2010; 2013) and elsewhere (Bock et al. 2006; Cease et al. 2012; Fartmann et al. 2012). Although vertebrate grazers are herbivorous competitors, many grasshoppers prefer grazed areas with a) reduced canopy and litter, and b) increased bare ground, because access to bare ground facilitates soil oviposition, and the warmer ground resulting from reductions in cover likely speeds development (Huntly and Inouye 1988; Fartmann et al. 2012; but see Spalinger et al. 2011). These mechanisms may have contributed to higher orthopteran abundances in our grazed meadows, which had lower canopy height, litter depth and cover, and more extensive bare ground relative to control meadows. Nutritional imperatives may also contribute to this pattern of grasshopper abundance. Cease et al. (2012) found that grazing in a grassland lowered the ratios of nitrogen and protein to carbohydrate and that these low ratios counterintuitively increase growth, survival, and habitat selection by acridid grasshoppers. Orthopteran herbivory can be substantial, particularly in high-altitude environments, where these animals remove up to 30% of above-ground biomass (Blumer and Diemer 1996); some taxa feed at the base of blades, which then fall to the substrate unconsumed, and ingest as little as 20% of removed material (Bailey and Riegert 1973; Thompson et al. 1995). There is thus also the potential for positive feedback (e.g., Rykiel et al. 1988; Cochrane et al. 1999) in that grazed patches are more likely to attract grasshopper herbivory that may in turn remove a disproportionate amount of canopy. Although overall grasshopper abundances were low in our

study, the biomass removed by grasshoppers can exceed grasshopper biomass by a factor of 33 (Blumer and Diemer 1996), so even a low density of grasshoppers can have a disproportionately large effect.

Vegetation type and annual effects, the latter likely driven by differences in both winter precipitation and stock activity, were both more important than grazing effects in terms of influence on arthropods. These results are analogous to those of an earlier study that found seasonal and annual effects to outweigh effects of grazing in these meadows (Holmquist et al. 2013). Roche et al. (2012) similarly found that differences in soil saturation and the associated vegetation assemblage were also more important than cattle grazing in structuring Yosemite toad (*Anaxyrus* [= *Bufo*] *canorus*) distributions in Sierra wetlands. There was clearly higher faunal diversity and abundance in sedge than reed grass, but this relationship was largely reversed when assessed after compensation for differing canopy height. Thus superior habitat was provided by sedge on a per-area basis, but by reed grass on a per-volume basis. In this sense, sedge provided greater habitat quantity, but reed grass provided better habitat quality if the habitats are considered as three-dimensional "patch bodies" (Johnston 1995) after accounting for differing canopy height. Although not a uniform result, many studies of arthropods in other comparatively simple habitats have also determined that the higher diversity and abundance found in taller-canopy habitats is reduced or reversed if compensation is made for canopy height and/or leaf-area index (e.g., Stoner 1983; Holmquist et al. 1989; Morris 2000; see also Reid and Hochuli 2007). Relationships in the current study were likely driven by the taller canopy (Cunha et al. 2012), low soil strength, high soil moisture (Neuman 1996), and high productivity (Stohlgren et al. 1989) in sedge, versus the greater green cover, higher plant species richness (Benedict 1983; Neuman 1996), and higher structural complexity

and heterogeneity (see also Denno 1977; Holmquist 1998; Cunha et al. 2012) in the reed grass assemblage.

Management Implications

The wetter sedge habitat is less common in these wetlands than is reed grass in combination with other drier vegetation assemblages. Differences in soil moisture (Neuman 1996) may have contributed to the significantly higher diversity and abundance of terrestrial fauna in sedge, irrespective of grazing. A number of the taxa found predominantly or exclusively in sedge have one or more life stages that make use of damp habitats, such as Saldidae (Hemiptera) and Dolichopodidae, Ephydriidae, Culicidae, Lonchopteridae, Micropezidae, and Sciomyzidae (all Diptera). Further, sedge habitats are flooded for a month or more during early and mid-season (Benedict 1983; Stohlgren et al. 1989; Loheide et al. 2009), during which time an assemblage of aquatic arthropods is also present (Holmquist et al. 2011a). Reed grass can also be flooded during early season, but these areas are much less extensive and persistent than flooded sedge habitat. Sedge has an emergent canopy during the flooded phase, which simultaneously supports a terrestrial assemblage, whereas areas of flooded reed grass have little or no emergent canopy to accommodate terrestrial fauna. Sedge habitat thus represents a strong terrestrial-aquatic interface (see also Haslett 1997; Wettstein and Schmid 1999; Holmquist et al. 2011a). On a per-area basis, sedge provides disproportionately more habitat for both terrestrial and aquatic fauna than does reed grass, and the value of sedge habitat in this context is noteworthy. Sedge patches are thus analogous to other vegetated and water-associated habitat elements that support high aquatic and terrestrial arthropod diversity and are of conservation importance, such as prairie or desert spring riparian habitat (Anderson and Anderson 1995; Sada

et al. 2005; Holmquist et al. 2011b). Although managers might overlook sedge habitats because of low botanical diversity, the contribution to overall arthropod diversity via habitat provision is clear.

Our Sequoia study wetlands appear to have tolerated grazing with only minor to moderate effects, likely in part due to management use of annual, wetland-specific assessments to determine meadow opening dates and allowable stock densities (McClaran 1989; Holmquist et al. 2010; 2013). There may, however, be fewer restrictions in other managed areas that contain sedge or other wetter, sensitive assemblages. A potential concern is that, if stock access is determined on the basis of drier, more dominant vegetation assemblages, sedge patches in opened meadows might remain in a wetter, more vulnerable state at opening. In such a scenario, a simple stipulation that stock users release animals into meadows as far from wetter habitats as possible might reduce effects on sedge habitats for some meadow configurations. Use of portable electric fencing (e.g., Hall et al. 1992), although impractical for large areas, might be useful for partial enclosure of smaller, heavily used sedge patches. This approach would be most practical in situations in which the fencing could be used in conjunction with natural impediments such as deeper ponds and streams or rock bands. Exclosure of animals is sometimes preferable to enclosure, as some packers who have used backcountry electric fencing report that enclosure is too confining and results in poor performance by stock, although enclosing only the lead animal may mitigate this concern. Another alternative would be the placement of a small number of logs in wetter habitat, as this novel approach has been shown to decrease usage by mammalian grazers to the benefit of vegetation, arthropods, and reptiles (Barton et al. 2011; Manning et al. 2013). Such approaches

could reduce effects on sensitive, wetter patches in heavily used areas while leaving meadows open for stock use.

Acknowledgements Rick Dodson and Steve Case were outstanding field assistants, and Marie French was her usual meticulous self while sorting samples. We thank Sequoia National Park for their excellent support, especially from Corie Cann, Erik Frenzel, Erika Jostad, and Charisse Sydoriak, and WMRC faculty and staff, especially Vikki DeVries, Frank Powell, and John Smiley. The paper was improved through review by, or discussion with, Liz Ballenger, Beverly Collins, Dave Graber, Rebecca Efroymson, Peggy Moore, Sarah Sheehan, Matthew Taylor, Harold Werner, and an anonymous reviewer. This project was supported by the National Park Service (J8R07080005), and the current study built upon earlier work funded by the NPS (J8C07100004, J8R07070006, and J8R07030011). Angela Evenden expertly assisted with agreement development via the Californian and Great Basin Cooperative Ecosystems Studies Units.

Ethical Standards This study complies with the laws of the USA. We obtained a Scientific Research and Collecting permit from the US National Park Service for work in Sequoia National Park for each year of the study. No protected species were sampled.

Conflict of Interest The authors declare that they have no conflict of interest.

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Figure Captions

Fig. 1. Sequoia National Park in the Sierra Nevada of California, USA. Each of the six pairs of meadows (blocks) was composed of a grazed (black circle) meadow paired with an ungrazed (white circle) meadow. Meadows of a given pair are separated slightly on the map for clarity where necessary. Modified from Holmquist et al. 2010 with permission from Springer

Fig. 2 Rank abundance plots for families, based on mean abundances, comparing grazed and control meadows as a function of vegetation type

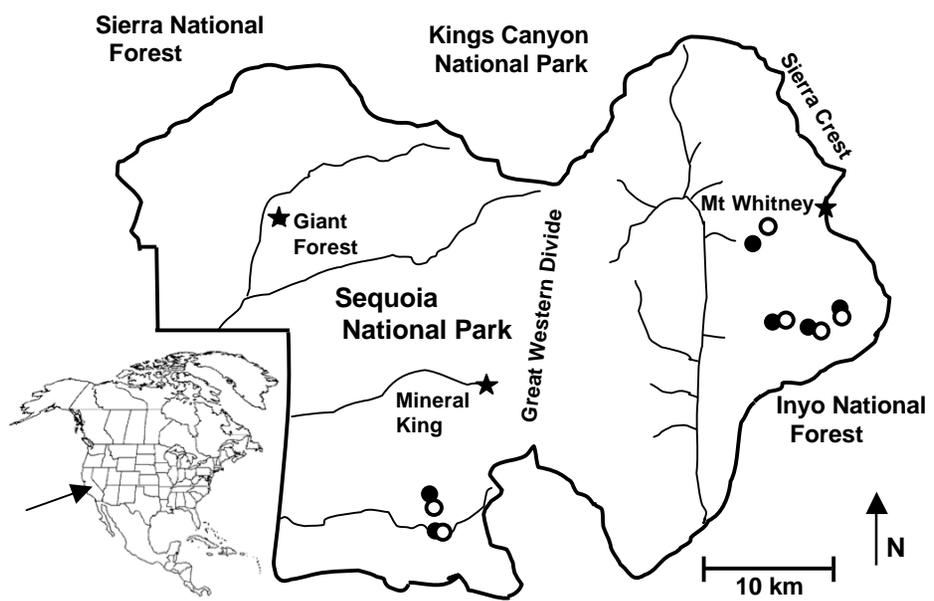


Fig 1

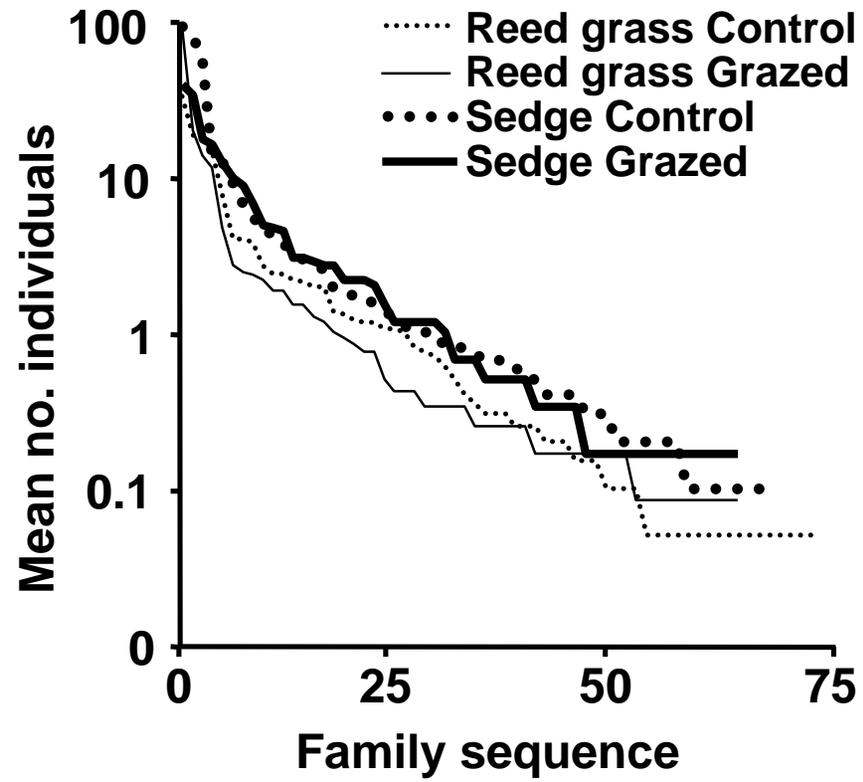


Fig 2

Table 1 Means (standard errors) for vegetation and physical metrics as a function of Treatment (T: Control, Grazed), Vegetation (V: Reed grass, Sedge), and Year (Y: 2010, 2011) and results of 2x2x2 blocked (B) ANCOVAs with elevation as a covariate

	Year	Reed grass		Sedge		ANOVA						
		Control	Grazed	Control	Grazed	T	V	Y	TxV	TxY	VxY	B
Canopy height (cm)	2010	17.8 (1.1)	11.4 (2.6)	44.5 (3.5)	27.5 (7.2)		**	**	*			**
	2011	7.88 (0.96)	6.14 (0.94)	28.7 (2.9)	21.0 (8.5)							
Litter depth (cm)	2010	1.25 (0.18)	0.250 (0.14)	3.13 (0.33)	0.250 (0.250)	**		*	*	**	**	**
	2011	1.33 (0.28)	1.00 (0.25)	0.708 (0.27)	0.500 (0.38)							
Litter cover (%)	2010	8.75 (3.3)	0.0 (0.0)	11.9 (7.9)	1.67 (1.7)	**				*		*
	2011	5.42 (2.2)	7.50 (3.8)	9.58 (3.1)	1.67 (1.7)							
Bare ground (%)	2010	1.88 (1.2)	25.0 (11)	0.0 (0.0)	35.0 (20)			**	*	**		
	2011	7.08 (1.4)	13.3 (8.3)	15.0 (3.1)	26.7 (14)							
Brown cover (%)	2010	7.50 (2.3)	5.83 (3.3)	7.50 (2.7)	10.8 (5.1)			**				**
	2011	18.3 (2.9)	15.8 (3.6)	17.1 (3.1)	20.0 (3.8)							
Green cover (%)	2010	81.9 (1.6)	69.2 (15)	80.6 (6.6)	52.5 (23)		**	**	*			**
	2011	69.2 (2.9)	63.3 (6.8)	58.3 (2.9)	51.7 (12)							
Soil strength (kg/cm ²)	2010	1.31 (0.23)	1.79 (0.25)	0.910 (0.12)	1.33 (0.77)	**	**				**	**
	2011	1.85 (0.062)	2.29 (0.49)	0.719 (0.22)	1.17 (0.98)							
Wind speed (km/hr)	2010	5.60 (1.6)	3.13 (2.4)	4.45 (0.68)	3.13 (2.4)							
	2011	5.72 (1.5)	5.97 (1.7)	5.03 (1.5)	5.97 (1.7)							
Air temperature (°C)	2010	19.0 (1.5)	17.0 (3.3)	19.1 (1.5)	17.0 (3.3)							*
	2011	16.9 (1.1)	18.7 (0.88)	16.9 (1.1)	18.7 (0.88)							

*P < 0.16 (see Methods); **P < 0.05.

Table 2 Means (standard errors) of faunal assemblage metrics as a function of Treatment (T: Control, Grazed), Vegetation (V: Reed grass, Sedge), and Year (Y: 2010, 2011) and results of 2x2x2 blocked (B) ANCOVAs with elevation as a covariate. All measures were based on 50-sweep samples

	Year	Reed grass		Sedge		ANOVA						
		Control	Grazed	Control	Grazed	T	V	Y	TxV	TxY	VxY	B
Total individuals	2010	157 (49)	80.3 (32)	369 (179)	208 (6.4)		**					
	2011	154 (35)	83.3 (40)	286 (109)	188 (70)							
Total individuals/cm canopy height	2010	9.28 (3.2)	9.88 (6.2)	8.54 (4.4)	8.50 (1.8)							
	2011	19.7 (4.0)	12.2 (4.6)	10.8 (4.5)	9.19 (0.29)							
Family richness	2010	19.0 (3.4)	13.3 (4.4)	28.8 (1.3)	24.0 (6.6)		**				*	
	2011	22.3 (3.1)	18.0 (4.2)	23.3 (3.6)	21.3 (6.7)							
Morphospecies richness	2010	28.5 (7.0)	16.7 (6.2)	40.1 (3.5)	38.3 (13)		**				*	
	2011	33.7 (6.0)	23.7 (7.6)	35.5 (6.3)	33.0 (12)							
Expected no. of morphospecies	2010	8.65 (1.9)	8.15 (3.0)	10.4 (2.2)	9.35 (2.7)			*			*	
	2011	10.6 (0.72)	11.0 (1.0)	9.20 (1.4)	10.1 (1.9)							
Expected morphospecies/cm canopy height	2010	0.484 (0.12)	0.652 (0.13)	0.236 (0.054)	0.356 (0.11)		**	**			**	
	2011	1.40 (0.12)	1.87 (0.33)	0.342 (0.068)	0.570 (0.12)							
Probability of interspecific encounter	2010	0.705 (0.16)	0.660 (0.20)	0.804 (0.13)	0.743 (0.17)			**				*
	2011	0.868 (0.030)	0.888 (0.025)	0.774 (0.078)	0.868 (0.067)							
% Family dominance	2010	44.5 (15)	49.9 (19)	35.5 (14)	42.5 (17)			*			*	
	2011	34.0 (3.7)	26.4 (2.3)	43.1 (11)	37.1 (7.2)							
% Species dominance	2010	43.3 (16)	48.4 (20)	30.7 (15)	42.0 (18)			**				
	2011	27.5 (6.1)	23.6 (3.5)	36.9 (10)	22.3 (11)							
% Predators	2010	12.9 (3.6)	13.6 (7.1)	17.6 (7.2)	9.13 (5.8)			**		*		
	2011	10.9 (2.2)	19.4 (2.2)	14.2 (3.2)	26.5 (12)							
% Herbivores	2010	10.5 (3.2)	8.56 (2.7)	23.6 (7.0)	15.8 (8.0)		*	**				
	2011	33.7 (4.4)	47.2 (7.5)	45.9 (12)	45.5 (10)							
% More motile fauna	2010	94.3 (1.5)	92.0 (3.4)	91.6 (3.2)	91.6 (5.5)			*				
	2011	79.9 (3.7)	87.4 (3.8)	73.4 (12)	85.8 (3.6)							
% Less motile fauna	2010	5.67 (1.5)	8.00 (3.4)	8.38 (3.2)	8.21 (5.6)			*				

2011	20.1 (3.8)	12.6 (3.8)	26.6 (12)	14.2 (3.6)
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*P < 0.16 (see Methods); **P < 0.05.

Table 3 Means (standard errors) for orders and ten most abundant faunal families as a function of Treatment (T: Control, Grazed), Vegetation (V: Reed grass, Sedge), and Year (Y: 2010, 2011) and results of 2x2x2 blocked (B) ANCOVAs with elevation as a covariate. All measures were based on 50-sweep samples

	Year	Reed grass		Sedge		ANOVA						
		Control	Grazed	Control	Grazed	T	V	Y	TxV	TxY	VxY	B
Orthoptera	2010	0.250 (0.25)	0.333 (0.33)	0.0 (0.0)	1.00 (1.0)	**						*
	2011	0.0 (0.0)	1.00 (0.0)	0.0 (0.0)	0.0 (0.0)							
Plecoptera	2010	0.0 (0.0)	0.0 (0.0)	0.250 (0.25)	0.0 (0.0)							
	2011	0.0 (0.0)	0.0 (0.0)	0.500 (0.50)	0.0 (0.0)							
Hemiptera	2010	10.5 (7.3)	3.33 (1.7)	81.8 (37)	33.3 (16)		**	**				*
	2011	53.7 (18)	44.7 (26)	178 (84)	92.7 (41)							
Cicadellidae	2010	5.75 (3.5)	2.00 (1.2)	70.8 (35)	13.3 (5.2)	*	**	**				*
	2011	29.2 (11)	16.7 (9.3)	84.2 (48)	53.0 (16)							*
Delphacidae	2010	2.25 (2.3)	0.333 (0.33)	1.75 (0.85)	4.00 (3.1)			**		*		*
	2011	7.50 (3.8)	21.7 (12)	1.83 (1.1)	28.0 (21)							
Aphididae	2010	0.750 (0.48)	0.0 (0.0)	2.25 (0.75)	3.00 (2.5)		*	**		*		
	2011	14.0 (7.6)	1.33 (0.67)	86.8 (80)	6.00 (5.0)							
Thysanoptera	2010	0.0 (0.0)	0.0 (0.0)	0.500 (0.29)	0.0 (0.0)	ID						
	2011	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)							
Coleoptera	2010	0.500 (0.29)	1.00 (1.0)	1.25 (0.75)	2.33 (1.5)	*				*		**
	2011	1.50 (0.62)	0.667 (0.33)	0.667 (0.33)	0.333 (0.33)							
Neuroptera	2010	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.333 (0.33)	ID						
	2011	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)							
Hymenoptera	2010	5.75 (2.2)	1.00 (0.58)	8.50 (1.7)	11.7 (5.8)						*	*
	2011	7.33 (3.7)	8.33 (4.6)	3.50 (1.1)	5.67 (3.7)							
Lepidoptera	2010	0.250 (0.25)	0.667 (0.67)	1.25 (0.75)	0.333 (0.33)							
	2011	0.167 (0.17)	0.0 (0.0)	0.667 (0.67)	0.333 (0.33)							
Diptera	2010	132 (50)	71.7 (36)	268 (162)	155 (29)		**	**				
	2011	83.5 (15)	21.3 (6.9)	92.8 (30)	80.3 (29)							
Dolichopodidae	2010	1.00 (0.71)	0.0 (0.0)	5.75 (2.8)	0.333 (0.33)	*	**	**				

	2011	3.67 (2.9)	1.67 (1.7)	16.8 (11)	19.0 (13)				
Anthomyiidae	2010	33.0 (16)	13.0 (8.1)	19.0 (2.8)	30.3 (14)	**	*		
	2011	10.7 (2.8)	1.00 (0.58)	2.33 (0.72)	4.00 (2.3)				
Muscidae	2010	3.50 (.87)	2.00 (1.5)	10.0 (4.7)	12.0 (6.1)	*		*	*
	2011	26.5 (16)	5.67 (2.4)	14.8 (4.7)	12.3 (7.5)				
Agromyzidae	2010	1.75 (0.76)	0.667 (0.67)	4.75 (1.9)	7.33 (1.2)	**	*	**	*
	2011	4.00 (1.3)	1.67 (0.88)	2.17 (0.48)	6.00 (2.6)				
Chloropidae	2010	5.00 (2.8)	2.33 (0.88)	2.25 (0.95)	4.33 (2.2)	*		*	**
	2011	3.50 (1.4)	1.67 (0.88)	1.67 (0.56)	0.0 (0.0)				
Ephydriidae	2010	70.8 (59)	41.3 (39)	190 (156)	63.3 (53)	**	**		
	2011	12.5 (5.4)	0.667 (0.33)	24.8 (11)	14.0 (11)				
Araneae	2010	7.25 (4.0)	2.33 (1.2)	7.50 (2.3)	4.00 (1.7)				
	2011	8.00 (3.0)	7.33 (6.3)	10.0 (5.4)	8.33 (4.5)				
Araneidae	2010	3.00 (0.82)	1.00 (0.58)	5.25 (1.9)	2.67 (1.2)	**		**	
	2011	3.00 (0.86)	6.00 (6.0)	0.333 (0.33)	0.0 (0.0)				

*P < 0.16 (see Methods); **P < 0.05; ID = insufficient data to test.

Online Resource 1 Overview of abundance relationships by habitat and treatment. R = Reed grass, S = Sedge, C = Control, G = Grazed. Absence of a given combination indicates zero abundance. Inequalities do not indicate statistical differences

Orthoptera		Lepidoptera	
Acrididae	RG = SG > RC	Coleophoridae	RG = SG > RC > SC
Plecoptera		Pyrilidae	RG
Chloroperlidae	SC	Hesperiidae	SC
Hemiptera		Noctuidae	SC > SG
Saldidae	SG > SC	Diptera	
Miridae	SG > SC > RG > RC	Tipulidae	SG > SC > RC
Nabidae	SG > SC > RC > RG	Ceratopogonidae	SC > SG > RG
Anthocoridae	SC	Chironomidae	SC > SG > RG > RC
Scutelleridae	RG = SG	Culicidae	SC = SG
Rhyparochromidae	RG > SC	Simuliidae	SG > RC > SC
Lygaeidae	SG > RC > SC > RG	Cecidomyiidae	RG > SC
Geocoridae	RG = SG > SC	Mycetophilidae	RG > SG
Cicadellidae	SC > SG > RC > RG	Sciaridae	SG > RC > SC > RG
Delphacidae	RG > SG > RC > SC	Empididae	RC > RG > SC > SG
Psyllidae	SC > RC > RG	Dolichopodidae	SG > SG > RC = RG
Aphididae	SC > SG > RC > RG	Lonchopteridae	SG > SC
Thysanoptera		Phoridae	SC > SG > RG > RC
Thripidae	SC	Pipunculidae	SG > RC > SC > RG
Coleoptera		Syrphidae	SC > SG = RG > RC
Staphylinidae	RC > RG > SC	Anthomyiidae	RC > SG > SC > RG
Melyridae	SC	Calliphoridae	SG
Coccinellidae	SG > SC > RG > RC	Muscidae	SC > SG > RC > RG
Mordellidae	RC = RG	Sarcophagidae	RC
Chrysomelidae	SG	Scathophagidae	SC > RC > SG
Neuroptera		Tachinidae	RC > RG > SC > SG
Hemerobiidae	SG	Psilidae	RC
Hymenoptera		Micropezidae	SC
Tenthredinidae	SG	Lonchaeidae	RC > SC
Braconidae	SG > SC = RC > RG	Tephritidae	RC > SC > RG > SG
Ichneumonidae	SC > SG = RC > RG	Chamaemyiidae	RG > SC
Pteromalidae	SG > RC > RG > SC	Sciomyzidae	SC
Eucoilidae	RC = SC	Sepsidae	SC > RG > SG > RC
Proctotrupidae	SG	Agromyzidae	SG > SC > RG > RC
Diapriidae	RG > SC > RC	Opomyzidae	RG
Bethyidae	SG	Chloropidae	RC > RG = SG > SC
Dryinidae	RC	Heleomyzidae	RG > SG > RC > SC
Pemphredonidae	SG	Sphaeroceridae	SG > SC > RC > RG
Apidae	RC	Drosophilidae	RG = SG > SC > RC
Formicidae	SG > RG > RC > SC	Ephydriidae	SC > SG > RC > RG

Araneae

Araneidae	SC > SG > RG > RC
Tetragnathidae	SC > SG > RC
Linyphiidae	SC > RG > RC
Dyctinidae	SC > SG
Oxyopidae	SG
Lycosidae	RC > SG > SC
Philodromidae	SG
Thomisidae	RC > RG > SC > SG
Salticidae	RC