
Experimental Demonstration of an Allee Effect in American Ginseng

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Abstract: *Harvesting of wild American ginseng (Panax quinquefolius) for the herbal trade has lowered natural population sizes. We tested for reproductive limitation due to small population size (a form of the Allee effect) by experimentally planting "natural" populations numbering 4, 16, and 64 using 4-year-old cultivated plants. Plant size traits and reproductive traits (bud, flower, green fruit, and mature fruit) were recorded through the ensuing summer. Fruit production per flower and per plant increased in proportion to flowering population size ($p = 0.0063$ and $p = 0.0017$, respectively), strongly suggesting that an Allee effect occurs in very small populations. The increase in fruit production was not explained by either plant or inflorescence size differences. Although population size-dependent pollination, through insufficient pollinator visitation rate or pollen transfer rate, seems the most likely cause of the observed effects, our limited observations of pollinators were not sufficient to demonstrate a change in pollination rates as a function of population size. Knowledge of the presence as well as the mechanism underlying this Allee effect may be especially useful for management and determination of minimum viable population size of the species in the wild.*

Demostración Experimental de un Efecto de Allee en el Ginseng Americano

Resumen: *El uso comercial del ginseng silvestre americano ha disminuido el tamaño de su población natural. Evaluamos la limitación reproductiva debida a una reducción en el tamaño poblacional (que es una forma de efecto de "Allee") experimentando con poblaciones "naturales" de 4, 16 y 64 plantas cultivadas por cuatro años. Censamos las características de tamaño y los rasgos reproductivos (yema, fruto verde y fruto maduro) al verano siguiente. La producción de fruto por planta y por flor aumentó proporcionalmente con el tamaño de la población ($p = 0.0063$ y $p = 0.0017$ respectivamente) sugiriendo enfáticamente que el efecto Allee ocurre en poblaciones muy pequeñas. El incremento en la producción de frutos no fue explicado por diferencias en tamaño de la planta, ni por diferencias en el tamaño de la inflorescencia. A pesar de que la polinización dependiente del tamaño, mediante una tasa de visita de polinizadores o una tasa de transferencia de polen insuficientes, parece ser la causa más probable de los efectos observados, nuestras limitadas observaciones de polinizadores no son suficientes para demostrar un cambio en las tasas de polinización como una función del tamaño poblacional. El conocimiento de la presencia, así como del mecanismo de acción de este efecto Allee puede ser especialmente útil para el manejo y determinación de un tamaño poblacional viable de las especies silvestres.*

Introduction

A basic tenet of conservation biology is that population size is inversely proportional to the probability of extinction (Shaffer 1981). The susceptibility of small popula-

tions to extinction is partially due to the proximity of population size, N , to zero. This explanation implies that small population size heightens the probability that some stochastic event (often "environmental" in the broad sense; Antonovics et al. 1988) will eliminate all individuals from the population (Menges 1991, 1992; Boyce 1992). A more subtle, deterministic disadvantage of small populations, described by Allee (Allee 1931, 1951; Boyce 1992), is that fertility and survival of individuals

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may be diminished once the population size descends below a critical threshold (Lande 1987; Caswell 1989; Lamont et al. 1993; Veit & Lewis 1996; Groom 1998). Only recently have the consequences of Allee effects been noted for their importance in the behavioral, ecological, and conservation biology of animals (Courchamp et al. 1999; Stephens & Sutherland 1999). The importance of Allee effects in plants needs further consideration.

As originally proposed, the Allee effect was conceived as a phenomenon whereby at low population densities reproductive opportunities are reduced because individuals are mate-limited (Allee 1931, 1951). In small plant populations, important mutualisms such as plant-pollinator interactions may be weakened, thereby resulting in lowered seed set (Lamont et al. 1993; Groom 1998). Jennersten (1988) and Bawa (1990) have emphasized the importance of changes in the composition and abundance of pollinators which may result in lowered seed set in plants.

In plants, pollinators may become less effective in two ways when N is reduced. First, small populations as a whole are less apparent, especially to specialist pollinators. As a result, plants are encountered at lower rates, and a lower number of pollinator visits may occur (Schemske 1980; Sih & Baltus 1987; Jennersten 1988). Alternatively, even if the number of pollinator visits does not decline when N is reduced, there may be a lower transfer rate of pollen (reduced "quality"; Kunin 1993). If pollinators are generalists and they visit flowers of many other species prior to visiting another individual in the same small population, seed production may be reduced by a low rate of intraspecific pollen transfer (pollen limitation). This effect may occur not only when plant densities are low (Silander 1978) but also when individuals are at low frequency—surrounded by flowering individuals of other species (Feinsinger et al. 1991; Kunin 1993, 1997; Aizen & Feinsinger 1994).

Many plant species naturally found in small populations have breeding systems that reduce their reliance on pollinators. Apomixis and autogamy, for example, bypass the pollinator requirement (Darwin 1876; Richards 1986; Feinsinger et al. 1991; Lloyd & Schoen 1992; Oostermeijer et al. 1992; Barrett 1996). The species most vulnerable to population size effects are likely to be obligate outcrossers that have been reduced in population size by whatever cause (Huenneke 1991). Nevertheless, even plants capable of selfing can be pollinator-limited if (1) selfing effectiveness is reduced by lower pollinator activity or lower pollen transfer rate (Karoly 1992; Lloyd & Schoen 1992), (2) enhancement of outcrossing increases seed set while selfing remains the same (Travis 1984), or (3) there is a genetic load (i.e., reduced fitness) associated with selfing (Darwin 1876; Schoen 1983; Charlesworth 1989).

Wild-harvested species may be particularly vulnerable

to the Allee effect if they were once abundant in nature. American ginseng (*Panax quinquefolius* L., Araliaceae) may fit this profile. Ginseng is an herbaceous perennial that has been harvested for its valuable fleshy root since the early 1700s (Carlson 1986). In 1995, wild ginseng harvest totaled 59,000 kg, with a total value of \$64.8 million at an estimated price of \$1099 per kg (Robbins 1998). This harvest equates to mortality (based on a range of mean root mass of 600–1100 roots per kg) of 35,400,000 to 64,900,000 individuals. The impact of this mortality is highly uncertain because it is not known whether this rate represents 0.1%, 1.0%, or 10% of all wild ginseng plants.

Regardless of the historical abundance of ginseng, in some locations it has been reduced to populations of one to a few dozen individuals (Van der Voort 1998). As an Appendix II plant species of the Convention on the International Trade in Endangered Species of Fauna and Flora (CITES), its trade is monitored by government regulatory agencies. The U.S. Office of Scientific Authority is required to issue a "no detriment" finding for harvest each year if trade is to be permitted.

We asked the following questions concerning the Allee effect in wild ginseng: (1) Do plants in small populations of ginseng experience lower pollinator visitation rates than plants in large populations? (2) Is the probability of producing fruit influenced by population size? (3) Is mean fruit production per flower and per plant lower in small populations than in large populations? These questions could be addressed in natural populations, but small N and low reproductive performance might be correlated due to a common underlying environmental cause rather than due to cause and effect. To avoid this problem, we addressed these questions by making observations of experimental populations of variable N that were planted randomly across a natural ginseng habitat.

Methods

Study Species

Wild ginseng occurs in the eastern deciduous forest of North America from Quebec, Canada, to northern Georgia and from Missouri to the east coast (Anderson et al. 1984; Robbins 1998). Ginseng seeds with immature embryos are dispersed from August through October (Anderson et al. 1984). Germination is delayed, requiring a protracted warm season followed by cold stratification (Lewis & Zenger 1983; Anderson et al. 1984; Schlessman 1985; Charron & Gagnon 1991; C. Baskin, personal communication). Therefore, germination usually occurs 18 months after dispersal.

Plants older than 3 years with more than two compound leaves emerge from the soil in late April to early

May, bearing an inflorescence. The inflorescence may develop as many as 70 buds (in four- or five-leaf plants), which reach anthesis in early to mid-June and continue to flower in a centripetal fashion until late July. The flowers are small and greenish-white, five-merous, entomophilous, and bisexual (Lewis & Zenger 1982).

Ginseng breeds by combining pollination within flowers (with or without pollinator assistance—autogamy), pollination between flowers within an inflorescence (with pollinator assistance—geitonogamy), and outcrossing (Carpenter & Cottam 1982; Lewis & Zenger 1983; Schlessman 1985). Two main pollinator groups have been observed: small bees in the family Halictidae and flies in the family Syrphidae (Carpenter & Cottam 1982; Lewis & Zenger 1983).

Berries begin to develop in early July and begin to mature to red fruits in mid-August (E.E.H., personal observation). Red berries may contain one to three seeds, with two being the most common (Lewis & Zenger 1982; Anderson et al. 1984).

Populations of ginseng typically have low fruit-to-flower ratios, so few fruits mature per plant (E.E.H., personal observation). In the absence of harvest, population growth rates (λ) are near 1.0 (Charron & Gagnon 1991). These growth rates are particularly sensitive to the behavior of the largest individuals in the population (Charron & Gagnon 1991); these individuals not only contribute the most to λ , but they are the most sought after by harvesters. Population viability analysis has led to estimates of minimum viable population size of 172 total plants (reproductive and nonreproductive; 1068, if seeds are included) at the northern edge of the species' range (Nantel et al. 1995).

Source Population

To create experimental populations varying in size, we obtained 596 "woods-grown" dormant plants in March 1997 from a local ginseng grower. The plants were descendants of a wild-collected seed stock. They were 4 years old, were cultivated in raised beds under a tree canopy, had been sprayed for insect pests and fungal pathogens, and treated with nutrient solutions and lime. The roots were layered in an organic soil mixture in random order. Prior to planting, roots were washed with tap water and placed in ziplock bags with moistened paper towels to prevent desiccation. All bags were stored in a "cold" room at 7.2°C until the field soil was ready for transplanting. Populations were stored in this manner for a maximum of 3 weeks while planting took place.

Field Site and Experimental Populations

Experimental populations were established on either side of two parallel, northeast-facing drainages at the

West Virginia University Forest on Chestnut Ridge, 15 km east of Morgantown, West Virginia. Three natural ginseng populations were found along one drainage during the course of the first summer's work, demonstrating that the study site was capable of supporting natural populations.

To generate populations representing a range of sizes, we planted three populations consisting of 4, 16, and 64 individuals, using the winter-dormant root material. Populations were placed approximately 100 m apart to minimize pollen flow among them. To avoid confounding density and population size effects, we constructed a planting template to assure equal spacing (25 cm) of individual plants within populations. Each root was washed with a 20% commercial bleach solution prior to planting. Transplanting began 18 March 1997 and was completed within 3 weeks. In all, 16 size-class 4 populations, 10 size-class 16 populations, and 5 size-class 64 populations were planted. As a hedge against failure to emerge or flower, two extra roots were planted within each of the $n = 4$ and $n = 16$ populations.

A survey of every plant was taken during each phenological stage. Stem height was measured, as an index of size, between 20 May 1997 and 10 June 1997. Buds were counted on each inflorescence from 11 June to 4 July. Open flowers were counted in the 3 weeks following 7 July, and green berries were counted from 7 July to 14 August.

Pollinator Observations

On 7 July, one population of 64 was observed from 0700 to 1800 hours to determine the peak hours of pollinator visitation. A pollinator visit was recorded if the pollinator alighted on the inflorescence of the plant. Pollinator activity was constant and high between 1000 and 1600 hours. Pollinator observations were carried out over a 17-day period beginning 7 July, during the peak flowering time of all populations. Each population was observed for 40 minutes, and the number of pollinator visits during this period was counted. Observations were terminated when most flowers on the inflorescence were beginning to lose, or had lost, their petals and ovaries had begun to swell.

Statistical Analysis

We functionally related probability of plant emergence to planted population size using log-likelihood tests; populations were nested within population size classes (4, 16, 64) (Sokal & Rohlf 1995). Because a different number of plants emerged in each population, subsequent tests treated population size as a continuous variable. We examined flowering probability by regressing the proportion of emerged plants that flowered (Y) on emerged plant population size using standard least-

squares regression, weighted by the number of emerged plants in each population.

If Allee effects operate through reduced fertility, we would expect significant declines in reproductive performance with decreasing numbers of flowering plants in a population. We analyzed the dependence of population mean fruit production and pollinator visitation on flowering population size with weighted regression (Christensen 1996). The weighting factor in all analyses was the number of observations used to compute the population mean, and the independent variable (X) was the number of flowering plants in each population. The dependent variables (Y) included proportion of flowering plants producing fruit, population mean number of green fruits per plant, population mean number of green fruits per flower, mean stem height, mean bud number, and mean pollinator number per population. Linear regression was also used to determine whether a relationship existed between weighted mean fruit production per flower and weighted mean number of visits per flower.

Yield component analysis was used to determine which stage—emerged plants, flower production, or berry production—explained most of the variation in seed production between populations (Fraser & Eaton 1983). The natural log of fruits per planted individual was the dependent variable, and the log of the fraction of plants that emerged, the log of the fraction of emerged plants that produced flowers, and the log of the fraction of flowering plants that produced fruits were the independent variables (yield components). One-half was added to each component to allow inclusion of observations whose values were zero. All analyses were performed with SAS JMP statistical software v. 3.1.5 (SAS Institute 1996).

Results

Of the 596 roots planted, 453 (76%) emerged, 284 (48%) flowered, and 224 (40%) produced fruit. The lack of 100% emergence is not surprising and may have been due to damage during collection and transplanting of individuals. The rate of flowering was unusually high for 4-year-old plants (Anderson et al. 1984), no doubt due to their cultivation, but it appeared to be comparable to that observed in natural populations in plants of similar size. All collected seeds were viable. Of the 31 planted populations, 26 persisted, and were followed from flowering to fruit production, and were therefore included in the analyses. The flowering plant population sizes of those 26 populations ranged from 1 to 52. Of the 26 populations, only 4 had flowering population sizes above 20.

As expected, probability of shoot emergence was not influenced by population size (log-likelihood analysis, $p = 0.9405$). Also as expected, for plants that emerged, the probability of flowering was unaffected by population

size (standard least-squares regression with weighting, $p = 0.8318$).

If small populations exhibit mate limitation, we would expect the quantity of fruit production to decline with smaller N . We chose to examine these relationships as a function of flowering plant population size rather than all plants, because attractiveness to pollinators presumably would not be influenced by nonreproductive individuals. In the population of plants that flowered, we found that the proportion of individuals producing fruit was significantly reduced at smaller N (weighted regression, $p = 0.0206$). In addition, the population mean number of fruits produced per flower decreased significantly as flowering population size declined, as indicated by a positive regression coefficient (weighted regression, $p = 0.0063$; Fig. 1). This lowered per-flower seed production resulted in the same pattern of reduced mean seed production at low N when expressed on a per plant basis (weighted regression, $p = 0.0017$, Fig. 2).

Consistent with the Allee-effect hypothesis, 69% of the variation between populations in green fruit production was explained by the rate at which flowers yielded green fruit, not the earlier stages of reproduction (yield component analysis). The variation among populations in fruit production was not due to variation in mean plant size among populations (bud number, $p = 0.1361$;

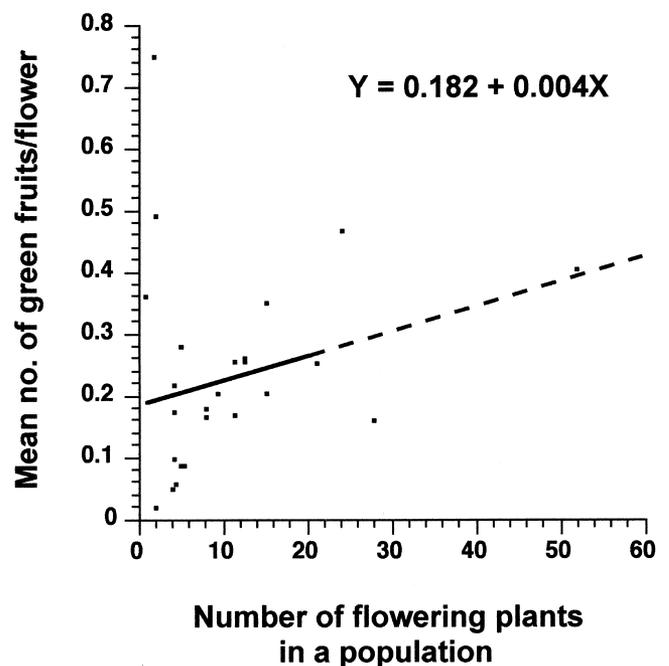


Figure 1. Reduction in fruit production per flower at small flowering population sizes in 26 planted populations of American ginseng. Regression lines extending above $N = 20$ are represented with dashed lines to indicate a level of uncertainty concerning the Allee effect at higher N (although points in that range are means based on a large N).

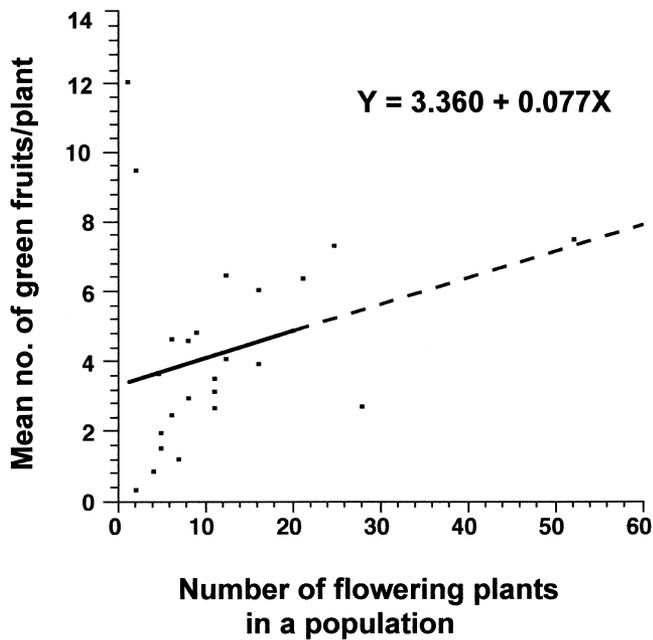


Figure 2. Reduction in fruit production per plant at small flowering population sizes in 26 planted populations of American ginseng. Regression lines extending above $N = 20$ are represented with dashed lines to indicate a level of uncertainty concerning the Allee effect at higher N (although points in that range are means based on a large N).

stem height, $p = 0.1101$), showing that initial plant size differences were not the cause of reproductive differences among populations.

One possible explanation for decreased fruit production at low N is mate limitation in small populations. Pollinators could be limiting fruit production in small populations by visiting them less frequently. Although this hypothesis is feasible, pollinator visitation rates did not vary as a function of flowering plant population size (weighted regression, $p = 0.7429$). There was a nonsignificant positive relationship between mean pollinator visitation rate per flower and mean number of fruits produced per flower in a population (regression, $p = 0.0993$).

Discussion

Reduced Fertility and Survival in Small Populations

Numerous studies have demonstrated reduced fertility and/or survival in small, natural populations. Many of the studies on small populations attribute this reduced fitness of individuals to genetic erosion (Heschel & Paige 1995; Oostermeijer et al. 1994; Fischer & Matthies 1998). Small population size is associated with substantial levels of genetic drift and inbreeding, which may lead to loss of heterozygosity and expression of deleterious al-

leles, thus leading to inbreeding depression (Frankel & Soulé 1981; Charlesworth & Charlesworth 1987). In particular, reduced seed weight, reduced seedling weight, and higher seedling mortality in small populations of *Gentiana pneumonanthe* were attributed to inbreeding depression (Oostermeijer et al. 1994). In *Gentianella germanica*, Fischer and Matthies (1998) found a reduction in seeds produced per fruit in smaller populations, and in small populations of *Ipomopsis aggregata* Heschel and Paige (1995) demonstrated a reduction in both seed size and germination, both ostensibly due to effects of inbreeding. Small populations may also have reduced resilience under environmental stress: small populations of *Ipomopsis aggregata* suffered higher mortality and reduced individual size under simulated ungulate herbivory (Heschel & Paige 1995). If any of the reduced fertility we observed is due to inbreeding, it would have to be a first-generation effect caused by increased abortion of seeds due to a higher selfing ratio because relatedness of adults did not vary with population size in our study. We cannot rule out higher early abortion rates due to greater selfing, but this seems an unlikely explanation in a species such as ginseng with a high natural rate of selfing (Schlessman 1985).

The reduced per-individual fertility we observed is most likely due to pollinator and/or pollen limitation, because small populations of animal-pollinated plants are less apparent than larger populations (Sih & Baltus 1987). Reduced apparency would lower pollinator visitation rate (i.e., pollinator limitation) and/or pollen transfer rate (pollen limitation). Through a series of hand pollinations, the observed lower seed set in isolated patches of *Dianthus deltooides* was ascribed to pollinator limitation (Jennersten 1988). Fragmented populations of *Banksia goodii* also have reduced seed set in small populations, a difference attributed to two possible causes, an increase in pollen transfer between incompatible siblings and/or a lowered number of effective pollinations (Lamont et al. 1993).

A difficulty in interpreting small population effects is that populations may actually be small because they are in poor physical environments that reduce fertility and survival. Therefore, studies that take into account the possible confounding effects of environment and population size by experimentally manipulating population size are better able to distinguish a true Allee effect from an environmentally caused correlation. Groom (1998) documented Allee effects in fragmented populations of the annual *Clarkia concinna* by experimentally manipulating patch size and isolation distances. Her results suggest that Allee effects resulting from pollinator limitation are responsible for extinctions in small, isolated patches.

The reduced number of fruits per flower and the reduced number of fruits per plant that we observed in small experimental populations of ginseng are consistent with the operation of an Allee effect. Because popu-

lation size “treatments” were randomly assigned to field sites, our study eliminated the potential confounding effects of the environment. For ginseng, a species that may be harvested heavily, this finding means that populations may be threatened by an Allee effect even in “good” environments. To judge the significance of the Allee effect, the consequences of reduced seed set need to be evaluated in a broader demographic context.

Consequences of Allee Effects in Natural Populations

Although Allee effects operate through reduced fertility or survival of individual plants, the important consequence is the net effect on the finite rate of increase of the population (λ). We propose that an Allee effect in plant populations may take one of two forms: (1) a “mild” Allee effect, in which λ decreases at reduced N , but remains above one, and (2) a “strong” Allee effect, in which λ decreases below one, thereby crossing an extinction threshold (Fig. 3). The extinction threshold (N_A ; A for Allee) is the population size below which N inexorably declines to zero. Stephens and Sutherland (1999) describe a similar classification scheme, citing that per capita growth rates are lower for populations with Allee effects than would be expected for typical logistic growth. In addition, populations with strong Allee effects exhibit two equilibria, upper (stable) and lower (unstable). The lower equilibrium point corresponds to our proposed N_A and results in ultimate extinction of the population.

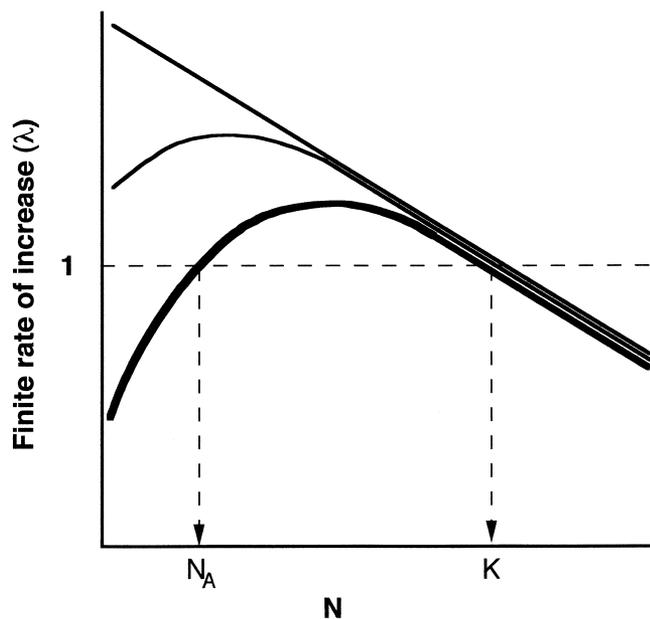


Figure 3. Effects of density on λ , illustrating no Allee effect (top curve), a mild Allee effect (middle curve), and a strong Allee effect (lower curve). N_A is the critical value of N below which $\lambda < 1$.

To determine whether the reduction in reproductive output we observed constitutes a mild or strong Allee effect, we would need complete data on natural populations, which are not presently available for the central Appalachian region. Therefore, we modified existing population projection matrices estimated for four ginseng populations (1–4) by Charron and Gagnon (1991; published again by Nantel et al. 1995). At $N = 60$, we assumed that fertility elements were the same as those published in the original study. Below $N = 60$, we reduced fertility elements by multiplying the original fertility values by the fractional fertility of individuals found in a population of that size. We determined the appropriate fraction by the ratio of fertility predicted at that N relative to the $N = 60$ value, using the regression of Fig. 2. We calculated a new λ at each population size between $N = 1$ and $N = 60$ using MATLAB v.4.2c.1 (The Math Works 1993).

As depicted by the theoretical exercises, populations 1, 2, and 4 would be classified as having mild Allee effects (Fig. 4) because, at low N , λ is reduced but remains above one. Across the range of population sizes from 60 to 1, the finite rate of increase (λ) was reduced by 4–6%. Population 3 had a λ below one for all population sizes and therefore appeared to be in decline regardless of harvest. These projections assume that the Allee effect operates linearly in a range from $N = 1$ to $N = 60$ and that it ceases to be an influence at that point. In fact, we have no evidence for a “break point” at $N = 60$. These projections therefore merely suggest the order of magnitude of the Allee effect in ginseng. It appears that popu-

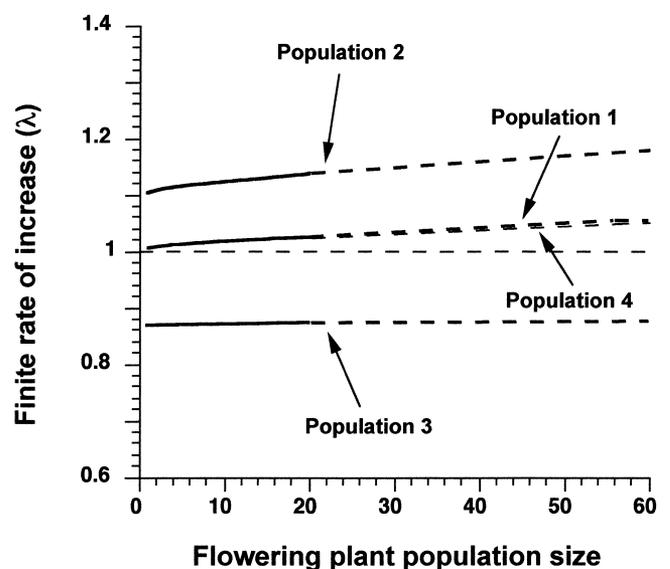


Figure 4. Theoretical consequences of Allee effects in natural populations adapted from projection matrices estimated for four ginseng populations by Charron and Gagnon (1991); populations 1, 2, and 4 have mild Allee effects.

lations with λ in the range of 1.00–1.04 could experience a strong Allee effect at sufficiently low N .

A Mechanism for Allee Effect in Plant Populations

Although we have demonstrated an Allee effect in ginseng, the mechanism remains unclear. The Allee effect has been attributed to a variety of causes in animals: less efficient feeding (Way & Banks 1967), reduced defenses (Kruuk 1964; Kenward 1978), and inbreeding depression (Ralls et al. 1986; Gilpin & Soulé 1986). In plants, little attention has been given to the occurrence of Allee effects (with the recent exception of Groom 1998); nevertheless, pollinator limitation-effectiveness is a likely mechanism in some cases. Pollinator visits, however, did not decrease in small populations of ginseng. On the other hand, fruit production did relate positively to pollinator visitation rate such that, as visits declined, fruit production per flower lessened. Thus, reduction in pollinator visitation could potentially reduce seed production in small populations.

Although inadequate observation of pollinators may explain the lack of differences in pollen visitation rate among populations, the alternative explanation of reduced pollinator effectiveness is more likely. Pollinator effectiveness may be reduced in small populations because pollinators transfer lower absolute relative amounts of conspecific pollen (Waser 1978; Thomson et al. 1981; Rathcke 1983; Campbell 1985). By manipulating plant densities with both conspecifics and heterospecifics, Feinsinger et al. (1991) found that seed set increased in stands with conspecific plants and decreased in mixed stands while pollinator visitation rates remained constant in both. This indicates that pollinator effectiveness was lowered by the excess of heterospecific pollen in the mixed stands. When spacing of individual plants was increased (Kunin 1993), a similar depression in seed set was demonstrated in *Brassica kaber*. A thorough study of pollinator effectiveness in the context of a ginseng breeding system study would provide further insight.

Implications for Conservation

Conservation biologists often aim to sustain populations of endangered or threatened species. Some species are endangered or threatened because they occur in small populations that are prone to extinction due to a variety of stochastic factors, including environmental, genetic, demographic, and natural catastrophes. By understanding the deterministic elements that may affect the long-term viability of populations, conservationists can reach a more sound estimate of the minimum viable population size.

Although demographic projections and population viability analyses have not been carried out for ginseng in the center of its range, our results suggest that it is unreasonable to assume that reproductive parameters will

remain constant when populations are reduced by harvest. With the inclusion of Allee effects, the detrimental effects of harvest on population viability may be greater than would normally be projected. Because harvest is presently a nearly ubiquitous part of the ginseng environment, the Allee effect should be incorporated in simulations of the effect of harvest in natural populations in the context of population viability analysis.

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