**Abstract**

**Introduction**

* ABT (currently very weak)
  + Spatial subsidies shape food webs in recipient habitats
  + And: subsidies generally have weak effects in forests
  + But: sargasso in the forest decomposes at a similar rate to beaches
  + Therefore: sargasso subsidies impact the plant and arthropod communities at the beach and likely impact the microbe communities in the forest
* Habitat subsidies shape food webs
* Subsidy impacts are habitat-specific
  + Impacts differ depending on
    - Magnitude
    - Pulse timing
    - Utilization
* Drivers of habitat-specificity
  + Abiotic / biotic
  + Supply and timing
  + Barriers / boundaries
* Humans impacts on processes, supply, boundaries leading to increased subsidies

Fishing – Aquatic to Terrestrial

Eutrophication (Fertilizers, run-off, Sewage) – Terrestrial to aquatic

Dumping – Terrestrial to terrestrial

Agriculture/Farming – Terrestrial to terrestrial

Aquaculture- aquatic to aquatic

* The human element in subsidies research is understudied
* Forests in Yucatan peninsula are less subsidized
  + Less nutrient limitation
  + Natural boundaries
* Impacts may differ if “subsidy” is not utilized
  + +/- impacts may be species dependent
* What we did:

**Methods**

**Sargassodecomposition experiments**

*Sargasso piles*

We conducted this study at two sites in Puerto Morelos, Quintana-Roo, Mexico, from August 2022 and August 2023. This region is among those impacted by increased beached sargasso. The beach location in which we established this experiment is an ungroomed strip of beach north of the resort. All sargasso used in this manipulative experiment was obtained from drift paddies collected and supplied by Moon Palace Environmental Services.

At each site, we created piles of sargasso (4.28 ± 0.37 m3) with paired, unmanipulated controls (i.e., sections of beach or forest based on the average footprint of sargasso piles). Plots were separated by a minimum of 9 m from the center of the nearest treatment. To simulate a natural deposition of beached sargasso, we created five piles and five controls on a beach dune, parallel to the water line, north of Moon Palace Resorts (20.99343° N, 86.82442° W). In order to minimize human disturbance and prevent natural sargasso deposition from altering the manipulation, we established these plots above the high tide line, in an area not frequented by tourists. The beach at this location is a relatively narrow (~10m) strip adjacent to an unmarinated section of coastal foliage.

To simulate forest dump sites, we repeated the experiment along the outer perimeter of a botanical garden (Jardín Botánico ECOSUR “Dr. Alfredo Barrera Marín”; 20.84400° N, 86.90278° W). The botanical garden occupies an area of 65ha of natural forest and consists of 204 species from 64 botanical families (Elizondo, 2013). The botanical garden treatments (hereafter, “forest”) were located along the outer edge of a clearing, adjacent to a natural forest assemblage similar to areas where sargassois dumped in this region. To obtain initial volumes of sargasso piles, we measured the longest length, perpendicular width, and height of each pile to estimate volume using the elliptic cone formula (*V=1/3 πabh).* In subsequent sampling trips (November 2022, March, and August 2023), we measured the piles using the same methods and calculated the percent volume relative to original values.

*Decomposition experiment*

To test relative contributions of bacterial and arthropod decomposition of sargasso*,* we placed two sizes of mesh bags containing sargasso at the beach and in the forest (sm 180µm, lg 1cm; n=10). Small mesh bags excluded all arthropods larger than 180µm and large mesh bags allowed for decomposition by bacteria and arthropods. We placed 234.66 ± 0.42g of sargasso in each bag and measured changes in biomass on subsequent trips. Initially, forest treatments were placed in a forested public area but were later moved to the botanical in November 2022, to ensure they would be left undisturbed. The beach treatment remained in the same location throughout the experiment, however, on March 2023, we were unable to recover the large mesh bags due to vandalism of the experiment.

*Soil nitrification*

To understand if sargasso degradation affects soil nitrification (the oxidation of ammonium into nitrate by bacterial decomposition), we used aquarium water quality test strips (SJ Wave ®) to measure NO3- . We collected sediment samples from all treatments using a modified 50 ml falcon tubes as coring devices (tapered end of the tubes were cut off). All sediment cores were collected from approximately 30 cm from the edge of plots by temporarily clearing sargassoand leaf litter from the surface and coring the sediment underneath. We homogenized sediment samples and mixed with ?ml of filtered water, then filtered it through filter type. Following instructions included with the test kit, we visually compared the color change of each strip using the chart provided.

*Soil respiration*

We used upside-down 1.87 L plastic containers with an approximate footprint area of 176.715 cm as gas collectors. We drilled a hole in each container and glued rubber septa plug to sample using syringes. We placed gas collectors approximately 30 centimeters from the perimeter into each plot, directly above the sediment. We collected gas samples at the initial timepoint (T0) and after 60-minutes (T1) in November 2022, using a 10cc syringe. To do this, we penetrated the septa plug and pumped it ten times to homogenize the air before extracting the sample. Gas samples were collected in 10 ml vacutainers and transported to San Diego State University for CO2 analysis. In August 2023, we used a respirometer (model #) to obtain *in situ* readings of CO2 at the center and 30cm from the edge of each plot.

**Plant surveys**

*Plot interior survey*

To assess the effect of sargassoon plant cover directly on piles, we conducted percent cover surveys on the interior and perimeter of all plots using 100-point 0.5 x 0.5m PVC quadrats. To estimate plot interior percent cover (August and November, 2022), we randomly sampled by blindly tossing a marker over the shoulder and haphazardly placing a quadrat where the marker landed (n=3). We standardized the sampling method (March and August, 2023) by placing one quadrat in the center and using two randomly selected cardinal directions (degrees) and placing the next two quadrats at the edge of the first. We decided to sample in this way to fully capture the treatment effect at the center of the piles as piles shrank over time. In situations where we encountered multiple species under quadrat cross hairs, we identified and counted the top layer only.

*Plot perimeter survey*

To assess the effect of sargasso beyond piles, we conducted two surveys to look at plant percent cover at the edge of all treatments. We placed a quadrat at the edge of the piles and controls (1.88 m, average radius), on opposing sides of the plots (“left” and “right”). We measured percent cover using the methods described in the section above. This was repeated at 0.75m and 1.5m from the edges (August and November 2022, and March 2023). In March 2023, we did not see variation between sampling distances at 0.75m and 1.5m from the plot and decided to drop this portion of the survey in the interest of sampling efforts and time. In the second survey, we placed a quadrat on front and back of each plot (hereafter called “low” and “high”) and conducted percent cover surveys as described above. Thus, we combined the 0 m points of both surveys to create a perimeter survey to detect the effect of sargasso directly adjacent to the piles. Additionally, because Bermuda grass was so prevalent at the beach sites and there were no obvious patterns observed in the forest, we decided to score these surveys by collapsing all non-Bermuda grass plants into one category in the forest (March 2023), and both sites in August 2023.

It should be noted that the beach site was located north of Moon Palace resort in an area that is not typically used by beachgoers, however, between November 2022 and March 2023, we found recreational vehicles that disturbed the edge of two sargassopiles*.* Due to this disturbance, surveys were adjusted to avoid the disturbed areas by moving quadrats to an adjacent side where the piles were undisturbed. We did not see any signs of unnatural disturbance on treatments in the forest.

**Arthropod Surveys**

*Crawling arthropods*

To assess the effect of sargassoon crawling arthropod abundance, we placed two yellow (210 ml) plastic cups at the edge of the lowest and highest points of each plot. Each cup was buried, flush with the substrate and filed approximately halfway with water and ~5 drops of dish soap to break the surface tension and prevent arthropods from escaping. We collected the entire contents of each trap after 24 hours, counted, and identified arthropods to order.

*Flying arthropods*

To assess the effect of sargassoon flying arthropod abundance, we placed two double-sided sticky cards (127mm x 76mm), attached to wire rods using cable ties on each plot. The sticky traps were placed ~ 130mm above the substrate or sargassopiles, ~1m from the center to the “high” and “low” sides of the plot.  After 24 hours, we photographed all sticky traps *in-situ* to process at a later time. Both sided of sticky traps were counted and averaged. Flying arthropods were identified to order.

**Results**

*Decomposition*

Although initial sargasso pile volumes differed between sites(rm-ANOVA), both beach and forest treatments decreased the most between August and November 2022 (3.98 SE at the beach and 1.86 SE at the forest). Although pile volumes did not differ between November 2022 - March 2023 and March – August 2023 sampling periods at the beach, there was a significant difference in pile volumes between November 2022 - March 2023 in the forest treatment.

*Soil nitrification*

None of the sediment samples from control plots at either site registered any nitrate levels in our tests. Nitrate levels were 6.5 ± 2.3 mg/L under sargasso piles at the beach after initial deployment and continued to increase to 18.6 ± 5.2 mg/L in November 2022, peaked at 79.5 ± 44 mg/L in March 2023, and declined to 24 ± 10.8 in August 2023. Due to logistical and time constraints, we were unable to sample the sediment under the forest treatments after installation. Forest nitrate levels at the forest were lower than those at the beach but generally following the same pattern (i.e., nitrate levels peaked in March 2023). Nitrate levels were 7.5 ± 4.03 mg/L in November 2022, increased to 20 ± 5.2 mg/L in March 2023, and declined to 10 mg/L in August 2023.

*Soil respiration*

In November 2022, initial soil respiration was ?? in beach controls and did not increase after an hour elapsed. Similarly, initial CO2 levels in sargasso treatments was ?? but significantly increased after one hour elapsed. CO2 were generally higher in forest soils than in the sand at the beach. Initial CO2 levels in the forest were generally higher than the beach in controls and sargasso treatments and both increased after an hour elapsed.

**Plant surveys**

*Plot interior*

Percent cover of grass increased in sargasso plots at the beach over time. During the second sampling period, grass percent cover was ??, and increased to ??, and ??, in March and August 2023, respectively. The effect of sargasso on grass percent cover in the plots was highest during March and August 2023, but no effect was observed for any other plants at the beach or the forest. We observed a slight increase in plant percent cover in the forest during the March 2023 sampling period, but the effect size was negligible (es).

*Plot perimeter*

Percent cover of grass also increased at the perimeter of sargasso plots at the beach over time. Initially, percent cover decreased between August and November (??) , then increased in March and August 2023. Grass cover generally followed the same pattern between sargasso plots and controls, however, sargasso had a large effect on grass percent cover between March and August 2023(??). Sargasso had a small effect on other plant percent cover at beach in November 2022 and March 2023 but the effect was negligible in August 2023. Overall percent cover of grass in the forest was initially minimal (Nov 2022ES) and then nonexistent on sampling dates thereafter, thus, sargasso had no effect on grass. Percent cover of all other plants generally increased over time in the forest in controls and sargasso treatment but there was a small effect in November 2022 and March 2023 and a medium effect in August 2023.

**Arthropod Surveys**

*Crawling arthropods*

Crawling arthropods in pitfall trap contents consisted of various arachnids and hymenopterans, mainly wolf spiders and ants at both sites, and tilirid amphipods at the beach. Sargasso addition at the beach initially had a large effect on amphipod abundances in August 2022 (M=195.3, SE = 57.11 sargasso, M=4.60, SE =1.93 control; *d*=1.49) and small effects in November 2022 (0 in sargasso and 1 individual in controls; *d*=-0.45) and March 2023 (1 individual in sargasso and 0 in controls *d*=0.45). Arachnids were more abundant on sargasso plots in August 2022 (M=1.90, SE=0.51 sargasso, M=0.70, SE=0.26 controls; *d*=0.95), and became less abundant in November 2022 (M=0.60, SE=0.16 sargasso, M=1.00, SE=0.26 control, *d*=-0.59) and March 2023 (M= 0.70, SE=0.26 sargasso, M=1.60, SE=0.43 control; *d*=-0.80). The effect of sargasso on hymenoptera abundance at the beach was initially small in August 2022 (M=3.70, SE= 1.94 sargasso, M=4.60, SE=1.94; *d*= 0.35), medium in November 2022 (M= 16.70, SE=10.55 sargasso, M=0.70, SE=0.40 control; *d* = 0.68) and March 2023 (M=12.80, SE=3.62 sargasso, M=5.90, SE=3.26; *d* = 0.63).

No amphipods were found in forest pitfall traps during any of the sampling periods. Sargass addition had negligible effects on arachnid abundance in August and November 2022 (*d*=0, *d*=0.11, respectively) and a small but negative effect in March 2023 (M=0.40, SE=0.16 sargasso, M=0.60, SE=0.27; *d*=-0.29). Sargasso effects on hymenoptera in the forest were also negligible in August and November 2022, but we detected a small effect size in March 2023 (M=5.60, SE=1.33 sargasso, M=2.65, SE=0.60 controls; *d*=0.44).

*Flying arthropods*

Flying arthropods on traps consisted of various dipterans and hymenopterans, mostly various species of flies and wasps. On the initial deployment of the experiment, amphipods were also captured on sticky traps at the Beach. Sargasso addiction had a large effect on amphipod densities on the initial sampling trip (M=21.00, SE=7.10 sargasso, M=0.90, SE=0.48 control; *d*=0.89) but no effects in November 2022 or March 2023. Diptera abundances were initially high higher on sargasso piles at the beach (M=223.75, SE=57.33 sargasso, M=10.35, SE=2.12 control; *d*=1.18) but the effect size was reduced in November 2022 (M=96.30, SE=22.63 sargasso, M=48.95, SE=8.08; *d=*0.62). On March 2023, diptera abundance was higher in control plots but were an order of magnitude lower than abundances on August 2023 (M=12.9, SE=1.98 sargasso, M=23.05, SE=4.12 control; *d*=-1.57).

No amphipods were found in forest sticky traps, however, one individual on a sargasso pile resulted a small effect size (*d=*0.32). Sargasso addition initially had a small effect on diptera abundance in August 2022 (M=4.10, SE=0.59 sargasso, M=3.00, SE=0.91 control; *d*=0.35) and peaked in November 2022 (M=14.95, SE=1.62 sargasso, M=3.90, SE=0.60 control; *d*=2.02). Diptera densities were similar between treatments in March 2023, resulting in a small, negative effect size (M=2.85, SE 1.04 sargasso, M=2.10, SE=0.38 control; *d=-*0.50). Sargasso initially had no effect on hymenoptera (M=0.85, SE=0.27 sargasso, M=1.05, SE=0.33 control; *d=-*0.15*)* abundance in the jungle but increased the effect size increased over time. Hymenoptera abundance increased in November 2022 (M=7.65, SE= 2.21 sargasso, M=2.25, SE=0.46 control, *d=*0.76) and peaked in March 2023 (M=5.6, SE=1.33 sargasso, M=2.65, SE=0.50 control; *d*=1.25).

**Tables**

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**A table with numbers and a number of objects

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**Figures**

Figure 1. Pile volume percent

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Figure 2. Mesh bag decomposition

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Figure 3. Nitrate content

A graph of a graph showing the number of days and months

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Figure 4. Soil respiration

A graph of different types of trees

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Figure 5. Plot interior percent cover and effect sizes

A graph of different seasons

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Figure 6. Plot perimeter percent cover and effect sizes

A graph of different types of data

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Figure 7. Arthropod counts and effect sizes

A graph of different types of numbers

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**Supplementary**

Figure 1. Plant percent cover from edges of sargasso piles

A graph of different sizes and numbers

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Figure 2. Interior survey percent cover

Forest

A chart of different colored squares

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Beach

A chart of different colored squares

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Figure 3 Perimeter percent cover

Beach

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Forest

A chart with different colored squares

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**Figure legends**

**Lit review**

**Marczak et al. 2007**

Meta-Analysis: Trophic Level, Habitat, and Productivity Shape the Food Web Effects of Resource Subsidies (see note later in this document)

Focused on biomass or density response of consumers in recipient habitats to a resource subsidy.

Excluded studies if they did not report consumer response OR if they reported consumer response in units other than density or biomass

Included studies that manipulated either subsidy amount OR used natural gradient in a subsidy as a proxy for manipulation.

|  |  |  |
| --- | --- | --- |
| Study | Donor | Responder |
| Gende and Willson 2001 | Salmon | Forest birds |
| Marczak unpublished data | stream insects | Forest spiders |
| Sabo and Power 2002 | stream insect | Forest lizard |

Note that in this meta-analysis, there was an emphasis on forest predators (spiders, birds, lizards). The meta-analysis revealed that subsidy effects were neutral for birds and spiders  (the exception being horizontal orb weavers). Further, subsidies had weaker effects on predators than detritivores. I think the fact that such few studies could indicate a lack of subsidies (studies would be rare if there weren’t suspected roles of subsidies). Also, this table was edited because I had to remove riparian forest subsidies (where impacts were much greater).

**Recalde et al. 2016**

Impacts of subsidies in the tropical forests.

Subsidy impacts were seen on vegetation-associated arthropods, not ground-associated. The lack of effect on ground-associated guys sounds like our pitfall trips. But the lack of effect in this study could because subsidy was aquatic insects. “We also predicted that vegetation-dwelling predators are more responsive to allochthonous inputs than those living on the ground (leaf litter), because the flow of emerging insects is likely intercepted higher in the air column (vegetation stratus) than close to the ground.”

**Collins and Baxter 2014**

"Salmon carcasses in un-vegetated habitats desiccated whereas in vegetated habitats  
they remained moist which likely facilitated rapid consumption"

And from that same paper "Similar effects have been

observed in tropical habitats, where desiccation

of reptile carcasses inhibited rates of consumption

by arthropods in dry versus wet habitats

(Cornaby 1974)."

**Anderson and Polis 1998**

-coastal individuals exhibited more strongly marine-based diets than inland individuals (using stable isotopes)

-“Flow of energy and nutrients across habitat boundaries is ubiquitous, and spatial subsidization of less productive habitats by more productive habitats often influences population and community dynamics of the less productive habitat (Polis et al. 1996, 1977a, Oksanen et al. 1997).”

“During years of high precipitation, for example the 1992-93 El Nino event, population dynamics and community interactions are different from those in dry years (Polis et al. 1997b, c). Increases in land plant biomass following heavy rains increase the absolute contribution of terrestrial productivity and diminish the relative importance of marine input to island and coastal communities.”

In a water limited system, adding water increases plant biomass, thus, reducing marine subsidy impact on arthropods. We have forests that are not water limited and little response from arthropods

**Greig et al 2012**

Human mediated climate change changes subsidies between aquatic and terrestrial habitats. Using mesocosm experiments they showed predatory fish reduce arthropod emergence and terrestrial detritus decomposition. Warming and nutrients resulted in higher emergence and decomposition rate especially without predators.

**Helfield and Naiman 2001**

Salmon carcasses subsidize trees which then improve stream quality through sediment and nutrient filtration and woody detritus production (which then maybe loops back to providing better spawning habitat for fish?). Uses stable isotope enrichment.

**Holt 2008**

Recurrent resource pulses can alter community structure, permitting coexistence that otherwise would not occur, or hamper coexistence mechanisms effective in stable environments.

**Jeffreis 2000**

Where large amounts of agricultural resources are transferred to natural habitats, trophic dynamics change: trophic cascades can occur and rare or uncommon species can become invasive.

Non native, nuisance grasses fertilized in dunes in our system…

**Kenny et al 2017**

Seaweed subsidies changed perching heights and movement rates of lizards on Bahamian islands. Terrestrial predators forage on seaweed subsidies (i.e. predator release to terrestrial prey).

**Marcarelli et al. 2011**

Literature review of studies (>90) about open water metabolism in lakes and streams. They concude that animals select higher quality food regardless of allochthonous vs autochthonous.

“ecosystem and food web effects of a subsidy depend on its quality and its quantity, yet the role of subsidies cannot be understood via either of these characteristics by themselves.”

**Zelnik et al. 2023**

Modeling paper using methods from a previous study (zelnik 2023) and data from Cebrian (199, 2004).

“The subsidies provide food for detritivores, which in turn increases predator populations, and lead to a trophic cascade where plants grow more as herbivory pressure is reduced by predators.”

The positive trend in the terrestrial ecosystem occurs because organic nitrogen supports a large detritivore community, which feeds the predators that in turn reduce the herbivores, thereby allowing plants to grow more. At higher organic fractions outside the coexistence range, NPP decreases when larger amounts of nitrogen flow into the brown food web instead of being used by primary producers.

“emphasizing that benefits of organic subsidies to primary production are context dependent”

**Reshamwala et al 2018**

Terrestrial to terrestrial subsidies via human trash as fox food. Foxes consumed less natural prey where there was an abundant human-produced subsidy.

**Piovia-Scott et al. 2013**

We found that both top-down, lizard-mediated, and bottom-up, plant-mediated pathways contributed to the long-term effect of chronic seaweed deposition on herbivory. ry. However, the bottom-up fertilization pathway overshadowed the effects of the top-down lizard-mediated pathways, resulting in a positive association between seaweed deposition and herbivory. In contrast, our previous experimental study indicated that a short-term increase in herbivory in response to a single, large pulse of seaweed deposition was due to the lizard diet-shift pathway. Thus, even though both chronic and pulsed subsidies increased herbivory, the mechanism underlying this response depended on the temporal pattern of subsidy inputs, with a predator-mediated pathway dominating short-term responses to pulsed subsidies and a plant-mediated pathway dominating long-term responses to chronic subsidy inputs.

**Piovia-Scott et al 2019**

Looked at the impact of seaweed deposition on the effect of lizards on the food web (insects and plants). Long-term strengthening of lizard effects was associated with lizard numerical responses and plant fertilization. Increased pulse frequency reinforced the strengthening of lizard effects on spiders and plants. These results underscore the temporally variable nature of top–down effects and highlight the role.

**Riggi and Bommarco 2018**

Effect sizes (log-ratio) of top-down (predation) and bottom-up (fertilization) forces across three fertilization treatments on aphid density per plant biomass and on plant biomass.

Subsidy is fertilizer and the treatment is Removal of the subsidy.

Leroux and Loreau, 2008

**Schnidler and Smits 2017**

“The lateral extent of biological aquatic subsidies is typically small, extending only a few meters into riparian habitat; however, terrestrial consumers often aggregate on shorelines to capitalize on these high-quality resources.”

Aquatic to terrestrial subsidies delivered hydrologically (floods, complex drainage), biologically (bears, salmon, insects, bats, lizards). Introduced lizards to island and fond that they have a top-down effect on leaf damage (reduce it).

“Lizards reduced leaf damage significantly; because they consume numerous kinds of arthropods, including many herbivores”

Note that, for a between-subjects effect, repeated-measures analysis is equivalent to using the time average in a simple analysis. The between-subjects statistics are used to test hypotheses about magnitudes; within-subject statistics (i.e., those involving time) are used to test hypotheses about temporal changes. Initially, we performed an ANCOVA with the premanipulation value on each island as the covariate. If the P value for the covariate was !.10, the ANCOVA, which adjusts for premanipulation plot differences, was given in the results. If (true for all variables except small P ∏ .10 aerial arthropods), the covariate was omitted from the analysis. Treatment (1–3) was a fixed effect. All analyses used Type III sums of squares and were executed with SAS software (Littell et al. 1991).

**Spiller et al. 2010**

For each response variable, mean values for each plot on each post-manipulation date were analyzed using repeated-measures MANOVA with block (island) and treatment (seaweed added, removed) as the main (between-subjects) factors and time (sampling date) as the repeated (within-subject) factor. We used rmMANOVA because it contains fewer assumptions (e.g., sphericity) than does rmANOVA.

To test each hypothesis, the P value for the overall treatment effect was used when the time 3 treatment interaction P value was .0.10. When the interaction P value was ,0.10, treatment effects from separate ANOVAs on each sampling date were used; significance levels were then adjusted for multiple comparisons using the step-down Bonferroni method (SAS Institute 1999).

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Relevant…see last sentence from Marczak et al. (No effect of subsidies on spiders for studies like ours).