Characterizing prevalence and ecological impact of non-native terrestrial isopods (Isopoda, Oniscidea) in tallgrass prairie

Caitlin Singer, Nora M. Bello, and Bruce A. Snyder

Published Version Information

Citation: Singer, C., Bello, N. M., & Snyder, B. A. (2012). Characterizing prevalence and ecological impact of non-native terrestrial isopods (Isopoda, Oniscidea) in tallgrass prairie. Crustaceana, 85(12), 1499–1511.

Digital Object Identifier (DOI): doi:10.1163/15685403-00003126

Publisher's Link: http://booksandjournals.brillonline.com/content/10.1163/15685403-00003126;jsessionid=1p4jfcu5em6o4.x-brill-live-01

CHARACTERIZING PREVALENCE AND ECOLOGICAL IMPACT OF NON-NATIVE TERRESTRIAL ISOPODS (ISOPODA, ONISCIDEA) IN TALLGRASS PRAIRIE.

BY

CAITLIN SINGER [1*], NORA M. BELLO [2], and BRUCE A. SNYDER [3]

[1]Arizona State University, Tempe, Arizona U.S.A.

[2]Department of Statistics, Kansas State University, Manhattan, Kansas, U.S.A.

[3]Division of Biology, Kansas State University, Manhattan, Kansas, U.S.A.

[*] Corresponding author. Tel.: +1 602 696 0550. E-mail address: caitlinsinger@gmail.com (C. Singer). Current address: Caitlin Singer, School of Environmental and Forest Sciences, Box 352100, University of Washington, Seattle, WA 98195-2100.

ABSTRACT

Isopods are terrestrial crustaceans whose role and impact in the tallgrass prairie ecosystem remains little explored despite being rather prevalent non-native inhabitants. To better understand this role, we conducted two related studies. The first was a rapid survey of isopods in experimental treatments at Konza Prairie LTER site to investigate the diversity and relative abundance of isopod species present. Of the four species known in Kansas thus far, all non-native, Armadillidium vulgare was the most abundantly found, accounting for 93% of individuals found. Armadillidium nasatum, Cylisticus convexus, and Porcellionides pruinosus were also found and we report the first record of Porcellio laevis in the State of Kansas. Survey results showed no evidence for a relationship between isopod abundance and fire frequency or grazing treatment.

The second experiment was a food preference study to explore granivory in non-native isopods and characterize their seed predator behavior on native plants. Individual isopods were placed in Petri dishes with food options including leaf litter and seeds from one of 15 species; dishes were then incubated for 6-12 days and preference was assessed based on pre- and post-trial weights of the feed and individual isopod. Isopods showed a significant preference for leaves compared to seeds in nine of the 15 seed species evaluated; no evidence for leaf-vs.-seed preference was apparent in the remaining six seed species. However, in all cases, isopods did consume some amount of seeds even when leaf litter was present. Taken together, the relatively low abundance of non-native terrestrial isopods and their lack of apparent preference for native plant seeds suggest that isopods are unlikely to pose considerable threat to tallgrass prairie ecosystems. More extensive research, including a preference study with greater representation of

seed species and a quantitative survey throughout the year, would be needed to further characterize the ecological role of isopods in the tallgrass prairie.

INTRODUCTION

Isopods of a broad spectrum of sizes and shapes can be found in both aquatic and terrestrial ecosystems (Brusca & Wilson, 1991). Terrestrial isopods, the focus of our experiments, are very adaptable and can be found in almost any environment provided there is sufficient moisture and food. They typically have minimal food constraints due to their generalist diet and opportunistic feeding (Causey, 1952; Hassall & Rushton, 1982; Saska, 2008), though they do seem to have a preference for microbially colonized decaying organic materials, including plant litter (Paoletti & Hassall, 1999; Ihnen & Zimmer, 2008). Isopods are historically widespread and abundant across North America, despite being non-native fauna, and have been described to aggregate in high densities, reaching as many as thousands per m^2 (Causey, 1952; Paoletti & Hassall, 1999) . Their plethoric numbers and synanthropic nature (Jass & Klausmeier, 2000) suggest that they are adaptable to most environments, with a recognized role in the ecosystem as an accelerator of plant matter decomposition (Hassall et al., 1987; Zimmer, 2002). This is likely achieved by mandibular fragmenting of leaves, which in turn executes chemical decomposition in the environment by stimulating the growth of microbes (Warburg, 1993; Zimmer et al., 2003).

Little is known about terrestrial isopod ecology and distribution in Kansas, especially in the highly fragmented and threatened tallgrass prairie ecosystem (Cully et al., 2003; Reed, 2004). Diversity and distribution of isopod species in Kansas has also received little attention; species known in Kansas prior to this study were Armadillidium nasatum Brandt 1833, Armadillidium vulgare (Latreille 1804), Cylisticus convexus (DeGeer 1778) and Porcellionides pruinosus

(Brandt 1833) (Jass & Klausmeier, 2001). These species are often found not only in disturbed areas, but also within relatively undisturbed prairie habitats (e.g., logs, stones, vegetation), so that encounters of isopods with plant seeds are quite plausible (Saska, 2008).

Seed predation can have a considerable impact on plant demography, potentially affecting population growth, dispersal and population structure (Saska, 2008). While several species of marine isopods are known to consume seeds (Fishman & Orth, 1996; Holbrook et al., 2000; Orth et al., 2006, 2007), terrestrial species have only recently been established as granivorous in laboratory experiments (Saska, 2008). Seed dispersal and establishment are known to be important events in plant populations (Benson & Hartnett, 2006), with select advantages being movement away from predation near parent plant and suitable germination microsites (Collins & Uno, 1985). Prairie insects can have a detrimental effect on seed dispersal and plant reproductive success (Evans et al., 1989); if terrestrial isopods were found to also act as seed predators, they could plausibly have a similarly detrimental effect on plant reproduction. Therefore, depending on their relative abundance, distribution, and food preference, non-native isopod species present in Kansas could pose a threat to the conservation of native plants in this ecosystem which has already been highly impacted by land-use change. Two studies were undertaken to address the potential conservation implications of terrestrial isopod presence. The specific objectives of the studies were: to investigate the diversity and relative abundance of non-native isopod species in the tallgrass prairie and to characterize their seed predator behavior on native plants. Preliminary sampling during summer 2010 indicated that the most commonly found isopod was Armadillidium vulgare; our objective was to test A. vulgare's preference for leaf litter versus native seed species of Konza Prairie.

MATERIAL AND METHODS

Site description

Konza Prairie Biological Station is a Long Term Ecological Research (LTER) site owned in partnership by The Nature Conservancy and Kansas State University. It is located in the Flint Hills of northeastern Kansas, within the largest area of unplowed tallgrass prairie in North America, retaining much of its native uniqueness. It is used as a field research station by Kansas State University Division of Biology, providing opportunities for study of tallgrass prairie ecosystems (Freeman & Hulbert, 1985). Konza Prairie is divided into watershed-scale treatments including watersheds that are either ungrazed or grazed by ungulates (American bison, Bison bison (Linnaeus 1758)), in combination with burn frequencies of 1-, 2-, 4- and 20-year intervals (Towne, 2002).

Survey

A rapid survey approach was employed across watersheds within a short period of time. This was primarily done to limit the effects of Kansas' highly variable weather on survey results. Sampling occurred during the week of 6 to 12 March 2011 on a total of 16 watersheds, so that each combination of prescribed fire frequency and grazing treatment was represented by 2 watersheds. Three sampling sites were selected a priori in each chosen watershed, thus yielding a total of 48 samples.

In order to maximize likelihood of isopod presence, the collectors made an effort to stratify the samples within each watershed by several factors: distance from disturbed areas (e.g., roads dividing watersheds), type of vegetation, and position on the landscape. Specimen collection was by hand and restricted to an approximate 5m x 5m area and 30 person-minutes (Snyder et al., 2006). Once collected, specimens were placed in a vial with soil and leaves to be taken back to the lab for identification.

Food preference study

Experiments were conducted during the summer of 2010 at Kansas State University (trials 1-3) and the fall of 2010 at Arizona State University (trial 4). Seeds and leaf litter were collected from Konza Prairie and Kansas State University campus. Petri dishes (100 x 15mm) were set up so that each contained one isopod, leaf (trials 1-3) or grass (trial 4) litter, and one native plant seed species. Each Petri dish was considered an experimental unit. This resulted in five experimental units per seed species in trials 1-3, and four experimental units per seed species in trial 4. Dishes were misted daily with water. Individual isopods (live biomass), litter, plant seeds and fecal pellets (air-dried) were weighed before and after each trial. Seeds and leaves were provided in standard and relatively large amounts to prevent confounding due to limited food availability, independent of trial duration. As consumption rates were unknown, trial durations were relatively short but varied between trials as we sought the ideal duration.

For trials 1-3, individuals of A. vulgare were collected from Konza Prairie during the summer of 2010 and data collection was conducted during 23 June – 27 July 2010. Trials 1 and 2 lasted 6 and 12 days respectively, with both using the seeds of five native Kansas plant species: Desmanthus illinoensis (Michaux) MacMillan (Illinois Bundleflower), Psoralidium tenuiflorum (Pursh) Rydb. (Scurfy pea), Helianthus maximiliani Schrader (Maximilian Sunflower), Solidago rigida (Linnaeus) (Rigid Goldenrod) and Sorghastrum nutans (Linnaeus) Nash (Indiangrass). The third trial lasted nine days and used the seeds of five native Kansas plant species: Zigadenus paniculatus (Nutt.) S. Watson (Death Camas), Tripsacum dactyloides (Linnaeus) Linnaeus (Gamagrass), Elymus canadensis Linnaeus (Canada Wildrye), Oenothera macrocarpa Nutt. (Missouri Evening Primrose) and Asclepias viridiflora Raf. (Green Milkweed).

Time constraints disallowed for the entire study to be completed during the primary investigator's 10-week Research Experiences of Undergraduates (REU) project during the summer of 2010 at Kansas State University; thus a further trial in the food preference study (trial

4) was conducted during fall of 2010 at the primary author’s home institution of Arizona State University. For trial 4, materials and specimens were mailed from the original collection site to Arizona State University.

Data collection for trial 4 was conducted during 14 October – 10 November 2010. Isopods were collected during a single day from Kansas State University campus, approximately 10 km from Konza prairie. A total of 27 individuals of A. vulgare were collected. Grass litter was collected from a mowed fire guard in the Konza Prairie Biological Station headquarters area during the spring of 2010, allowed to air dry, and stored until the initiation of the experiment. Seed decay was attempted for the purpose of enhancing consumption given isopods’ well described preference for decaying matter (Paoletti & Hassall, 1999; Ihnen & Zimmer, 2008). Seed decay was initially induced for 4 days for the first three seed species listed below, with the remaining four seed species added after this pre-testing was determined unnecessary, for a total of 20 days for the first three seed species, and 16 for the remaining four (see next paragraph). Seeds of each species were moistened and allowed to sit in a Petri dish in a warm location. This was intended to facilitate decomposition, but appeared ineffective, as no visible evidence of decay could be found.

Trial 4 lasted nine days and evaluated seeds from the following seven native Kansas plant species: Zizia aurea (Linnaeus) W.D.J. Koch (Golden Zizia), Desmanthus illinoensis (Illinois Bundleflower), Sporobolus heterolepis (A. Gray) A. Gray (Prairie dropseed), Silphium laciniatum Linnaeus (Compass Plant), Panicum virgatum Linnaeus (Switchgrass), Dalea candida Michx. ex Willd. (White Prairie Clover), and Elymus canadensis (Canada Wildrye).

Statistical Analysis

For survey data, a generalized linear mixed model was fitted to count of isopods recorded on each survey sample. The response was fitted using a Poisson distribution with a log link function. The linear predictor included the fixed effects of grazing and prescribed fire frequency treatments. The interaction between grazing and prescribed fire frequency was evaluated as a fixed effect but was excluded from the final model based on evidence for model overspecification. The random effect of watershed nested within grazing and prescribed fire frequency treatment was also specified to recognize technical replication in the design and to appropriately recognize experimental units.

The experimental setup for food preference Trials 1, 2 and 3 was similar; thus, we analyzed their data in a joint analysis. A general linear mixed model was fitted to the response variable "Feed consumption" defined as the difference between weight of initial feed offered and weight of refuse feed (measured in grams) for Trials 1, 2 and 3. The linear predictor of the model used for analysis included the fixed effects of feed source (seed or leaf), seed species and their 2-way interaction, along with the covariates initial feed weight and initial isopod bodyweight. Additional interactions were evaluated but were not included in the final model based on non-significant P-values, maximum-likelihood-based model fit criteria and an attempt to prevent model overparameterization. A random effect of isopod nested within seed species for each trial was fitted to the model to recognize the appropriate experimental unit for seed species and the blocking factor for feed source. A random effect of trial was evaluated as a potential blocking factor. However, the corresponding variance component converged to zero and thus the random trial effect was dropped from the model. Heterogeneous residual variances as a function of trial were fitted in the model, as granted by improved model fit assessed using Bayesian Information Criteria.

The experimental design and conditions for Trial 4 differed considerably from Trials 1-3, and thus was analyzed separately. A general linear mixed model was fitted to the response variable “Feed consumption" as described previously for data from trials 1-3. We note that only 7 seed species were evaluated in this trial.

Statistical models were fitted to the survey and food preference data using the GLIMMIX and MIXED procedures of SAS (Version 9.2, SAS Institute, Cary, NC), respectively. For general linear models, studentized residual plots were evaluated and model assumptions were considered to be appropriately met. Estimated standard errors were bias corrected using Kenward Roger's or Morel's Sandwich estimator, as implemented by SAS for general and generalized linear mixed models. Also, degrees of freedom were estimated using Kenward Roger's approximation. Results are presented as estimated least square means and corresponding standard errors. Pairwise comparisons of interest were conducted using Tukey-Kramer's or Bonferroni's adjustment, as appropriate, to avoid inflation of Type I error rate.

RESULTS

Isopod diversity, relative abundance and distribution at Konza Prairie

Our survey of Konza Prairie found only 15 individuals of two species, Armadillidium vulgare and Cylisticus convexus. Armadillidium vulgare was much more common, comprising 14 of 15 specimens (93%), and was found under shrubs, in leaf litter, moist soil, ungulate fecal matter and under rocks.

Isopod specimens were collected from 6 out of the 16 watersheds (table I). Most notably, no isopods were recovered from watersheds with 20-year fire frequency intervals and only 1 and 2 individuals were collected in 2- and 4-year fire frequency treatments, respectively. However, we found no evidence of significant differences between grazing treatments ($P = 0.90$) or prescribed fire frequencies ($P = 0.25$) in the count of isopod specimens.

Additional collections in the headquarters area of Konza Prairie Biological Station and the Kansas State University campus yielded Armadillidium nasatum, Porcellionides pruinosus and Porcellio laevis Latreille 1804. Our identification of Porcellio laevis constitutes a new state record for Kansas and was found at Konza Prairie, within watershed N1B under aged bison fecal matter.

Food preference study

For Trials 1-3, the joint analysis showed evidence for a significant interaction between seed species and feed source ($P<0.0001$) on feed consumption. In particular, the question of interest related to differences in consumption between feed sources (i.e., leaves vs. seeds) within each seed species. Significant differences in feed consumption between sources (fig. 1) were apparent for the following native plant species: Tripsacum dactyloides (Gamagrass), Oenothera macrocarpa (Missouri Evening Primrose), Helianthus maximiliani (Maximilian Sunflower), and Sorghastrum nutans (Indiangrass). For these native plant species, seed consumption was decreased compared to leaf consumption. As a side note, we point out that gamagrass exhibited a negative estimate for consumption due to minimal consumption combined with the growth of fungi and bacteria, resulting in a positive change in mass.

Across all plant species evaluated in this study, initial amount of feed offered was positively associated with feed consumption ($P < 0.0001$), whereby every 1 gram increase in feed offered increased feed consumption by an estimated 0.15 ± 0.02 grams for a given isopod. After adjusting for initial feed consumption, there was no evidence for any association between initial isopod bodyweight and feed consumption ($P = 0.84$).

For trial 4, data corresponding to native plant species Zizia aurea (Golden Zizia) and Elymus canadensis (Canada Wildrye) were excluded from analysis due to the high isopod mortality rate. In this trial, a main effect of feed source on feed consumption was identified (P =

0.0112). For the five remaining seed species considered in this experiment, isopods appeared to consume more leaves than seeds (fig. 2). There was no evidence of interaction between seed species and feed source (P= 0.19) on feed consumption. Also, there was no evidence for an association between initial isopod bodyweight and feed consumption (P = 0.62) nor for any association between initial feed availability and feed consumption (P = 0.82).

DISCUSSION

Due to widespread land-use change, the tallgrass prairie ecosystem is threatened and highly fragmented (Cully et al., 2003). Thus the conservation of native plant species is important to the maintenance of this ecosystem's distinctive character and ecosystem functioning. Invasive plant and animal species are a major threat; insects, in particular those known as seed predators, pose a special challenge by limiting seed dispersal (Evans et al., 1989). Due to the realization of a similar niche, isopods may fulfill a comparable role to seed predating insects, potentially by harming reproductive or dispersal abilities of native plant species. Past studies have recognized the role isopods have as decomposers in the tallgrass prairie ecosystem (Hassall et al., 1987; Zimmer, 2002) and have explored food preferences (Dudgeon et al, 1990; Rushton & Hassall, 1983). Granivory behavior of isopods has been described (Saska, 2008; Honek et al., 2009; Farmer & Dubugnon, 2009) and determined to be facultative (Koprdova et al., 2010). Moreover, isopod granivory behavior seems to be driven by seed abundance, nutrition and accessibility (Saska, 2008). If isopods are abundant and widespread seed predators, they could prove to be a threat to native plants of the tallgrass prairie.

Survey

Isopods were found to be widely but unevenly distributed, minimally abundant, and very depauperate at Konza Prairie. It was initially hypothesized that more isopods would be found in less frequently burned watersheds because of the protection and food provided by the higher abundance of plant detritus. We did not find evidence to support this claim; potential explanations include food quality, favorability of drier environments and/or open habitats. These preliminary data suggest that more work is needed to assess the effects of prescribed fire, grazing, and other land use changes on terrestrial isopods. In particular, other survey techniques should be considered, such as pitfall traps to complement manual searches as their combination may enhance effectiveness of the search (Snyder et al., 2006).

Food preference studies

This study showed a preference against consuming seeds relative to plant litter for nine of the 15 seed species present; no evidence for differential source preference was apparent for the other six native plant species. This supports the observations and conclusions of Saska (2008), including granivory in terrestrial isopods despite the presence of litter, which is possibly indicative of non-starvation based granivory, but may also be due to factors such as size, climate, season, and decomposition state of feed source (Hassall & Moss, 2011; Szekeres et al., 2011). This lack of evidence for associations between feed consumption and initial isopod bodyweight further link the two studies. We therefore hypothesize a difference in seed palatability, compatibility, and preference for consumption amongst different seed species.

Easily available litter-colonizing microbiota becomes a valuable resource to isopods when population density is driven by food quality (Zimmer & Topp, 2000; White, 1978). Access to highly nitrogenous foods is known to be limited for saprophagous, soil-dwelling animals (Rushton & Hassall, 1983; White, 1978). This available supply of a vital nutrient such as nitrogen may therefore affect feeding preference (Zimmer & Topp, 2000), with consumption due to the nutritional content of the microorganisms residing on the different leaf species, rather than the nutrition of the leaf species themselves (Zimmer & Topp, 1997). Chemical composition of the food source as well as amount of colonization by microbes may both influence their consumption by isopods. Indeed, chemical composition of leaf litter has been addressed when looking at food source utilization by sympatric woodlice species Porcellio scaber Latreille 1804 and Oniscus asellus (Linnaeus 1758), with results showing a better performance associated with a lower litter C:N ratio, higher pH levels, and lower levels of tannins and other phenolics (Zimmer & Topp, 1997).

Future food preference experiments should take into account the morphology (Pulliam & Brand, 1975) and chemical composition (Zimmer & Topp, 2000) of seeds consumed, offer an assortment of leaf species and shapes (Dudgeon et al., 1990), and test for litter quality through factors such as microbiota colonization, pH levels, and nutrient ratios (Zimmer & Topp, 1997, 2000). While this study examined seeds that were accessible during the time frame of the study, there are hundreds of species of vascular plants (Freeman & Hulbert, 1985) on Konza Prairie that could provide food for isopods. Species where seed-based reproduction is important or species whose seeds are used in restoration would be high priority for future studies.

Conclusions

Conservation of native plants is critical for protecting the remaining fragments of North American tallgrass prairie. Large populations of granivorous invertebrates could negatively affect the survival rates of native plants. However, it appears that isopods are at low densities regardless of the fire regimes evaluated herein, namely historical, more frequent (as is used for cattle management across much of the Flint Hills region), and less frequent (fire suppression near urban areas). Also, the most common isopod, A. vulgare, did not seem to exhibit any particular preference for native plant seeds. Taken together, this evidence suggest that isopods may pose little, if any, threat to the native plants of Konza Prairie, as representative of tallgrass prairie systems.

ACKNOWLEDGEMENTS

The authors would like to acknowledge the assistance of Arizona State University, Dr. Ron Rutowski, Dr. James Elser, Dr. Ari Jumpponen, Konza Prairie Biological Station, Konza Prairie LTER, Adam Skibbe, Dan Carter, Ben VanderWeide, and members of the Kansas State University Summer 2010 Biology and Engineering REUs. This work was funded by the Biology REU (NSF DBI-0851835) and SUROP programs at Kansas State University. We thank anonymous reviewers for constructive comments.

LITERATURE CITED

BENSON, E.J. & D.C. HARTNETT, 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecology, **187**: 163-177.

BRUSCA, R.C. & G.D.F. WILSON, 1991. A phylogenetic analysis of the Isopoda with some classifactory recommendations. Memoirs of the Queensland Museum. **31**: 143-204.

CAUSEY, D., 1952. The terrestrial Isopoda of Arkansas. Proceedings of the Arkansas Academy of Science, **5**: 25-30.

COLLINS, S. & G.E. UNO, 1985. Seed predation, seed dispersal, and disturbance in grasslands: a comment. American Naturalist, **125**: 866-872.

CULLY, A., J. CULLY JR. & R. HIEBERT, 2003. Invasion of exotic plant species in tallgrass prairie fragments. Conservation Biology, **17**: 990-998.

DUDGEON, D., H.H.T. MA & P.K.S LAM, 1990. Differential palatability of leaf litter to four sympatric isopods in a Hong Kong forest. Oecologia, **84**: 398-403.

EVANS, E.C. SMITH & R. GENDRON, 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. Oecologia, **78**: 220-230.

FARMER, E.E. & L. DUBUGNON, 2009. Detritivorous crustaceans become herbivores on jasmonate-deficient plants. Proceedings of the National Academy of Sciences of the United States of America, **106**: 935-940.

FISHMAN, J.R. & R.J. ORTH, 1996. Effects of predation on Zostera marina L. seed abundance. Journal of Experimental Marine Biology and Ecology, **198**: 11-26.

FREEMAN, C. & L. HULBERT, 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. Transactions of the Kansas Academy of Science, **88**: 84-115.

HASSALL, M. & S.P. RUSHTON, 1982. The role of coprophagy in feeding strategies of terrestrial isopods, Oecologia, **53**: 374-381.

HASSALL, M., J.G. TURNER & M.W.R. RANDS, 1987. Effect of terrestrial isopods on the decomposition of woodland leaf litter. Oecologia, **72**: 597-604.

HASSALL, M., A. MOSS. 2011. Effects of simulated climate change on ecology and behaviour of terrestrial isopods. Proceedings of the 8th International Symposium of Terrestrial Isopod Biology. Bled, Slovenia, Ljubljana: pp. 85-86.

HOLBROOK, S.J., D.C. REED, K. HANSEN & C.A. BLANCHETTE, 2000. Spatial and temporal patterns of predation on seeds of the surfgrass Phyllospadix torreyi. Marine Biology, **136**: 739-747.

HONEK, A., Z. MARTINKOVA, P. SASKA & S. KOPRDOVA, 2009. Role of post-dispersal seed and seedling predation in establishment of dandelion (Taraxacum agg.) plants. Agriculture, Ecosystems and Environment, **134**: 126-135.

IHNEN, K. & M. ZIMMER, 2008. Selective consumption and digestion of litter microbes by Porcellio scaber (Isopoda: Oniscidea). Pedobiologia, **51**: 335-342.

JASS, J. & B. KLAUSMEIER, 2000. Endemics and immigrants: North American terrestrial isopods (Isopoda, Oniscidea) north of Mexico. Crustaceana, **73**: 771-799.

JASS, J. & B. KLAUSMEIER, 2001. Terrestrial isopod (Crustacea: Isopoda) atlas for Canada, Alaska and the contiguous United States. Milwaukee Public Museum Contributions in Biology and Geology, **95**: 1-105.

KOPRDOVA, S., P. SASKA, A. HONEK & Z. MARTINKOVA, 2010. Seed consumption by millipedes. Pedobiologia, **54**: 31-36.

ORTH, R.J., G.A. KENDRICK & S.R. MARION, 2006. Predation on Posidonia australis seeds in seagrass habitats of Rottnest Island, Western Australia: patterns and predators. Marine Ecology Progress Series, **313**: 105-114.

ORTH, R.J., G.A. KENDRICK & S.R. MARION, 2007. Posidonia australis seed predation in seagrass habitats of Two Peoples Bay, Western Australia. Aquatic Botany, **86**: 83-85.

PAOLETTI, M. & M. HASSALL, 1999. Woodlice (Isopoda:Oniscidea): their potential for assessing sustainability and use as bioindicators. Agriculture, Ecosystems and Environment, **74**: 157-165.

PULLIAM, R. & M.R. BRAND, 1975. The Production and Utilization of Seeds in Plains Grassland of Southeastern Arizona. Ecology, **56**: 1158-1166.

REED, A.W., 2004. Granivory in the prairie of Central North America. Dissertation, Kansas State University.

RUSHTON, S.P. & M. HASSALL, 1983. Food and feeding rates of the terrestrial isopod Armadillidium vulgare (Latreille). Oecologia, **57**: 415-419.

SASKA, P., 2008. Granivory in terrestrial isopods. Ecological Entomology, **33**: 742-747.

SNYDER, B.A., M.L. DRANEY & P. SIERWALD, 2006. Development of an optimal sampling protocol for millipedes (Diplopoda). Journal of Insect Conservation, **10**: 277-288.

SZEKERES, S., D. FÜLÖP, P. SZABÓ, E. HORNUNG & F. VILISICS. 2011. Intra-population differences in litter consumption of Porcellio scaber Latreille, 1804. In: Zidar, P. & J. Strus (szerk.) Proceedings of the 8th International Symposium of Terrestrial Isopod Biology. Bled, Slovenia, Ljubljana: pp. 143-144.

TOWNE, E.G., 2002. Vascular Plants of Konza Prairie Biological Station: An Annotated Checklist of Species in a Kansas Tallgrass Prairie. Sida, **20**: 269-294.

WARBURG, M.R., 1993. Evolutionary Biology of Land Isopods: 1-159. (Springer, New York).

WHITE, T.C.R., 1978. Importance of a relative shortage of food in animal ecology. Oecologia, **33**: 71-86.

ZIMMER, M. & W. TOPP, 1997. Does leaf litter quality influence population parameters of the common woodlouse, Porcellio scaber (Crustacea:Isopoda)? Biology and Fertility of Soils, **24**: 435-441.

ZIMMER, M. & W. TOPP, 2000. Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea). Journal of Animal Ecology, **69**: 1071-1082.

ZIMMER, M., 2002. Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. Biological Reviews of the Cambridge Philosophical Society, **77**: 455-493.

ZIMMER, M., G. KAUTZ & W. TOPP, 2003. Leaf litter-colonizing microbiota: supplementary food source or indicator of food quality for Porcellio scaber (Isopoda: Oniscidea)? European Journal of Soil Biology, **39**: 209-216.

FIGURE CAPTIONS

Figure 1: Feed consumption in trials 1-3 of the food preference study, presented as least square mean estimates ± estimated standard errors (SE). Asterisks indicate native plant species for which seed consumption was significantly reduced relative to leaf consumption ($P < 0.05$). IB = Desmanthus illinoensis (Illinois Bundleflower), SP = Psoralidium tenuiflorum (Scurfy pea), MS = Helianthus maximiliani (Maximilian Sunflower), RG = Solidago rigida (Rigid Goldenrod), SOR = Sorghastrum nutans (Indiangrass), DC = Zigadenus paniculatus (Death Camas), GAMA = Tripsacum dactyloides (Gamagrass), CR = Elymus canadensis (Canada Wildrye), MEP = Oenothera macrocarpa (Missouri Evening Primrose), MW = Asclepias viridiflora (Green Milkweed).

Figure 2: Feed consumption in trial 4 of the food preference study, presented as least square mean estimates ± estimated standard errors (SE). *IB* = Desmanthus illinoensis (Illinois Bundleflower), PV = Panicum virgatum (Switchgrass), SH = Sporobolus heterolepis (Prairie dropseed), SL = Silphium laciniatum (Compass Plant), and WPC = Dalea candida (White Prairie Clover). Species Zizia aurea (Golden Zizia) and Elymus canadensis (Canada Wildrye) were excluded.

Figure 1:

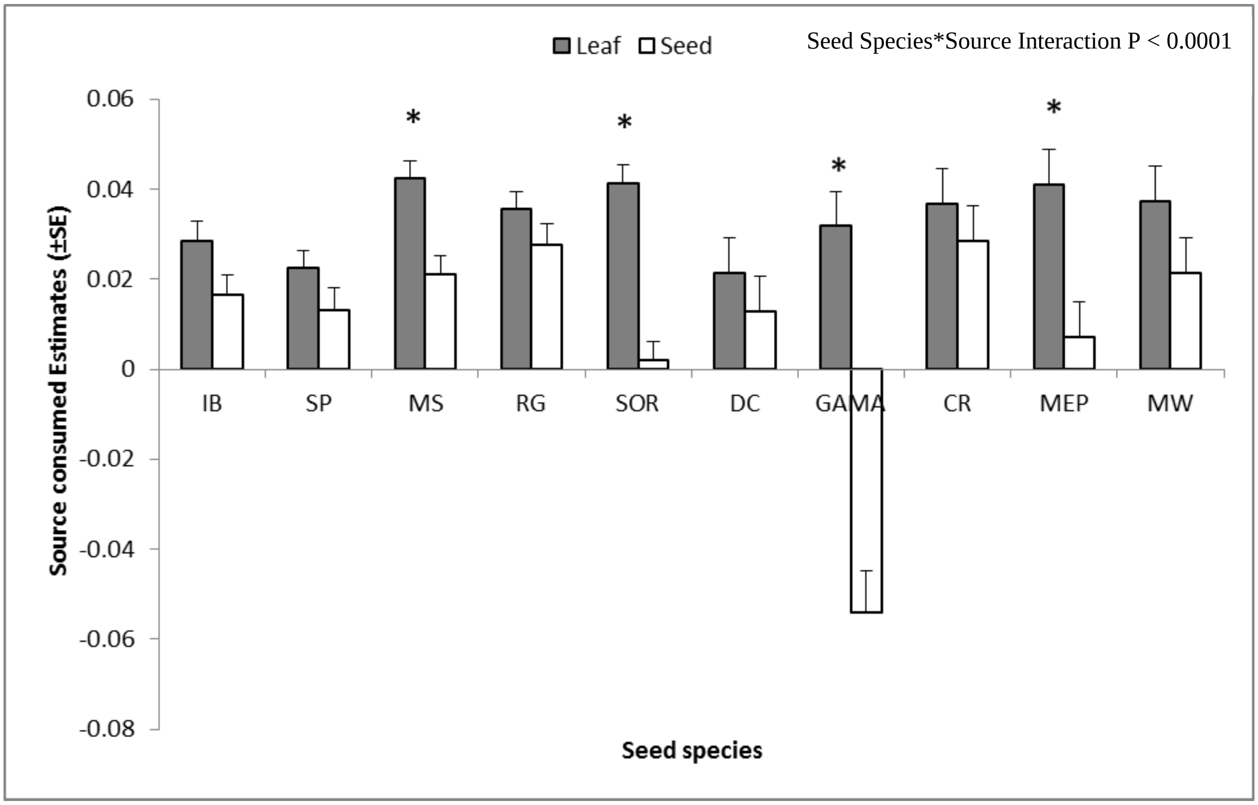
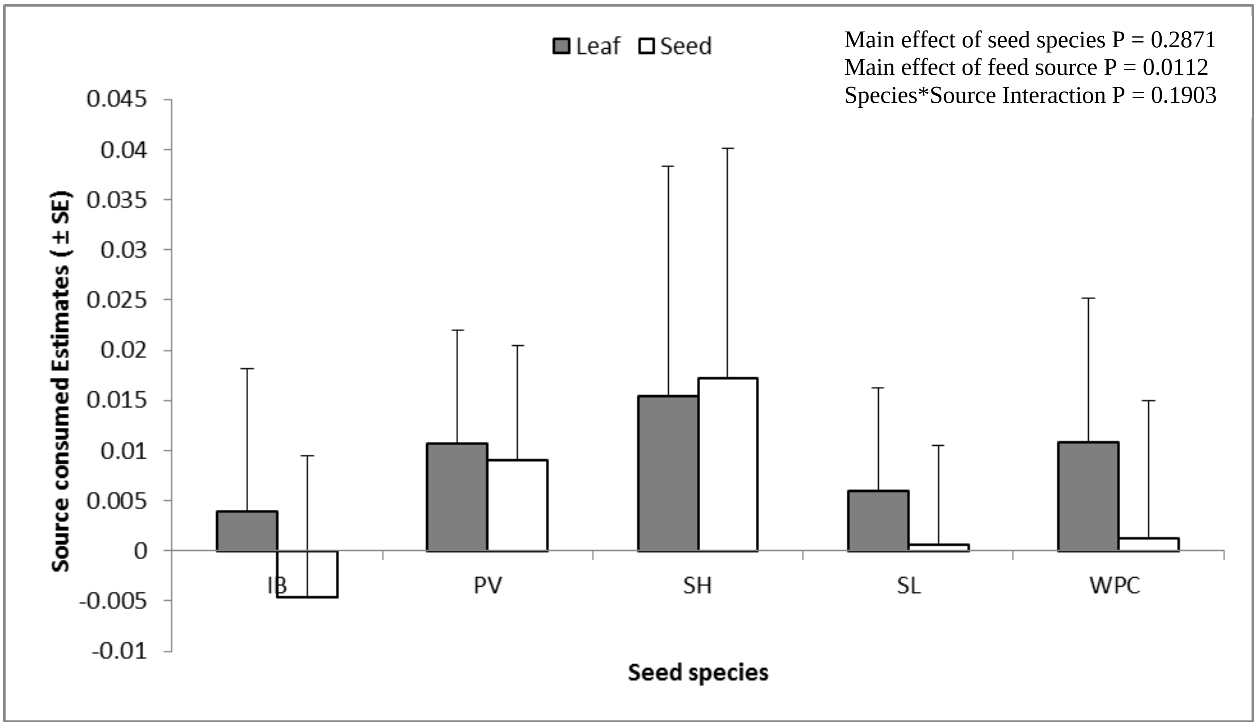

Leaf
Seed
Seed Species*Source Interaction P < 0.0001
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
Source consumed Estimates (±SE)
IB
SP
MS
RG
SOR
DC
GAMA
CR
MEP
MW
*
*
*
*
Seed species

Figure 2:



Leaf
Seed
Main effect of seed species P = 0.2871
Main effect of feed source P = 0.0112
Species*Source Interaction P = 0.1903
0.045
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
-0.005
-0.01
Source consumed Estimates (± SE)
IB
PV
SH
SL
WPC
Seed species

Table I: Number of isopod individuals and species found in each fire and grazing regime.

Main effect of grazing treatment P = 0.90
Main effect of fire frequency P = 0.25

Fire Frequency (years)	Grazing Treatment	Individuals Found	Species Found
1	Grazed	5	Armadillidium vulgare
	Ungrazed	7	Armadillidium vulgare
2	Grazed	1	Cylisticus convexus
	Ungrazed	0	--
4	Grazed	1	Armadillidium vulgare
	Ungrazed	1	Armadillidium vulgare
20	Grazed	0	--
	Ungrazed	0	--