Deer Indirectly Alter the Reproductive Strategy and Operational Sex Ratio of an Unpalatable Forest Perennial

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ABSTRACT: Environmental conditions impose restrictions and costs on reproduction. Multiple reproductive options exist when increased reproductive costs drive plant populations toward alternative reproductive strategies. Using 4 years of demographic data across a deer impact gradient, where deer alter the abiotic environment, we parameterize a size-dependent integral projection model for a sexually labile and unpalatable forest perennial to investigate the demographic processes driving differentiation in the operational sex ratio (OSR) of local populations. In addition to a relative increase in asexual reproduction, our results illustrate that nontrophic indirect effects by overabundant deer on this perennial result in delayed female sex expression to unsustainably large plant sizes and lead to more pronounced plant shrinkage following female sex expression, effectively increasing the cost of reproduction. Among plants of reproductive age, increased deer impact decreases the size-dependent probability of flowering and reduces reproductive consistency over time. This pattern in sex expression skews populations toward female-biased OSRs at low deer impact sites and male-biased OSRs at intermediate and high deer impact sites. While this shift toward a male-biased OSR may ameliorate pollen limitation, it also decreases the effective population size when coupled with increased asexual reproduction. The divergence of reproductive strategies and reduced lifetime fitness in response to indirect deer impacts illustrate the persistent long-term effects of overabundant herbivores on unpalatable understorey perennials.

Keywords: age-from-stage modeling, Arisaema triphyllum, cost of reproduction, integral projection model, operational sex ratio, reproductive strategy.

Introduction

The opportunity and ability to reproduce is necessary for life to persist but comes at a cost. While this idea is well known, the cost of reproduction is an elusive metric. In addition to sexual and asexual forms of reproduction, hermaphroditic species divide reproductive investment between male and female function. Plants are well known to employ all these reproductive tactics—often by a single individual within a season (e.g., monecious plants) or over its lifetime (e.g., sequentially hermaphroditic plants; Willson 1983)—and the balance in effort directed toward male or female function (Gregg 1975; Doust and Cavers 1982; Meagher 1988) or between sexual and asexual reproduction (Abrahamson 1975; Honnay and Bossuyt 2005; Van der Merwe et al. 2010) can highly depend on the local environment. Differential effort and resource demand to each of these dimensions of reproduction can interact and trade off in ways that complicate general statements regarding the cost of reproduction.

Environmental sex determination and environmentally induced shifts in sexual and asexual reproduction have been demonstrated for many plant (e.g., Charnov and Bull 1977; Thompson and Eckert 2004) and animal (e.g., Bull 1981; Purcell and Aviles 2007) species and can influence the operational sex ratio (OSR) of local populations (Sinclair et al. 2012). For dioecious species, variation between the sexes in resource requirements and energetic investments may cause shifts in the OSR of populations distributed along a resource gradient. In support of these expectations, recent work has shown that altered biotic interactions can differentially affect male and female plants (reviewed in Cornelissen and Stiling 2005), and abiotic conditions can skew the OSR of plant populations (Petry et al. 2016; Simancas et al. 2018). As environments become degraded, changing biotic and abiotic conditions may have a particularly pronounced impact on the OSR and reproductive strategy for hermaphroditic species with environmental sex determination.

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Variable environments have well-documented impacts on plant population dynamics (Elderd and Doak 2006; Torang et al. 2010; Kalisz et al. 2014). As environmental conditions become stressful and resources become limited, plants can accumulate and store resources more slowly and delay reproductive maturity until achieving a greater size (Stearns and Koella 1986; Barrett et al. 2010). Since male and female functions have different investment costs and allocation patterns (i.e., pollen production vs. fruit/seed maturation), the compounding effects of environmental stress on future resource reserves can alter an individual's lifetime trajectory of sex expression and thus individual fitness via sex-specific survival-growth-reproduction trade-offs that equate to lifetime reproductive success (Stearns and Koella 1986; Obeso 2002; Canelles et al. 2018). This may be particularly true for sequential hermaphroditic species where male and female functions are optimized at different sizes and sex expression is highly influenced by abiotic conditions (Doust and Cavers 1982).

To characterize the costs of male and female reproduction and evaluate the effects of altered abiotic conditions on the OSR and the population dynamics of plants require examination of a species with highly variable reproductive strategies that occur in varied environments (Field et al. 2013). Here we employ *Arisaema triphyllum* (hereafter, *Arisaema*) as an ideal species for addressing such questions. *Arisaema* exhibits labile sex expression (i.e., size-dependent sequential hermaphroditism) and reproduces both sexually and asexually (Bierzychudek 1984). In addition, *Arisaema* populations are known to exhibit variation in the amount of asexual versus sexual reproduction as well as differences in the OSRs of local populations (Doust and Cavers 1982; Bierzychudek 1984; Heckel et al. 2010).

Here we build on previous work using demographic data from *Arisaema* populations that occur along a large herbivore-mediated gradient of habitat quality. At sites with high deer impact, overabundant deer increase soil compaction and light availability (Sharrow 2007; Heckel et al. 2010; Heberling et al. 2017), decrease leaf litter deposition (Heckel et al. 2010), and alter soil and microbial community composition and structure (Waltert et al. 2002; Burke et al. 2019). *Arisaema* is unpalatable and is rarely browsed by deer at our field sites (Heckel et al. 2010). Modification in abiotic conditions and direct consumption of leaves, flowers, and fruits by overabundant deer reduce plant fitness of palatable herbaceous understory species (Knight 2004; Kalisz et al. 2014; Bialic-Murphy et al. 2019). Thus, we may expect that the negative effects of deer on the population dynamics of palatable species would result in competitive release of co-occurring unpalatable herbaceous species (Keane and Crawley 2002; Rooney and Waller 2003). However, the responses may be complex (Wiegmann and Waller 2006). For example, rather than competitive release of this unpalatable species, we found that indirect effects on abiotic quality by overabundant deer decreased population-level seed production and altered the OSR of *Arisaema* (Heckel et al. 2010). Under favorable common garden conditions, transplants from these same sites exhibit higher relative growth and smaller female flowering size than plants from low deer impact sites, suggesting an evolutionary response to increased environmental stress by overabundant deer (Heckel and Kalisz 2017). Together, our previous work demonstrates that the effects of overabundant deer on abiotic conditions reduce fecundity and growth and alter OSRs of *Arisaema*. What remains unknown is the mechanism by which increased deer impact affects OSR, and how variation in OSR affects population dynamics.

In this study, we use a size-dependent integral projection model (IPM) to map the indirect effects of overabundant deer to demographic rates and sex expression of *Arisaema*. We then predict even-aged cohort and equilibrium population dynamics to characterize the pattern and timing of sex expression across the levels of deer impact and compare projected OSRs with observed differences in OSRs at the field sites. To further explore the cost of reproduction, we compare within-site differences in plant size following female versus male sex expression. Surveys of local plant populations across a deer impact gradient for four consecutive years inform our model and allow us to evaluate how standing variation in reproductive strategies and OSRs of plant populations influences the fitness of this sex-labile, resource-limited, unpalatable understory perennial. We expect plants in sites with high deer impact will grow more slowly, delay both male and female sex expression until a greater plant size, and reproduce more sexually compared with plants in sites with low deer impact. Since female function requires a greater resource pool (Doust and Cavers 1982), female sex expression is likely suppressed by the scarcity or inaccessibility of resources at high deer impact sites. Therefore, we predict that the OSR of populations will be increasingly male biased in high deer impact sites. Furthermore, we predict that male-biased populations will have lower sexual net reproductive rate. Finally, we expect that *Arisaema* population fitness will be lowest in high deer impact sites.

**Material and Methods**

**Study System**

*Arisaema triphyllum* (L.) Schott (Araceae) is a sequentially hermaphroditic perennial herb native to eastern North America (Bierzychudek 1982). Each spring, *Arisaema* produces one to two leaves from an underground perennial corm, and if reproductive, it produces a leaf-like spathe.
surrounding a columnar spadix bearing minute flowers. The first year *Arisaema* becomes reproductively mature, and it typically produces male flowers (Bierzychudek 1982). In later years, following biomass accumulation, an individual can shift sex and produces female flowers. Individuals are sex labile and can shift between male and female function multiple times over their lifetime as they gain (male → female) or lose (female → male) biomass (Vitt et al. 2003). *Arisaema* is insect pollinated primarily by fungus gnats (Mycetophilidae and Sciaridae; Bierzychudek 1982). Previous studies provide strong support for the size advantage hypothesis for *Arisaema* (Bierzychudek 1982; Vitt et al. 2003), suggesting that sequential size-dependent sex change is an adaptive strategy that optimizes individual genetic contribution. Plants produce an overwintering bud at the end of the growing season composed of leaf and inflorescence primordia. In addition to sexual reproduction, *Arisaema* propagates asexual cormlets that grow as vegetative side shoots from the corm (Bierzychudek 1982). In subsequent years, cormlets detach from the main corm and become self-sustaining individuals. Previous work suggests that sexual reproduction is resource limited (Levine and Feller 2004). Conversely, asexual reproduction has been shown to remain relatively constant across an environmental gradient, suggesting that asexual reproduction is less resource dependent (Levine and Feller 2004). The single best predictor of *Arisaema* sex is current plant size (Bierzychudek 1984; Heckel and Kalisz 2017). Discrimination models suggest that previous years’ plant size, sex, and seed set can improve the predictive strength of current plant sex. However, these variables were highly correlated and varied by site and year (Bierzychudek 1984).

**Study Sites**

Our three study sites were in mature beech-maple forests in northwestern Pennsylvania (within 5–25 km of each other) and are a subset of the six *Arisaema* sites used in previous studies (Heckel et al. 2010; Heckel and Kalisz 2017). All sites were selected on the basis of similarity of understory community composition and general physical characteristics. We previously showed that our field sites differ consistently in browse rates on co-occurring *Trillium* species but that deer browse on *Arisaema* individuals rarely occurred (only 0.6% of 9,746 *Arisaema* stems; Heckel et al. 2010). Further, using a principal component (PC) analysis of abiotic variables measured at the sites (i.e., soil compaction, leaf litter depth, and soil moisture), we showed that PC1 and PC2 combine to explain 87% of the variance among sites in these abiotic variables (app. D in Heckel et al. 2010). Specifically, PC1 was positively correlated with soil penetration resistance (a measure of soil compaction) and litter depth, while PC2 was positively correlated with light level and negatively with soil moisture. Importantly, PC1 decreased with increasing *Trillium* browse level, signifying that high deer browse sites have more compact soil with less leaf litter than low-browse sites. High soil compaction alters soil hydrology and aggregation and has deleterious effects on plant vital rates, leading to physiological dysfunction, reduced water and soil nutrient absorption, and altered root respiration (Kozlowski 1999). Increased soil compaction by deer has known negative effects on forest plant abundance and diversity (Sabo et al. 2017). For *Arisaema*, our previous work demonstrates that plant vital rates decline as abiotic site impacts by deer increases (fig. 1E in Heckel et al. 2010).

**Demographic Data Collection**

We collected 4 years (2006–2009) of *Arisaema* demographic data (i.e., growth, survival, and fecundity) for a total of three annual transition years. Before data collection, in 2005, we established a 50 × 50-m plot at each study site. To increase our sample size and capture size-dependent vital rates across plant ontogeny, we installed three additional 1 × 50-m belt transects at each site during the 2006 annual census. Annually through 2009, all new recruits and previously unobserved plants were tagged and monitored. Over the study period we monitored a total of 1,539 unique individuals (*N* = 678 low, *N* = 588 intermediate, and *N* = 273 high deer impact sites). For each tagged *Arisaema*, we annually recorded the size, flowering status, and sex expression (i.e., male or female function) by visual inspection of the inflorescence. To estimate the annual number of seeds produced per female plant, we collected a subset of infructescences following seed maturation in 2005 and 2007 and counted the total number of seeds. All collected seeds were placed below the parent plant within 30 days of collection. To identify the best nondestructive predictor of total plant mass, we measured aboveground leaf and stem size metrics and then excavated, washed, and dried a subset of *Arisaema* from outside the study plots in 2006. Stem diameter (mm) at the soil surface is the best nondestructive metric of plant size (Pearson’s *r* = 0.70, *P* < .0001, *n* = 137) and is used as our metric of plant size. If a tag was found but there was no associated aboveground tissue found in subsequent years, then the plant was scored as dead. Plants that were not found in one year but that reappeared in subsequent years were scored as being alive; this dormancy was documented for 5.6% of 2,938 demographic transitions across the three sites. Given the relative rarity of dormancy in our data set, we did not explicitly include it in our model.
Drivers of Reproductive Differentiation

To quantify the indirect effect of deer on *Arisaema*, we use an IPM, which describes how a continuous size structured population changes from time $t$ to $t + 1$ (Easterling et al. 2000; Ellner and Rees 2006). The basic model structure is

$$n(y, t + 1) = \int_{a}^{b} K(y, x, \theta_q) n(x, t) dx,$$

where the vector $n(x, t)$ represents the size distribution of the population at time $t$ and $n(y, t + 1)$ is the size distribution at time $t + 1$. The kernel $K(y, x, \theta_q)$ is the sum of two components, the growth-survival function $p(y, x, \theta_q)$ and the fertility function $f(y, x, \theta_q)$. The growth-survival $p(y, x, \theta_q)$ component of the kernel is given by

$$p(y, x, \theta_q) = s(x, \theta_q) g(y, x, \theta_q),$$

where $p(y, x, \theta_q)$ represents the size and deer impact index (i.e., categorical variable $\theta_q$ is low, intermediate, or high deer impact index) dependent probabilities of surviving $s(x, \theta_q)$ and growing $g(y, x, \theta_q)$ from state $x$ to state $y$ through discrete time. The fecundity function is given by

$$f(y, x, \theta_q) = p'_s(x, \theta_q) f'_s(x, \theta_q) f'_a(y, x, \theta_q) p_c(\theta_q) + p'_s(x, \theta_q) f'_s(x, \theta_q) f'_a(y, x, \theta_q) p_c(\theta_q).$$

The first term of the equation represents sexual reproduction, where $p'_s(x, \theta_q)$ gives the probability of a size $x$ plant flowering as a female, $f'_s(x, \theta_q)$ is the number of seeds produced by a size $x$ female, $f'_a(y, x, \theta_q)$ gives the size distribution of recruits from seed produced by size $x$ females, and $p_c(\theta_q)$ is the establishment probability of new recruits. This model assumes a female-dominant mating function (Caswell 2001, chap. 17). The second term of equation (3) represents asexual reproduction, where $p'_a(x, \theta_q)$ is the size $x$ dependent probability of asexual recruitment, $f'_a(x, \theta_q)$ represents the mean number of cormlets produced by a size $x$ plant, $f'_a(y, x, \theta_q)$ gives the size distribution of cormlets produced by size $x$ plants, and $p_c(\theta_q)$ is the establishment probability of asexual cormlets.

Population Dynamics and Environmental Sex Determination

To evaluate the IPM, we discretized the continuous size space into 300 bins using the midpoint rule at an interval from 0.9 $\times$ minimum plant size (2.53) to 1.1 $\times$ maximum plant size (3.28) and employed standard matrix projection model analyses (Easterling et al. 2000; Ellner and Rees 2006). The dominant eigenvalue of the discretized IPM kernel at each site (= level of deer impact) represents the long-term asymptotic population growth rate $\lambda$. The corresponding right eigenvector represents the stable size distribution (SSD), and the left eigenvector represents reproductive value (Caswell 2001). To obtain the OSR at SSD for each site, we used our field data to calculate the probability of producing a flower (either male or female) $p'_s$ and the probability of being female $p'_a$ conditional on flowering. To calculate the probability of being vegetative ($p_v = 1 - p'_s$) and the probability of flowering and being male ($p'_s = 1 - p'_v$), we used the complements of $p'_s$ and $p'_v$, respectively. All probabilities were dependent on size and deer impact index. To classify SSD at each site into vegetative, male, and female categories, we multiplied the right eigenvector by a probability vector, which we discretized to match the dimension of the eigenvector. By summing this sex-classified SSD, we obtained the proportion of the population that was either vegetative or flowering and the proportion of flowering plants that were either male or female. The proportion of the flowering plants that were either male or female represents the OSR of the population at equilibrium.

To characterize the cost of reproduction at each deer impact index site, we compared the change in plant size from time $t$ (x) to $t + 1$ (y) between vegetative and male plants and between male and female plants. Separate comparisons between vegetative and males and between males and females were done because *Arisaema* has strong size-dependent sex expression, with little overlap in size between vegetative and female plants (5% at the low, 2% at the intermediate, and 0% at the high deer impact site, respectively). We used the following criteria to subset our data and then made these comparisons within each deer impact site: (1) the minimum size of male plants and maximum size of vegetative plants and (2) the minimum size of female plants and maximum size of male plants. To compare differences in the energetic cost of achieving and maintaining a large enough size to sexually reproduce between the low, intermediate, and high deer impact sites, we compared the change in the predicted size range for each sex with the projected shrinkage at that size. Since we used log-transformed size, we back-transformed size at time $t$ (x) and $t + 1$ (y) to calculate the change in size in its native dimension, $\Delta x = e^y - e^x$. Note that we distinguished reproductive costs associated with decreased plant size following sex expression from energetic costs associated with reaching and maintaining a large enough size necessary to reproduce.

To translate the hypothesized size delay to a time delay and to visualize the age dependence of reproductive status, we used age-from-stage procedures (Horvitz and Tuljapurkar 2008). We projected a cohort of newborns 50 years into the future using the $p(y, x, \theta_q)$ component of $K$. At each iterative time step, we multiplied the size distribution by the size-dependent probabilities of reproductive status (i.e., vegetative, male, or female). To capture reproductive consistency over time, we also calculated the probability.
of a flowering plant remaining reproductively mature the following year using individual based models (app. B; apps. A, B are available online).

To quantify the net reproductive rates of individuals across the levels of deer impact, we also calculated the per generation growth rate \( R_0 \), (including sexual and asexual) and the proportional contribution of asexual reproduction \( R_{\text{dim}}/R_{\text{total}} \) (Caswell 2001; Ellner and Rees 2006). The net reproductive rate \( R_0 \) represents the mean number of offspring an individual produces over its life span.

Vital Rate Functions

The size-dependent vital rate functions that we used to construct the kernel \( K \) were estimated from demographic field data from 2006 to 2009 using generalized linear mixed effect models. All models were fitted in R 3.0.1 (R Development Core Team 2014), using the glmer function in package lme4 (Bates et al. 2009). The full vital rate models included plant size \( x \) at time \( t \), deer impact index \( \theta_v \) and the interaction term as fixed effects and year as a random factor. To improve nonlinearity in the survival \( s \) and growth \( g \) functions and normalize the residuals, size was log transformed. We used a logistic regression for the survival model and fertility components, \( p_f(x, \theta_v), \ p_s(x, \theta_v), \) and \( p_a(x, \theta_v) \). We used Poisson regression for the number of seeds, \( f_s(x, \theta_v) \), and number of cormlets, \( f_t(x, \theta_v) \). To account for size-dependent variance in the growth model, we used generalized least squares and compared the fits of models with and without exponential variance. We used maximum likelihood in generalized least squares for model comparison and then report generalized least squares estimates using restricted maximum likelihood (Bolker et al. 2009).

To retain all potentially important fixed effects and interaction terms for the \( p(x, \theta_v) \) and \( f(x, \theta_v) \) functions, we first constructed a fully parameterized model for each vital rate function. We then reduced model complexity by removing variables and interaction terms in a stepwise fashion, creating a set of candidate models. To identify all potentially important fixed effects, we used Akaike information criterion (AIC), selecting the most complex model with a \( \Delta \text{AIC} \) value <2. The best-supported model for each vital rate function was then used to estimate our regression coefficients. Model selection \( \Delta \text{AIC} \) values and regression coefficients of the selected models are reported in tables A1 and A2, respectively (tables A1, A2, B1, B2 are available online).

Results

Plants in high and intermediate deer impact index sites have a reduced probability of survival, particularly for small vegetative individuals (fig. A1A; figs. A1, B1 are available online). Regardless of the level of deer impact, plants grow when small and shrink when large. Indirect deer impact enhances this pattern through an interactive effect on plant growth (fig. A1B). As environmental quality decreases, plant growth increases for small individuals and decreases for large individuals. While high deer impact does not influence the size-dependent probability of asexual reproduction (fig. A1C), it does increase the mean number of cormlets an asexually reproductive plant produces (low = 1.18, intermediate = 1.74, high = 1.91). High deer impact and plant size have an interactive effect on the probability of flowering, \( p_f \). Across levels of deer impact, only large individuals flower (inflection point for \( p_f \) at log size 1.88, 1.99, and 2.31 at sites with a low, intermediate, and high deer impact index, respectively). As deer impact increased, the size range over which plants transition from vegetative to flowering increases (i.e., the vertical region of the curve becomes less steep). In the low deer impact site, the probability of flowering curve shifts to a larger size but converges to 100% more rapidly (fig. A1D). However, the size at which a flowering plant became female is narrower at the low deer impact sites (fig. A1E). Across the levels of deer impact, female seed set increases with plant size (fig. A1F). Seed set is also positively associated with deer impact, with higher seed set at sites with higher deer impact (fig. A1F).

To characterize the indirect effects by deer on current and future sexual reproduction for Arisaema, we calculated the size-dependent probability of plants being vegetative, male, or female. Overall, we find that plants in the intermediate deer impact site have a gradual size-dependent transition from vegetative to flowering and a high probability of producing a male flower at intermediate sizes (fig. 1B). Plants at the site with a high deer impact index share this pattern, but all probabilities shift toward larger sizes. Interestingly, this pattern is not mirrored for plants at the site with a low deer impact index (fig. 1A). As opposed to the broad male probability peak in response to intermediate and high deer impact (fig. 1B, 1C), plants at the site with low deer impact delay flowering to larger sizes, at which point they are more likely to be female than male (fig. 1A). Together, these results indicate two responses to reduced abiotic quality by overabundant deer: an increase in the size requirement of female sex expression (fig. 1F) and an increase in male sex expression at intermediate sizes (fig. 1E). We also find more pronounced plant shrinkage for large-sized individuals at high deer impact sites than at low deer impact sites (fig. A1B). However, analysis of our individual-based model shows that the magnitude of plant shrinkage at the low deer impact site does not preclude female sex expression the following year (fig. 2A). Conversely, at the high deer impact site, plant shrinkage is more pronounced and results in a high likelihood...
of regressing to a size at which they will be male or vegetative the following year (fig. 2C). We find evidence of a greater energetic cost of female reproduction, with consistently lower growth following female sex expression than male sex expression for similar-sized individuals (fig. 3). For males, we do not find a consistent trend across the deer impact gradient (fig. 3). At the low deer impact site, there was no difference in plant growth following male sex expression compared with vegetative plants. At the intermediate deer impact site, small-sized males grew faster than similar-sized vegetative plants, and large-sized males grew slower than similar-sized vegetative plants (fig. 3). At the high deer impact site, plant growth was greater for male plants than for vegetative individuals. Together, these results show that high deer impact lowers the ability to reach and maintain the size required for female sex expression (fig. 2).

At the population level, increased deer impact results in a decreased proportion of large vegetative individuals and an increased representation of small vegetative individuals in the population (fig. 4A.1–4C.1). As deer impact increased, the reproductive status of the population at SSD skews toward a male-biased OSR (percent male-to-female ratio: low = 42%, intermediate = 73%, high = 87%; fig. 4A.1–4C.1). The skewed male bias OSR is similar to field conditions, with a 5-year mean of 66% at the low deer impact site, 82% at the intermediate site, and 93% at the high deer impact site. The 5-year mean is based on 1 year of count data collected in 2005 and 4 years of demographic data collected from 2006 to 2009. The reproductive value (the sum of the left eigenvector) is highest in the high deer impact site, being six times greater than the reproductive value of individuals in the intermediate deer impact site and five times greater than in the low deer impact site (table B1), which means fewer individuals contribute to future generations at sites with high deer impact. An even-aged cohort levels off at a quasi-stationary stage distribution dominated by vegetative individuals, especially at sites with a high deer impact index (fig. 4A.2–4C.2). As cohorts age, we find that the probability of sexual reproduction decreases as habitat quality increases. Together, these changes in sexual reproduction shift the

![Figure 1: Probabilities of being vegetative, male, or female for Arisaema triphyllum plants at low, intermediate, and high deer impact index sites. The probability of being vegetative ($p_v = 1 - p$) and the probability of flowering and being male ($p_s = 1 - p_f$) are the complements of the probability of producing a flower (either male or female: $p_f$) and the probability of being female ($p_v$), respectively.](image-url)
OSR from male biased in the high and intermediate deer impact sites to more female biased in the low deer impact site (fig. 4A–4C). Using individual-based models, we find that reproductive consistency over an individual’s lifetime decreases as deer impact increases (fig. 4A–4C). Individuals from low deer impact sites are more likely to survive to flower as a female (35% at low deer impact sites vs. 4% at high deer impact sites), are more consistently reproductive once they reach reproductive age (29% vs. 15%), and are more often female when reproducing (55% vs. 7%; fig. B1; table B2). Across the three deer impact indices tested, asexually produced offspring (i.e., cormlets) produce flowers 1 year earlier on average than sexually produced offspring (i.e., seedlings; app. B; table B2). Increased site impacts by deer also alter an individual’s net reproductive rate (including sexual and asexual), $R_{\text{net}}$, and increases an individual’s relative contribution of asexually reproduced offspring over its life span (fig. 5B). Overall, these changes in Arisaema’s vital rates and reproductive strategy reduce population fitness, with a 15% difference in the population growth rate $\lambda$ between the low and the high deer impact sites (fig. 5A).

**Discussion**

There is growing evidence that environmental stress can influence the OSR of native plant species (Retuerto et al. 2017). Yet it remains unclear whether these observed changes are driven by short-term responses rippling through plant populations (e.g., from a recruitment burst) or the result of more permanent changes in life-history dynamics (but see Petry et al. 2016; Eberhart-Phillips et al. 2018). We used an IPM to assess the nontrophic indirect effects of deer on the population dynamics of a sex-labile understory perennial (Arisaema) and present evidence of altered life-history dynamics in response to habitat modifications by overabundant deer. Our results clearly link changes in Arisaema’s life cycle to deer-induced differences in habitat quality, causing long-term negative effects on population dynamics and mean lifetime fitness. Furthermore, our work demonstrates that increased deer impact alters the reproductive strategy of Arisaema in the following ways: (1) it delays female sex expression until plants reach a large size; (2) it leads to more pronounced shrinkage for large-sized individuals, the sizes at which plants are sexually reproductive; (3) it results in greater shrinkage.

**Figure 2:** Median (and 95% confidence interval [CI]) change in size from time $t$ to $t+1$ measured in natural units (diameter; mm) in relation to the logarithm of size at time $t$ (the scale at which we represent size in our integral projection model [IPM]) at sites with low (A), intermediate (B), and high (C) deer impact. The colored bar at the bottom of each plot shows the reproductive status at time $t$ and corresponds to the vertical dotted lines that indicate the size thresholds for sex expression. The colored area within the range of growth indicates the reproductive status at time $t+1$, given size at $t$ and the magnitude of growth. Median and 95% CI represent quantiles of 10,000 random individuals (sample paths) projected from birth to death using an individual-based model built from our IPM.

- **A. Low deer impact**
- **B. Intermediate**
- **C. High deer impact**
following female sex expression than male sex expression; and (4) it reduces reproductive consistency. These changes in Arisaema’s life cycle explain observed variation in the OSRs of local populations.

**Resource Allocation and Costs of Sexual Reproduction**

Sexual reproduction is a costly endeavor, placing a premium on efficiency when resources are limited. Sex expression can be either genetically fixed or permanently determined by chemical or physical environmental cues (Bai and Xu 2013). For some plants and animals, sex expression is sequentially labile, shifting between male and female function over an individual’s lifespan (reviewed in Munday et al. 2006; Vega-Frutis et al. 2014). The most prominent hypothesis to explain the evolution of sequential sex changing for plants and animals is the size advantage hypothesis (Ghiselin 1969), which sets up the expectation that reproductive success of males and females is optimized at different sizes and that sex expression is constrained by resource availability. In support of the size advantage for female sex expression at large sizes, research demonstrates that the energetic cost and resource demand of maternal investment is substantially greater than the prezygotic cost of male reproduction for many species (Doust and Cavers 1982; Cruden and Lyon 1985; Barrett et al. 2010). In addition to immediate reproductive costs, an individual’s sex expression can have downstream impacts on its physiology, morphology, and behavior that in turn influence current and future life-history dynamics.

Our results indicate that Arisaema operates using both resources paid up front for the opportunity to reproduce (reaching and maintaining a large enough size to reproduce), and as more commonly reported in the literature, Arisaema incurs an energetic cost of reproduction through a loss in size following female sex expression. Specifically, we find that Arisaema has a greater size requirement for female sex expression at sites with high deer impact and

**Figure 3:** Relationship between size and reproduction for Arisaema triphyllum individuals at each deer impact index. For A.1–C.1, the data were subset by the minimum size of male plants and the maximum size of vegetative plants at each site. For A.2–C.2, the data were subset by the minimum size of female plants and the maximum size of male plants. An asterisk indicates a significant difference of the main effect or interaction term, and ns indicates no significant difference at $P = .05$. 

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has more pronounced shrinkage following female sex expression than male sex expression. Regardless of the level of deer impact, Arisaema grows when small and shrinks when large. However, we also find that there is more pronounced shrinkage for large-sized plants at high deer impact sites, indicating a greater resource constraint associated with reaching and maintaining a large enough size to reproduce at high deer impact sites. Together, a greater size requirement for sexual reproduction, a more pronounced decrease in plant size following female sex expression, and greater shrinkage for large-sized individuals suggest either a greater cost of nonrecoverable energetic expenditure or greater depletion of resource reserves at high deer impact sites. These results complement previous research, which found a nonlethal growth cost of flowering and a prolonged size-dependent reproductive delay in low light environments for a simultaneous hermaphrodite, Orchis purpurea (Miller et al. 2012).

Interestingly, in a common garden without resource constraints, Arisaema plants from high deer impact sites

Figure 4: A.1–C.1, Stable size distribution (SSD) and operational sex ratio (inset pie chart) of the population at SSD. A.2–C.2, Projected time delay of sexual reproduction for Arisaema triphyllum at low, intermediate, and high deer impact index sites from time $t$ to $t + 50$ years, using age-from-stage modeling procedures. A.3–C.3, Probability of flowering plants remaining reproductively mature the following year (i.e., reproductive consistency over time).
exhibited faster growth and produced female flowers at a smaller plant size (Heckel and Kalisz 2017). Faster growth in a common garden suggests that either plants from sites with high deer impact have different resource allocation patterns (invest more in growth at the cost of reduced reserves) or they are more efficient at nutrient and water uptake and/or photosynthesis. Put another way, environmental stress and resource limitation favor plants that accomplish more with the same budget, increase their budget, or some combination of both. Similar to increased growth rate, female sex expression at a smaller plant size under common garden conditions not only suggests a proportional increase in reproductive expenditure but also indicates evolutionary change favoring early reproduction in response to increased stress by overabundant deer (Heckel and Kalisz 2017). The lack of differences in the effective population sizes of Arisaema among the field sites further implicates local adaptation over genetic drift as the primary force of evolutionary change (Heckel and Kalisz 2017). The apparent contradiction between previous common garden results (Heckel and Kalisz 2017) and our field studies (Heckel et al. 2010; this study) demonstrates the importance of using both of these approaches to more fully understand how abiotic degradation may alter life-history strategies of native species. The “grow fast, flower early” strategy displayed by plants from high deer impact sites in the common garden appears to be masked in the field by resource limitation. Selection favoring increased mobilization of resources in high deer impact sites may account for the observed increase in growth for small-sized plants in the field. The associated decrease in survival is suggestive of a shift in resource allocation toward more rapid growth and reproduction, effectively depleting stored reserves to buffer against mortality. Reduced reproductive consistency and more pronounced shrinkage at high deer impact sites further indicate reproductive resource constraints and the depletion of reserves following sex expression. Altogether, this evidence may suggest a shift in resource allocation over improved efficiency as the primary dimension of differentiation. On the basis of our findings and the previous common garden results, we expect that plants from low deer impact sites would have lower fitness if transplanted into the high deer impact sites.

**Asexual Reproductive Assurance**

Previous work suggests that asexual reproduction can provide reproductive assurance because, relative to seedlings, clonal offspring have advanced physiological and anatomical attributes that enable them to better tolerate resource limitation and environmental stress (Daly 1978; Hartnett and Bazzaz 1983; Salzman and Parker 1985; Matlaga and Horvitz 2009). While asexually produced offspring (e.g., bulbils, cormlets) are often more well provisioned than seedlings before separating from the parent plant, they are also partially self-sustaining, with established root systems and photosynthetic capacity (Slade and Hutchings 1987). This may suggest that for some species, asexual reproduction is advantageous because it allows for the production of individuals that are better equipped to cope with resource limitation and environmental stress.

![Figure 5: A, Arisaema triphyllum population growth rate (λ) at low, intermediate, and high deer impact index sites. B, Per-generation growth rate (R0) for sexual and asexual reproduction and the proportional contribution of asexual reproduction (R0asexual/R0sexual) for individuals at low, intermediate, and high deer impact index sites, respectively.](image-url)
reproduction requires less energetic costs per equal-sized recruit compared with sexual reproduction. A high cost of sexual reproduction may be particularly true for plants that produce large floral displays to attract pollinators and/or invest in large fleshy fruits and seeds (Daly 1978). From a theoretical perspective, asexual reproduction is more advantageous than sexual reproduction, having a twofold increase in individual fitness due to genetic transmission (Smith and Maynard-Smith 1978). However, obligate asexual reproduction reduces genetic diversity, particularly for self-incompatible species (Honnay and Jacquemyn 2008), and decreases a species’ ability to purge deleterious mutations, which leads to high mutation load accumulation (Kondrashov 1994; Caetano-Anollés 1999; Paland and Lynch 2006). Still, a lower energetic cost and/or a higher establishment rate of asexually produced offspring likely explains why there is commonly higher representation of clonal offspring at our high deer impact site. From our individual-based cohort analysis, we found that asexual cormlets reach reproductive age on average 1 year earlier than seedlings (app. B). Together, our findings are congruent with previous studies (Morris et al. 2004; Gaoue et al. 2018) demonstrating that reduced habitat quality by overabundant deer can decrease reproductive effort toward sexual reproduction and increases an individual’s net contribution of asexually produced offspring to the next generation.

**Sex Ratio and Reproductive Value**

The OSR for plants is typically examined in dioecious species, where the mechanism is described as differential sex mortality leading to spatial segregation of the sexes (Bierzchudek and Eckhart 1988). Work with *Valeriana edulis*, a species with genetically based sex expression, has shown that differentiation in water use efficiency between male and female plants can be an explanatory mechanism driving variation in the sex ratio along a geographical gradient (Petry et al. 2016). With OSRs ranging between 26% and 48% male, they found that the strongly female-biased populations were pollen limited, and an increase in male frequency reduced pollen limitation and increased seed set (+11.2% seed set; Petry et al. 2016). Conversely, more even OSR populations appeared to be pollen saturated. An increase in male frequency for these populations had little effect on female seed set (+2.6% seed set), but the population-level seed production was reduced by a net decrease in the proportion of females in the population. In contrast to previous studies, in which OSR is a result of sex-specific mortality, we demonstrate that OSR can result from environment-specific size requirements for sex expression and altered growth dynamics. Similar to Doust and Cavers (1982), we find that abiotic conditions can alter the OSR of this sexually labile perennial, shifting the proportion of males at equilibrium from 42% male at sites with low deer impact to 87% male at sites with high deer impact. These predicted OSRs at SSD are congruent with observed 5-year mean OSRs at our field sites. We also show that sites with high deer impact and male-biased OSRs have higher female seed set than populations with female-biased OSRs, suggesting that individuals at low deer impact sites are more pollen limited. However, the net reproductive rate of individuals from male-biased OSR populations is also lower than the net reproductive rate in female-biased OSR populations. Congruent with the results of Audzijonyte and Richards (2018), we find that the probability of flowering plants remaining reproductively mature the following year decreases as deer impact increases, indicating a trade-off between current and future reproduction. Together, these results suggest that reduced population fitness in response to overabundant deer is mediated in part by a shift in OSR in favor of males and an inability of plants to reach and maintain a large enough size to consistently reproduce over time (i.e., decreased reproductive consistency).

From sex allocation theory, we expect that the strength of selection for size-dependent sex expression will be dependent in part on the OSR of a population. In a highly male-dominated population, natural selection should favor a shift from male to female function at a smaller plant size to optimize population fitness (Cole 1954; Charnov 1982). On the other hand, if reproduction is costly and leads to high mortality of small individuals with low fecundity, selection should favor delayed maturation (Bell 1980). Our results suggest that overabundant deer have the potential to influence both of these selective forces. The reproductive value of *Arisaema* individuals from male-dominated populations is five times higher than individuals from female-dominated populations, emphasizing the large fitness reward gained by an individual producing female flowers before dying (e.g., flowering earlier or at a smaller size) in highly skewed male-biased populations. Our results also show that small-sized individuals (seedlings, small vegetative plants) in sites with high deer impact have lower survival but higher growth than plants from sites with low deer impact. These results may suggest that *Arisaema* populations have a
more risky allocation strategy that optimizes the probability of reaching reproductive age in resource-limited environments.

In this study, we show that the indirect nontrophic effects of overabundant deer on the life cycle of *Arisaema* cause a greater size requirement for female sex expression, reduced reproductive consistency, increased asexual reproduction, and highly male-biased OSRs. One important implication of our results is that over long time periods, indirect effects by overabundant deer have the potential to strongly impact the genetic composition of *Arisaema* populations. This may be particularly true for highly fragmented populations with reduced gene flow. Our future research will investigate the eco-evolutionary implications of these results. Specifically, we aim to test whether a loss in genetic variation occurs because of deer impacts on the underlying demographics described here. Ultimately, few individuals disproportionately contributing to recruitment (both sexual and asexual) may increase the rate of inbreeding and reduce *Arisaema*’s adaptability in an era of extreme change.

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**Data and Code Availability**

Vital rate coefficients and the R code for the integral projection models and individual-based models are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.gv0420c; Bialic-Murphy et al. 2020).

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Sexually labile forest perennial, *Arisaema triphyllum*, with a male inflorescence. Researchers show that increased deer impacts alter *Arisaema*’s reproductive strategy and skew populations toward a male bias operational sex ratio. Photo credit: Christopher D. Heckel.