

Consequences of sex-selective harvesting and harvest refuges in experimental meta-populations

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Harvesting for food or sport is often non-random with respect to demographic state, such as size or life stage. The population-level consequences of such selective harvesting depend upon which states are harvested and how those states contribute to population dynamics. We focused on a form of selective harvesting that has not previously been investigated in an experimental context: sex-selective harvesting, a common feature of exploited, dioecious populations. Using simple metapopulations (two patches connect by dispersal) of sexually dimorphic Bruchid beetles in the laboratory, we contrasted the effects of female-selective, male-selective, and non-selective harvesting over six generations of population dynamics. We also tested the ability of a harvest refuge (one patch of the metapopulation free from harvesting) to mitigate the effects of harvesting, and whether refuge effects interacted with sex selectivity. Sex-selective harvesting significantly perturbed operational sex ratios and harvest refuges dampened these perturbations. Metapopulations assigned to male-selective and non-selective treatments were able to fully compensate for harvesting, such that their dynamics did not differ from non-harvested controls. Only female-selective harvesting led to significant reductions in population size and this effect was completely offset by dispersal from a harvest refuge. A two-sex model confirmed that population dynamics are more sensitive to female vs. male harvesting, but suggested that higher levels of male harvest than included in our experiment would cause population decline. We discuss the roles of density-dependent competition and frequency-dependent sexual processes in the population response to sex-selective harvesting.

Many natural populations are subject to human harvesting, which can threaten their persistence. There is pressing need to better understand how different harvesting methods and intensities affect population dynamics, and to develop sustainable harvest strategies based on this understanding. In structured populations, harvesting is often non-random with respect to demographic state, such as size class or life stage. For example, large, mature individuals may be preferred or disproportionately encountered (Tenhumberg et al. 2004), whereas in other cases juveniles or eggs may be targeted (Hunter and Caswell 2005, Butler et al. 2009). Because individuals in different demographic states make unique contributions to population dynamics, accounting for size- or stage-selectivity can be important for understanding and predicting the dynamical effects of harvesting (Freckleton et al. 2003, Cameron and Benton 2004, Wallace et al. 2013).

While size- or stage-selective harvesting has been well studied, less is known about a different form of demographic structure that is relevant for many exploited populations: sex structure. Studies on the effects of harvesting often assume similar harvest rates between the sexes (Tenhumberg et al. 2004). Yet, sex-selective harvesting may be common when females and males differ in morphology, behavior, and / or monetary value. For example, males are often prized for their sex-specific ornaments (Ginsberg and Milner-Gulland 1994,

Whitman et al. 2004, Milner et al. 2007). Sex-selective harvesting could perturb the operational sex ratio (sex ratio of individuals available for mating). Therefore, predicting the effects of sex-selective harvesting requires an understanding of how sex ratio variation affects population dynamics. While most traditional approaches in population ecology ignore sex ratio and focus only on females (Caswell and Weeks 1986, Rankin and Kokko 2007), recent work suggests that perturbations to the operational sex ratio can significantly affect population dynamics (Miller and Inouye 2011, 2013).

The effects of selective harvesting may be buffered by harvest refuges, or local areas protected from harvest. If refuge and non-refuge areas are connected by dispersal in a metapopulation context, then harvest refuges could 'rescue' local populations from extinction in exploited areas. Harvesting refuges have been shown to mitigate the effects of general harvesting and size-selective harvesting (Fryxell et al. 2006, Tenhumberg et al. 2004). We predicted that harvest refuges could similarly mitigate the effects of sex-biased harvesting on the operational sex ratio and hence population dynamics.

The nature of density-dependent regulation can determine how populations respond to selective harvesting. If density dependence is sufficiently strong, then removing individuals may release remaining individuals from density-dependent

competition, potentially compensating for losses to harvest (Sandercock et al. 2011, Peron et al. 2012). Counter-intuitively, harvesting could even have positive effects on population densities if density dependent competition is strongly over-compensatory (Abrams 2009, Zipkin et al. 2009, Miller and Rudolf 2011, Strevens and Bonsall 2011). This has been coined the 'Hydra effect' after the mythical beast that grew two heads for every one removed (Abrams 2009). In structured populations, the occurrence and magnitude of compensatory and over-compensatory responses may depend upon which demographic states are harvested and how these states contribute to density dependence (Schroder et al. 2009). For example, an experimental study of soil mites showed that selective harvesting usually decreased population densities, except for egg harvesting, which increased densities (Benton et al. 2004). In sex-structured populations, sexually antagonistic interactions, such as costs of excessive mating or male harassment, could lead to positive effects of male removal for females, until the point where female fertility becomes limited by male availability.

Replicated, field-based harvesting experiments may be limited by practical or ethical concerns. For these reasons, laboratory systems and mathematical models have assumed an important role in ecological studies of harvesting (Benton et al. 2004, Fryxell et al. 2006, Strevens and Bonsall 2011). In this study, we used the bean beetle *Callosobruchus maculatus* (Coleoptera: Bruchinae) to test the effects of sex-selective harvesting and harvest refuges on laboratory metapopulations, and we used a sex-structured population model to explore the effects of harvest intensities not included in our experiment. To our knowledge, this is the first experimental study to examine the consequences of sex-selective harvesting. Specifically, we addressed the following questions: 1) How do the effects of harvesting on population dynamics differ when harvesting is restricted to females, restricted to males, or random with respect to sex? 2) Do harvest refuges buffer local populations from the effects of harvesting and do refuge effects interact with sex selectivity? 3) Do beetle populations exhibit compensatory or over-compensatory responses to harvesting?

Material and methods

Study species

Callosobruchus maculatus is a stored grain pest and a laboratory model species in ecology and evolution, including studies of sex-structured population dynamics (Miller and Inouye 2011) and experimental harvesting (Strevens and Bonsall 2011). Gravid females deposit eggs on seeds of various cultivated legumes (Fabaceae). Larvae burrow into beans, pupate and emerge as adults; the egg-to-adult developmental period is 30–35 d under our incubator conditions (27.5°C and a 16 h: 8 h photoperiod). The adult lifespan is approximately one week and adults do not need to eat. Adult sexes can be readily distinguished by their size (females are larger), color, and patterning on their elytra. Our stock populations were reared exclusively on mung beans *Vigna radiata*. A previous study showed that *C. maculatus* is highly polygynous and exhibits density-dependent population dynamics (Miller and Inouye 2011).

Harvesting experiment

We tested the effects of sex-selective harvesting and harvest refuges with a multi-generation laboratory experiment in which treatments were applied to simple metapopulations. One replicate metapopulation consisted of two patches (petri dishes filled with 5 g of mung beans) connected by one bout of dispersal per generation. Each metapopulation was assigned to one of six factorial combinations of harvest sex (female / male / random) crossed with harvest refuge (present / absent). We also included a non-harvested control for a total of seven treatments, each replicated 12 times ($n = 84$ experimental populations). Metapopulations were initiated with five female and five male virgin beetles (≤ 48 h old) in each of the two patches.

Every 32 d, new female and male recruits in both patches were counted. Harvest treatments were implemented following the census. For all but the control treatment, we removed a fixed fraction (0.33) of the total beetles (female + male) in a local patch starting at the generation 2 census, and for each subsequent generation through generation 6. For metapopulations assigned to the no-refuge treatment, harvesting was applied to both patches and we removed 33% from each patch independently. For metapopulations assigned to the refuge treatment, we removed 33% from one patch and the other was designated a harvest refuge, with no beetles removed. The total number of beetles harvested was concentrated exclusively among females (female harvest), exclusively among males (male harvest), or evenly split between the sexes (random harvest). If the harvest fraction rounded to an odd integer in the random treatment, we alternated harvesting one extra female or male from replicate to replicate. While the random harvest was not applied in a literally random way, it approximated indiscriminate harvesting in a population with an unbiased sex ratio. The 0.33 harvest fraction was chosen to insure sufficient numbers of each sex available for harvest (with stochastic sex ratio variation, either sex can comprise less than 50% of the total population). We consider alternative harvest fractions in our modeling work (below). We did not experimentally explore different harvest strategies (e.g. fixed quota vs fixed number), which has been done by others this system (Strevens and Bonsall 2011).

Following harvest, patches were connected with 1 cm of plastic tubing for 24 h of dispersal, then separated. Control (no-harvest) metapopulations were similarly connected for dispersal once per generation. In generation three, we recorded post-harvest and post-dispersal counts to quantify how harvesting and dispersal affected the operational sex ratio at the start of the mating phase. Both patches of all metapopulations were replenished with 5 g of fresh beans following dispersal. Beetles were then left to mate and oviposit, and dead adults were removed before the next generation was censused.

Data analysis

We used data from generation 3 (when we re-censused following harvest and dispersal) to quantify the effect of our harvest treatment on pre-breeding, operational sex ratios and to ask whether dispersal from refuge patches mitigated the perturbation. We tested the main and interactive effects

of harvest sex and harvest refuge on the local sex ratio (arc-sine-square root-transformed proportion female) in a focal, non-refuge patch (designated arbitrarily for the no-refuge treatment). We used planned contrasts with Bonferroni-adjusted significance values to test for differences in sex ratio with and without harvest refuges for each harvest sex.

We analyzed the bean beetle population dynamics data in two steps. First, we tested for effects of sex-selective harvesting on total metapopulation size across the control and harvest sex treatments, excluding populations with a harvest refuge. Because both patches were treated identically in these populations, we summed beetle densities across patches. Second, we tested the interactive effect of harvest refuges and harvest sex on local population size in a focal, non-refuge patch (designated arbitrarily for the no-refuge treatment). For both analyses, we accounted for temporal dynamics across five generations (excluding the first generation, to which harvest treatments were not applied) using a repeated-measures analysis of variance (rmANOVA). We used Bonferroni-adjusted contrasts to test for differences among harvest treatments and controls (in the first analysis), and to test for refuge effects at each level of harvest sex (in the second analysis). Beetle counts were square root-transformed, which stabilized variances. Statistical analyses were conducted in SAS ver. 9.3. We report the occurrence of local patch and metapopulation extinctions but because these were very rare we did not statistically analyze extinction data.

Modeling effects of sex-specific harvest

Experimental results revealed that beetle populations were quite robust to the harvesting at the level used in our experiment (33%). We therefore conducted a simulation experiment with a two-sex model to explore a greater range of harvest intensity than was included in our experiment. The model takes the form:

$$N_{t+1} = \frac{\lambda b \frac{2F_t b^{-1} M_t}{F_t b^{-1} + M_t}}{1 + (b_F F_t)^{\gamma_F} + (b_M M_t)^{\gamma_M} + (b_O \frac{2F_t b^{-1} M_t}{F_t b^{-1} + M_t})^{\gamma_O}} \quad (1)$$

This function predicts total population density in the next generation (N_{t+1}) based on the contributions of females (F_t) and males (M_t) to recruitment via pair formation and mating (in the numerator) and density-dependent feedbacks (in the denominator). Parameters λ and b represent the per-mating birth rate and degree of polygyny (number of female mates per male), respectively. Parameters b and γ represent the strength and functional form of density dependence, respectively, and are subscripted to reflect unique contributions of female, male, and offspring (O_t) densities. The last term in the denominator uses mating density as a proxy for offspring density, which is difficult to quantify directly (larvae develop inside beans). Values of $\gamma > 1$ correspond to over-compensatory density dependence. In a previous study, this model provided the best fit to beetle population dynamics (Miller and Inouye 2011).

We simulated population dynamics using 95% confidence intervals for the maximum likelihood parameter estimates of this model (Table 2 in Miller and Inouye 2011).

We estimated the equilibrium density for harvest fractions ranging from 0 (no harvest) to 0.5 (50% of total population harvested). We applied the same three sex-selective treatments in the simulation experiment as in the lab experiment. We expected extinction at 50% harvest for female- and male-selective removal (because populations cannot persist in the absence of either sex) but were interested in the shape of the response to harvest intensity under different selective harvest regimes. We incorporated parameter uncertainty by drawing parameter values from uniform distributions defined by the maximum likelihood confidence intervals. We assume an unbiased birth sex ratio, consistent with empirical results (Miller and Inouye 2011). We present the confidence region of equilibrium population size as the inner 95% quantile of the distribution of population sizes for each harvest fraction and from 1000 samples of parameter values. Note that Eq. 1 and our parameter estimates focus on local population dynamics, so we did not use the model to explore the role of harvest refuges or the effects of dispersal.

Results

Harvesting experiment

Sex-selective harvesting modified operational sex ratios following harvest and dispersal (Fig. 1). There was a significant interactive effect of harvest sex and refuge on operational sex ratios during the mating phase ($F_{2,63} = 20.42$, $p < 0.001$), indicating that the effects of sex-selective harvest on sex ratio depended on the presence or absence of a refuge. As expected, females were under-represented in metapopulations with female-selective harvesting and over-represented in metapopulations with male-selective harvesting. Dispersal from harvest refuges significantly dampened the sex ratio perturbation in local patches under female harvesting ($t_{63} = -5.42$, $p < 0.001$) and male harvesting ($t_{63} = 3.26$, $p < 0.03$).

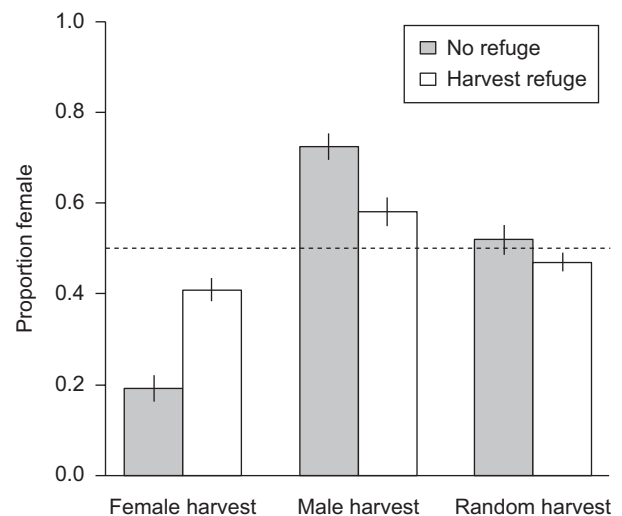


Figure 1. Operational sex ratio (proportion female) of local patches after harvesting and dispersal under different combinations of harvest sex and the presence or absence of a harvest refuge in the metapopulation. Dashed line indicates an unbiased sex ratio.

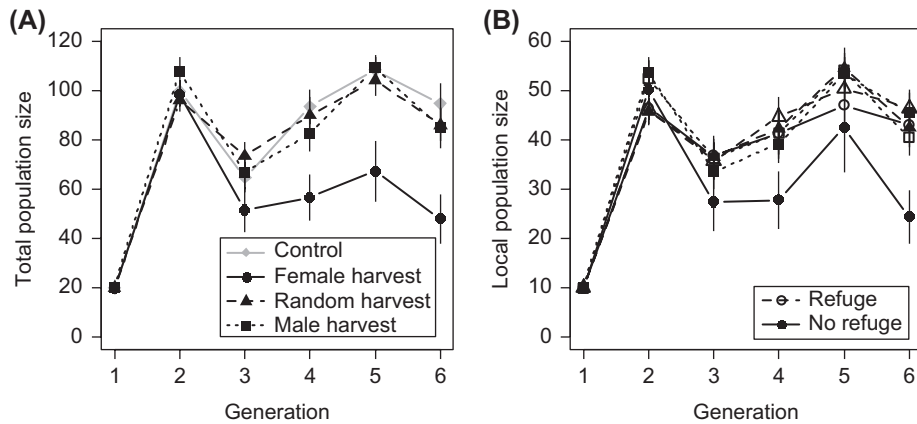


Figure 2. Results of sex-selective harvesting with harvest refuges. (A) Time series of total beetle abundance (sum across both patches of the metapopulation) in relation to the sex-specific harvest treatment. Metapopulations with a refuge are excluded. (B) Time series of local beetle abundance in the non-refuge patch for metapopulations in which the other patch was (open symbols) or was not (closed symbols) a harvest refuge. Control treatment excluded. Sex-specific harvest treatments are represented by shapes as in (A). Point and bars show mean \pm 1 SE.

Harvest refuges did not affect the sex ratio of randomly harvested metapopulations ($t_{63} = 1.07$, $p < 0.99$).

Out of the 84 metapopulations, there was one total extinction, with no recruitment in either patch, and three local extinctions, with no recruitment in one of the two patches. Locally extinct patches were rescued through dispersal from the persistent patch. All four extinctions occurred in the female harvest / no refuge treatment.

Beetle densities exhibited an initial peak and decline followed by oscillatory dynamics over six generations, consistent with over-compensatory density dependence (Fig. 2). Harvesting significantly affected metapopulation densities through time, relative to no-harvest controls, and the influence of harvesting depended on the harvest sex treatment (Generation \times Harvest sex: $F_{12,208} = 1.91$, $p < 0.03$). Contrasts indicated that only the female-harvested populations experienced reduced densities, and only in later generations (4 and 5; $p < 0.001$). The temporal dynamics of male-harvest and randomly harvested metapopulations did not differ significantly from control metapopulations (Fig. 2A).

Considering only harvested metapopulations, dispersal from harvest refuges mitigated the impact of harvesting on local densities in focal, harvested patches (Fig. 2B). Because only the female-harvest treatment was affected by harvesting, only this treatment was affected by a harvest refuge, hence a Harvest sex \times Refuge interaction ($F_{2,317} = 7.11$, $p < 0.0001$). The two- and three-way interactions with time were not statistically significant. Harvest refuges completely compensated for female-biased harvesting, such that female-harvested populations with a refuge were not significantly different from other refuge and non-refuge harvest sex treatments.

Two-sex harvest model

Our experimental results indicated that, for most treatments, beetle populations were remarkably robust to harvesting. We conducted a simulation experiment to ask how local population densities would respond to lower and

greater harvest fractions than included in our experiment (33% of total population). Equilibrium densities were similarly affected by harvesting across harvest sex treatments, indicated by the overlap in uncertainty ranges for most of the range of harvest fraction (Fig. 3). Densities declined monotonically from the non-harvested state, indicating neither compensatory nor over-compensatory responses to harvesting. At a simulated harvest fraction of 0.33 (the level used in our experiment), the equilibrium densities of harvested populations were reduced by approximately 10–20 individuals relative to the non-harvested state. Sex-selective

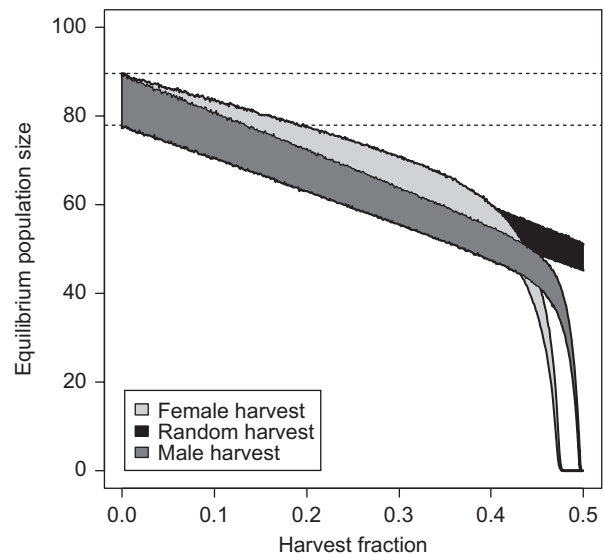


Figure 3. Simulations of sex-selective harvesting based on a two-sex population model parameterized for *C. maculatus*. Shaded areas show the inner 95% quantiles of the distributions of equilibrium population size for each level of harvest fraction (proportion of total population harvested) and harvest treatment (females harvested, males harvested, or random harvest). Dashed lines show the confidence region for equilibrium densities in the absence of harvesting.

harvest treatments diverged significantly only at very high (> 0.45) harvest fractions, at which point female-harvested populations began to decline, followed by male-harvested populations. Sex-selective harvesting was predicted to cause deterministic extinction, with female-harvest populations crashing at lower harvest fractions than male-harvest populations (Fig. 3). Thus, the minimum number of females necessary for population persistence exceeded the minimum number of males. Randomly harvested populations were predicted to persist at reduced densities even at 50% harvest.

Discussion

Previous experimental and theoretical studies have demonstrated the importance of selective harvesting based on size or life stage (Benton et al. 2004, Cameron and Benton 2004, Hunter and Caswell 2005). Our study builds upon this work by demonstrating effects of sex-selective harvesting, a potentially important factor in the dynamics of exploited populations but one that has not yet been experimentally examined. Our results indicate that female-biased harvesting had more severe negative effects than non-selective or male-selective harvesting and could even cause extinction at the patch or metapopulation levels. Our results also indicated that the presence of a harvest refuge connected by dispersal could completely offset the negative effects of the female-selective harvest on local populations.

Our experimental metapopulations were remarkably robust to male-biased and random harvesting, as these treatments exhibited statistically identical dynamics to the control (non-harvested) metapopulations. Two processes likely contributed to the resilience of male-selective and randomly harvested populations. First is compensatory density dependence, whereby surviving individuals experienced enhanced per capita demographic rates following harvesting. For randomly harvested populations, removal of males may have released females from negative effects of copulation and harassment (Crudginton and Siva-Jothy 2000, den Hollander and Gwynne 2009) while female removal likely reduced per-bean egg load and hence larval competition (Guedes et al. 2007). Second, *C. maculatus* is highly polygynous (Miller and Inouye 2011), meaning that a single male can fertilize many females. Thus, few males may be required to fertilize all females in the population. It is possible that these two mechanisms contributed differently to randomly harvested and male-selective treatments (where the role of polyandry may have been more important) but generated similar qualitative patterns. These density- and frequency-dependent processes are likely to operate in other dioecious populations subject to sex-selective harvesting. Further studies to quantify their relative roles in responses to harvesting would be valuable.

Low sensitivity of polygynous species to male removal suggests a capacity for these populations to sustainably absorb some degree of male culling. Indeed, wild populations can show resilience to male-selective harvesting and female-biased sex ratios (McLeod et al. 2004, Milner et al. 2007). However, it is important to recognize that the effects of sex ratio perturbations depend sensitively on the social mating system (Miller et al. 2011) and that the sustainability

of male-selective harvesting has its limits, even in a highly polygynous mating system, as demonstrated by our simulation results and by studies in nature (Ginsberg and Milner-Gulland 1994, Milner-Gulland et al. 2003). Additionally, systems in which males provide parental care could be extra sensitive to male removal (Whitman et al. 2004).

Prior work has demonstrated that harvest refuges can 'rescue' local populations from negative effects of harvesting (Fryxell et al. 2006). Here, too, we found that dispersal from refuges eliminated negative effects of harvesting on local patches. The dispersal distance between our experimental patches was short and the dispersal window (24 h) was long; thus, we suspect dispersal rates were high. Under greater, more realistic distances and lower dispersal rates, it could be important to consider how sex differences in dispersal might modify the role of refuges. For example, male bean beetles disperse significantly farther distances than females (Miller and Inouye 2013). Male-biased dispersal could make refuges less effective, especially under female-selective harvesting, since it would exacerbate male-biased operational sex ratios. While structured harvesting and harvest refuges have both received attention, little is known about structured dispersal (sex-, size- or stage-specific) and its influence on the efficacy of refuges under selective harvesting.

The sex-structured population model allowed us to explore the effects of sex-selective harvesting over a wider range of harvest intensities than included in our experiment. Model results showed that population density and persistence were most sensitive to female-selective harvesting, consistent with experimental results. However, theoretical and experimental results differed in some quantitative details. First, the uncertainty intervals for equilibrium density under female, male, and random harvesting over-lapped around the harvest intensity used in the experiment (0.33). Second, equilibrium densities for all treatments were significantly lower than the control condition; thus, the model did not predict fully compensatory responses, as we observed for most treatments. Parameters used in the model were estimated from the same beetle population used in our experiment, so these departures were surprising. However, our experimental metapopulations had not yet reached density equilibria. It is possible that the responses we observed were transient and that a longer time-series would have converged upon model predictions. It is also possible that mating and density-dependent dynamics of the model were somehow mis-specified such that effects of male-biased operational sex ratios and the strength of density dependence were under-estimated, which could explain the discrepancy.

There is much current interest in Hydra effects (positive responses to reductions in density), the conditions under which they occur, and their role in the dynamics of exploited or managed populations (Zipkin et al. 2009, Miller and Rudolf 2011, Strevens and Bonsall 2011). While our experimental results indicated compensatory responses to harvesting, densities of harvested populations never exceeded densities of non-harvested populations; thus, we found no evidence for Hydra effects. In reviewing the mechanisms that give rise to Hydra effects, Abrams (2009) emphasized that density dependence must be over-compensatory (meaning that increasing densities cause decreased recruitment) and that harvest mortality must precede the operation of density

dependence. Both of these factors appear to be in place in the bean beetle system. Prior demographic work indicates over-compensatory density dependence (Miller and Inouye 2011) and, in the present study, harvesting occurred prior to larval competition within beans. However, adult bean beetles may also experience density-dependent costs of mating (den Hollander and Gwynne 2009) or competition for oviposition sites. Stage-structured life histories with sequential phases of strong density dependence are less likely to exhibit Hydra effects (Abrams 2009), and this may have contributed to our results. It is also possible that harvesting a different life stage would have had different (and potentially more strongly over-compensatory) effects, as has been shown in other experimental systems (Benton et al. 2004).

In summary, we show that sex-structure is an important dimension of selective harvesting that warrants further experimental and theoretical work. Female harvesting significantly reduced population densities whereas male harvesting was less consequential, relative to non-selective harvesting, in our experimental system. Harvest refuges can reduce or eliminate negative effects of sex-selective harvesting. Density-dependent competition and sex frequency-dependent mating processes can be important determinants of population responses to harvesting.

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