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THE EFFECTS OF POPULATION SIZE AND DENSITY ON THE REPRODUCTIVE OUTPUT OF *ANEMONE CANADENSIS* L. (RANUNCULACEAE)

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We studied the effects of population density and population size on stigma pollen load and fruit set in *Anemone canadensis*, a xenogamous self-incompatible species. In 1993, 1994, and 1995, we examined 13–17 populations, with densities ranging from one to 39 flowering ramets per square meter and sizes ranging from 25 to 27,000 flowering ramets. In 1993, stigmas received fewer pollen grains than in 1994 or 1995. In 1993 and 1995, population size and fruit set were significantly and positively related, and in 1993, both population density and stigma pollen load were significantly and positively related to fruit set. Stigma pollen load was not significantly related to population density or size. Our results indicate that the effects of population density and population size on plant reproduction in *A. canadensis* represent a range of outcomes influenced by differences between years in the quality (self vs. outcross) of pollen moved. We hypothesize that small populations typically have poor fruit set because they consist of relatively few genets and infrequently receive large amounts of outcross pollen, particularly when they are relatively close to large populations in protected areas.

Keywords: population size, population density, plant reproduction, prairies, *Anemone canadensis*.

Introduction

Much emphasis in conservation biology has been placed on understanding the role of population size in the reproductive success of species because reductions in contiguous habitat caused by fragmentation typically lead to reductions in population size (Harris 1984; Saunders et al. 1991). Many studies of plants have shown that, compared with small populations, large populations have higher fruit set, seed set, and seed germination rates (Jennersten 1988; Menges 1991; Hendrix 1994; Byers 1995; Heschel and Paige 1995; Ågren 1996). In outbreeding species, reductions in these measures of reproductive success in small populations are often attributed to decreases in the quantity or quality of pollinator service (Jennersten 1988; Aizen and Feinsinger 1994; Byers 1995; Ågren 1996).

In addition to population size, density of plants in a population may also affect plant-pollinator interactions and hence plant reproduction (Platt et al. 1974; Feinsinger et al. 1986; Kunin 1992; Roll et al. 1997). Several studies have shown that low reproduction is associated with low densities because of low pollinator-visitation rates (Platt et al. 1974; Kunin 1993). However, high plant densities may also result in decreased reproductive output in outbreeding species because short pollinator flights between plants or flowers (Beattie 1976; Handel 1983; van Treuren et al. 1993; Karron et al. 1995a) may decrease the likelihood of flowers receiving outcross pollen (van Treuren et al. 1993; Karron et al. 1995b). Although the effect

of density on plant reproduction appears to be mediated through the process of pollen movement, relatively few studies have directly related plant or flower density to the number of pollen grains or pollen tubes per flower (see Feinsinger et al. 1991; Kunin 1993). Furthermore, few studies have separated the effects of population size and population density on pollen movement (see Ågren 1996; L. Rigney and S. D. Hendrix, unpublished manuscript).

Over a 3-yr period, we examined the effects of population density and population size on the reproductive success of *Anemone canadensis*, a perennial herbaceous forb of prairies. The specific questions addressed were, (1) Is reproductive success directly related to pollen arrival? (2) Is population density or population size related to reproductive success in *A. canadensis*? (3) Does the effect of population density or population size, if any, on reproductive characteristics, vary from year to year? (4) Is the relationship between population size and density consistent from year to year?

Material and Methods

Study Species

Anemone canadensis L. (Ranunculaceae) is a self-incompatible (Douglas and Cruden 1994) rhizomatous perennial, commonly found in moist open areas such as wet prairies and roadside ditches in the central and northeastern United States and Canada (Sutherland 1986). The flowering period in Iowa is late May to June. Flowers are solitary or in a cyme, and a ramet may have more than one flower open at the same time. Flowers have white showy sepals with numerous pistils and stamens. *Anemone canadensis* is pollinated by generalists such as solitary bees and syrphid flies (Douglas and Cruden 1994; Williams 1996). Because the flowers do not produce nectar,

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pollen is the only reward for visitors. Maturing pistils develop into achenes by mid-July.

Study Sites, Plant Collections, and Measurements of Population Characteristics

We conducted this study in 1993, 1994, and 1995 in 13–17 populations and patches in Dickinson County, Iowa, located adjacent to unimproved roads, in state preserves, or, in one case, adjacent to an active railway (table 1). Over the 3 yr of this study, population sizes ranged from 25 to ca. 27,000 flowering ramets, and densities ranged from one to 39 flowering ramets per square meter. The size of the area occupied by roadside populations was never >100 m². All roadside populations and the railway population were isolated from other such populations by at least 1 km. Sizes of patches on preserves ranged from 500 to 2500 m² and were isolated from each other by no less than 500 m. Edges of roadside populations and preserve patches were very distinct, possibly because of the clonal nature of *A. canadensis*.

At the beginning of each flowering season, we haphazardly selected and tagged in each population 30 ramets with unopened flower buds. We collected these ramets at the end of the fruiting season and used them to estimate mean percentage of fruit set and mean percentage of aborted fruits.

In each population, we determined the number and density of flowering ramets at the peak of the flowering season. In all populations, the occupied area was mapped and measured each year. We defined population or patch size as the absolute number of flowering ramets because the inclusion of nonflowering ramets in measures of population size could obscure important relationships between size and aspects of the reproductive process. We measured size by direct counting in small populations (<500 flowering ramets), and we calculated population density in small populations from ramet counts and

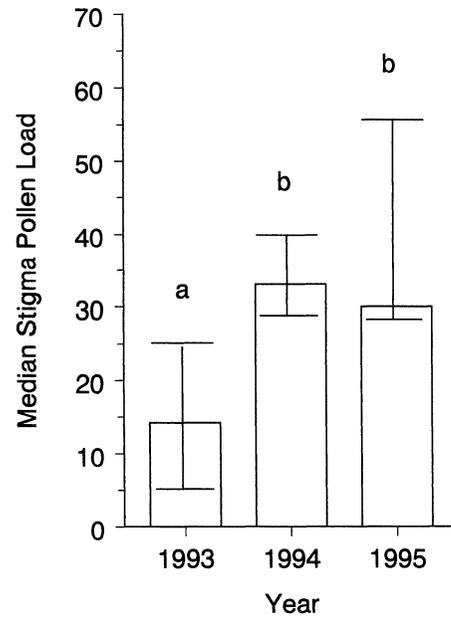


Fig. 1 Stigma pollen loads (number of pollen grains per stigma \pm 75% and 25% quartiles) in populations of *Anemone canadensis* in 1993, 1994, and 1995. Histogram bars with different letters differ significantly ($P < 0.05$).

area measurements. In large populations (>500 flowering ramets), we estimated size and density from the number of flowering ramets in not fewer than 100 1-m² quadrats placed along parallel transects that were equally spaced throughout the population.

Table 1

Location and Characteristics of Study Populations of *Anemone canadensis* in 1993, 1994, and 1995

Population address	Remnant type	Size ^a			Density ^b		
		1993	1994	1995	1993	1994	1995
180 Street, no. 3	Roadside	...	64	25	...	2.86	6.27
170 Street	Roadside	...	57	99	...	3.07	6.07
130 Street	Roadside	...	75	40	...	1.52	2.19
100 Street	Roadside	...	47	8.47	...
120 Street, no. 2	Roadside	40	82	116	0.98	1.91	3.21
180 Street, no. 1	Roadside	43	47	77	19.11	8.39	6.29
120 Street, no. 1	Roadside	50	42	107	3.21	1.82	3.21
140 Street, no. 2	Roadside	52	...	232	2.38	...	15.16
190 Street	Roadside	68	67	149	13.57	3.55	6.73
210 Avenue, no. 2	Roadside	74	...	87	2.24	...	2.54
140 Street, no. 1	Roadside	80	80	94	6.02	1.73	2.61
210 Avenue, no. 1	Roadside	104	107	165	3.15	2.98	4.82
140 Street, no. 3	Roadside	110	...	39	4.73	...	0.77
180 Street, no. 2	Roadside	553	718	872	7.18	8.70	10.11
120 Street, no. 3	Roadside	690	564	859	38.98	15.06	35.79
Railroad	Railroad	5056	7998	8174	8.85	10.77	8.37
Cayler	Preserve	5156	7181	12,020	13.09	14.42	24.14
Freda Haffner	Preserve	22,943	26,101	27,030	11.31	10.09	10.74

^a Number of flowering ramets.

^b Number of flowering ramets/m².

Table 2
Stigma Pollen-Load and Percentage of Fruit Set in *Anemone canadensis* Populations in 1993, 1994, and 1995 (\pm SD)

Population address	Stigma pollen load			Percentage of fruit set		
	1993	1994	1995	1993	1994	1995
180 Street, no. 3	39.31 (14)	42.56 (28)	...	19.6 (21)	1.6 (3)
170 Street	63.77 (20)	86.57 (55)	...	14.5 (20)	17.8 (21)
130 Street	33.05 (25)	28.36 (30)	...	47.1 (28)	10.0 (22)
100 Street	24.18 (19)	58.6 (16)	...
120 Street, no. 2	25.00 (14)	34.91 (18)	32.80 (17)	4.7 (7)	22.4 (30)	1.1 (1)
180 Street, no. 1	2.92 (4)	...	8.48 (7)	62.5 (13)	0.0 (0)	31.5 (24)
120 Street, no. 1	23.25 (14)	32.78 (25)	29.38 (14)	1.9 (2)	1.4 (5)	0.4 (2)
140 Street, no. 2	2.58 (4)	...	3.36 (6)	0.0 (0)	...	0.0 (0)
190 Street	14.25 (12)	27.16 (24)	30.03 (16)	37.8 (20)	0.0 (0)	24.6 (19)
210 Avenue, no. 2	3.50 (6)	...	17.02 (30)	3.4 (4)	...	2.5 (3)
140 Street, no. 1	7.25 (7)	...	69.92 (61)	13.9 (15)	0.0 (0)	23.7 (15)
210 Avenue, no. 1	12.30 (6)	27.44 (15)	26.65 (15)	6.7 (9)	7.7 (12)	12.5 (15)
140 Street, no. 3	14.17 (9)	...	28.96 (23)	24.6 (18)	...	22.2 (17)
180 Street, no. 2	30.34 (19)	39.84 (15)	99.82 (50)	0.0 (0)	0.8 (1)	1.4 (2)
120 Street, no. 3	58.60 (36)	41.09 (23)	52.47 (18)	62.6 (32)	0.7 (2)	3.6 (4)
Railroad	5.09 (7)	26.91 (16)	32.60 (28)	67.2 (21)	56.6 (17)	67.1 (19)
Cayler	40.30 (35)	47.53 (20)	116.39 (49)	50.0 (20)	36.6 (22)	32.1 (16)
Freda Haffner	24.37 (29)	29.86 (20)	28.97 (19)	52.4 (20)	19.9 (19)	31.7 (29)

Estimating Stigma Pollen Load

To estimate stigma pollen load per population (i.e., mean number of pollen grains per stigma), we haphazardly collected 10–30 flowers per population at the peak of the flowering season. We stored flowers in a 3 : 1 solution of 95% ethanol : acetic acid. Up to five pistils were removed from each flower and prepared for fluorescence microscopy by soaking in NaOH for 12 h to soften the tissue before staining with 0.1% aniline blue in 0.1 M K_3PO_4 (Martin 1959). We mounted pistils on slides in glycerol and scored them for the total number of pollen grains per stigma. It is not possible to distinguish outcross from self-pollen on the basis of pollen tube formation in *A. canadensis* because of its gametophytic self-incompatible

system (Douglas and Cruden 1994) in which rejection of self-pollen occurs after pollen tubes are formed. Furthermore, it is not possible to distinguish pollen tubes that enter the ovary from those that do not because of trichomes on the style and ovary.

Statistical Analysis

Population densities and sizes, as well as population means of percentage of fruit set, percentage of aborted fruits, and stigma pollen loads were not normally distributed. Therefore, we used Kruskal-Wallis tests followed by Dunn's test for pairwise comparisons to examine for differences between years.

We used Pearson's product-moment correlations to test for

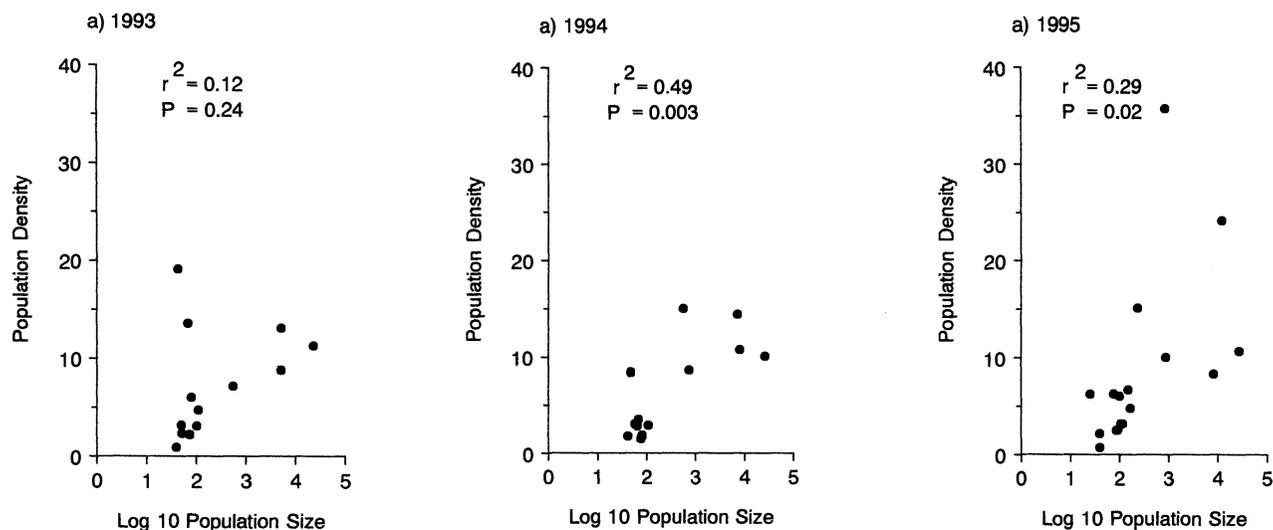


Fig. 2 Relationship between population density (flowering ramets/m²) and population size (number of flowering ramets) in *Anemone canadensis* populations in 1993, 1994, and 1995.

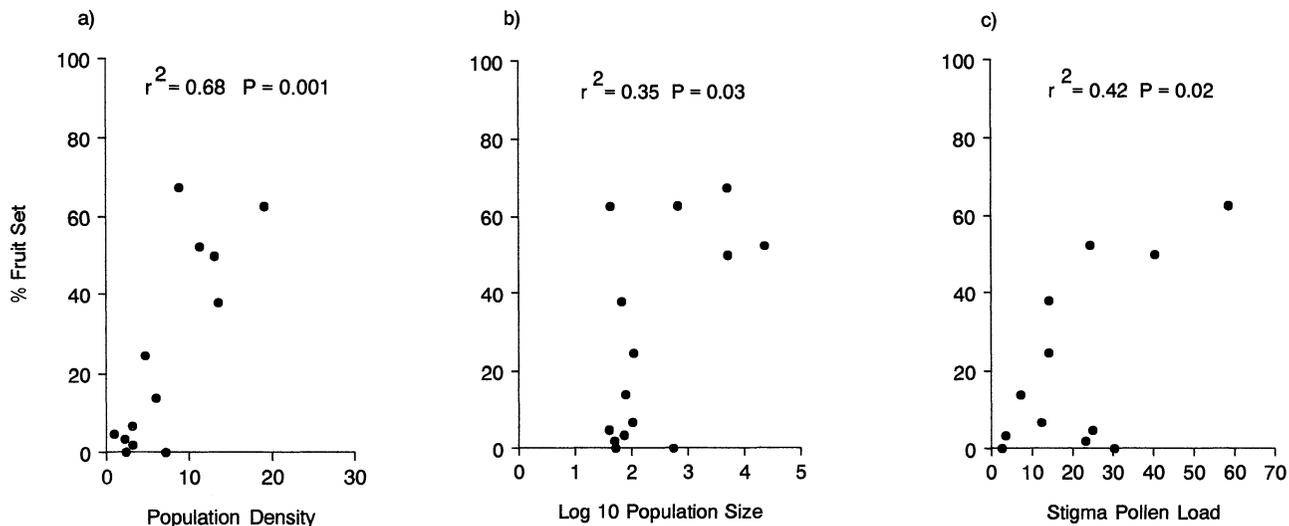


Fig. 3 Relationship between percentage of fruit set and (a) population density, (b) population size, and (c) stigma pollen load in *Anemone canadensis* populations in 1993.

a relationship between population density and population size in 1993, 1994, and 1995. Population sizes were log transformed before statistical analyses. We used ANCOVA to compare the slopes of the significant size-density relationships found for 1994 and 1995. Multiple regressions were used to distinguish between the correlated effects of population size and density in 1994 and 1995 on percentage of fruit set. In preliminary regressions, population density was not related to percentage of fruit set in either 1994 ($r^2 = 0.14$, $P = 0.49$) or 1995 ($r^2 = 0.42$, $P = 0.98$), but it was related to the residual of size on density in 1995 ($r^2 = 0.42$, $P = 0.01$). Therefore, we regressed percentage of fruit set against population size and the residual of density on size.

We used regression analysis to test for relationships in each year between population density or size and population means of percentage of fruit set, percentage of aborted fruits, and stigma pollen load. We also used regression analysis to test for relationships between stigma pollen load and percentage of fruit set. We checked all data sets for statistical outliers using Cook's D -test, and when found, they were eliminated from the analyses. All tests were performed using SAS version 6 (SAS Institute 1989).

Results

Differences between Years in Reproductive and Demographic Characteristics

Stigma pollen load varied significantly between years (Kruskal-Wallis test, $H_2 = 10.79$, $P = 0.01$), with stigmas receiving fewer pollen grains in 1993 than in 1994 or 1995 (Dunn's test, $P < 0.05$) (fig. 1; table 2). This indicates major differences in pollinator service over time. Population density, population size, percentage of fruit set, and percentage of aborted fruits did not vary significantly between years (Kruskal-Wallis tests, all H values < 1.36 , all P values > 0.51).

Relationship between Population Density and Population Size

Population density and population size were significantly and positively correlated in 1994 and 1995 but not in 1993 (fig. 2). The slopes of the regression lines for the relationship between density-size relationships did not differ significantly between 1994 and 1995 (ANCOVA, $F = 1.00$, $df = 1, 28$, $P = 0.33$), indicating that as density increased, size increased to a similar degree in both years.

Patterns in Reproductive Output in 1993, 1994, and 1995

In 1993, percentage of fruit set was significantly and positively related with population density, population size, and stigma pollen load (fig. 3; table 3). Stigma pollen load was not significantly related with population density or size in 1993 (both r^2 values < 0.20 , and P values > 0.13) (table 3). The percentage of aborted fruits in 1993 was not related with population density or population size (all r^2 values < 0.02 , and P values > 0.67) (table 3).

In contrast to 1993, percentage of fruit set was not significantly related with population density or size (both r^2 values < 0.10 , and P values > 0.31) in 1994 (fig. 4; table 3). In the multiple-regression analysis, neither population size nor the residual of the regression of density on size was significantly related to percentage of fruit set ($r^2 = 0.14$, all $P > 0.20$). Similarly, stigma pollen load was not significantly related with population density, population size, or percentage of fruit set (all r^2 values < 0.06 , and P values > 0.43) (fig. 4; table 3). Percentage of aborted fruits was not significantly related with population density or population size in 1994 (all r^2 values < 0.19 , and P values > 0.11) (table 3).

In 1995, percentage of fruit set was significantly and positively related with population size as in 1993, but not with population density ($r^2 = 0.00004$, $P = 0.98$) (fig. 5; table 3).

Table 3
Regression Coefficients and Significance Levels of Relationships among Population Size, Population Density, and Reproductive Characteristics in *Anemone canadensis* in 1993, 1994, and 1995

Year/regression	r^2	P
1993:		
Population size vs. stigma pollen load	0.195	0.131
Population size vs. percentage aborted fruits	0.018	0.664
Population size vs. percentage fruit set	0.346	0.034
Population density vs. stigma pollen load	0.007	0.792
Population density vs. percentage aborted fruits	0.003	0.864
Population density vs. percentage fruit set	0.682	0.001
Stigma pollen load vs. percentage fruit set	0.420	0.020
1994:		
Population size vs. stigma pollen load	0.001	0.976
Population size vs. percentage aborted fruits	0.038	0.488
Population size vs. percentage fruit set	0.079	0.311
Population density vs. stigma pollen load	0.005	0.826
Population density vs. percentage aborted fruits	0.188	0.106
Population density vs. percentage fruit set	0.038	0.486
Stigma pollen load vs. percentage fruit set	0.058	0.427
1995:		
Population size vs. stigma pollen load	0.112	0.191
Population size vs. percentage aborted fruits	0.136	0.145
Population size vs. percentage fruit set	0.292	0.025
Population density vs. stigma pollen load	0.118	0.176
Population density vs. percentage aborted fruits	0.124	0.166
Population density vs. percentage fruit set	0.00004	0.983
Stigma pollen load vs. percentage fruit set	0.003	0.823

In the multiple-regression analysis, population size was significantly related to percentage of fruit set ($r^2 = 0.42$, $P = 0.02$), but not the residual of the regression of density on size ($r^2 = 0.42$, $P = 0.10$). As in the other 2 yr of the study, stigma pollen load in a population was not significantly related with population density, size, or percentage of fruit set (all r^2 values < 0.12 , and P values > 0.18) (fig. 5; table 3). This indicates no significant effect of population characteristics on the pollination process and subsequent reproduction. In addition, percentage of aborted fruits in 1995 was not related with population density or population size (all r^2 values < 0.14 , and P values > 0.15) (table 3).

Discussion

In contrast to other studies that have shown consistent effects over time of population size and density on reproduction in plants in natural populations (Ågren 1996; Kyhl 1997; L. Rigney and S. D. Hendrix, unpublished manuscript) or experimental settings (Kunin 1997), our results indicate that these population characteristics are only intermittently related to reproduction in *Anemone canadensis*. In 1993, when population size and density were not related, both were significantly correlated with fruit set. However, in 1994 neither was related to fruit set. In 1995, when size and density were correlated, we hypothesized that the significant effect on fruit set was due mostly to population size. These results contrast with the strong effects of density rather than size in the experimental studies of Kunin (1997), possibly because densities in many of our populations were higher than the most dense experi-

mental array that he used. Furthermore, in contrast to pollen addition experiments (Byers 1995) and a broad survey of many tropical plant species (Aizen and Feinsinger 1994), we find only marginal evidence supporting the hypothesis that decreased reproduction in small or less dense populations is related to low pollen arrival to stigmas. In the one year of our study in which reproduction was related to both population density and size (1993), we found that the amount of pollen arriving to stigmas was related to percentage of fruit set but not to population size or density, indicating that population characteristics were not substantially influencing the quantity of pollen moved.

For a self-incompatible species such as *A. canadensis*, the amount of self versus outcross pollen arriving to stigmas or the quality of pollinator service may be more important than the amount of pollen moved. Because *A. canadensis* has vigorous vegetative reproduction and can form large clonal patches in most years, the flowers available to donate or receive pollen at any one time in a small patch could represent a small number of genets. In the self-incompatible species, *Eupatorium resinosum*, Byers and Meagher (1992) suggest a similar cause for low reproduction in small populations. Thus, successful pollination with outcross pollen in small populations of *A. canadensis* would depend on infrequent, long-distance movement of pollinators between patches of relatively few genets. This scenario could account for the fact that two-thirds of populations with < 1000 flowering stems had 20% or less fruit set, while two-thirds of the populations with > 5000 stems consistently had fruit sets of over 30%. Landscape features, particularly the distance to large populations (Spear 1987), may

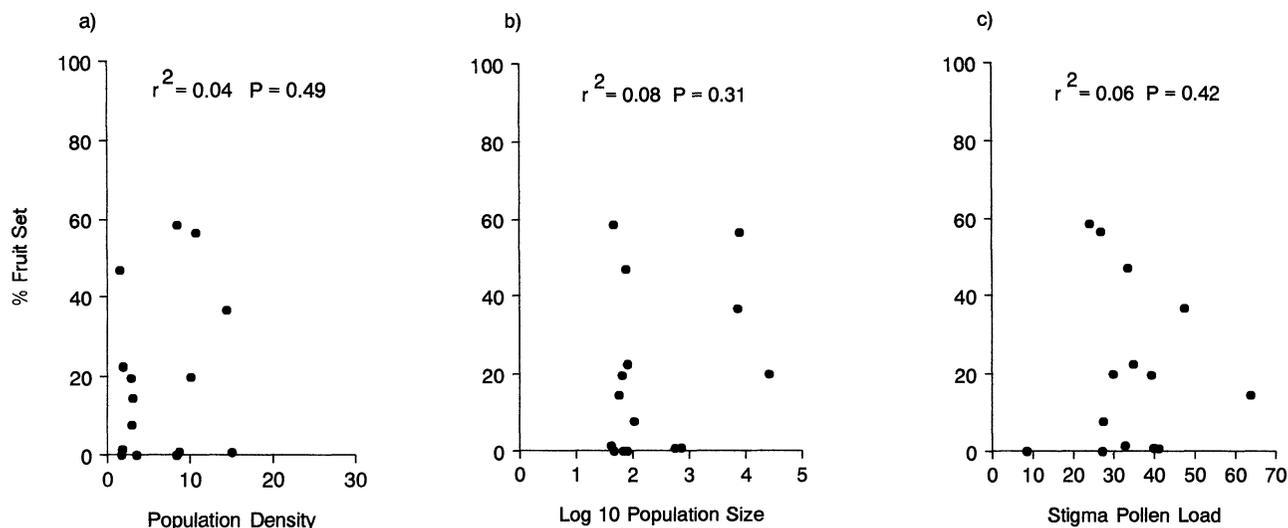


Fig. 4 Relationship between percentage of fruit set and (a) population density, (b) population size, and (c) stigma pollen load in *Anemone canadensis* populations in 1994.

also be important given that small populations with high fruit set were within 1 km of preserves or wildlife management areas that harbor large populations.

Variation between years and sites in the structure of pollinator guild (S. D. Hendrix and L. Anderson, unpublished data) may also affect quality of pollinator service. In general, different pollinators (i.e., beetles, bumblebees, honeybees) may visit different numbers of flowers per plant and therefore differ in their likelihood of performing geitonogamous (between flowers on the same plant) pollinations (Kunin 1993; Robertson and Macnair 1995). Furthermore, different pollinators differ in their behavioral responses to patch size (Sih and Baltus 1987; Kunin 1997), indicating that variation in patch size or density (Bateman 1956; Ellstrand et al. 1978) from year to

year will interact with changes in pollinator guild structure in complex ways that may be difficult to unravel.

Some of the inconsistencies between years in the effects of population size and density on the reproduction in our study likely reflect yearly variation in weather conditions affecting pollinator abundance or activity. For example, low pollen movement in 1993 may have resulted from the effect of unusually wet and cool weather in May and June on pollinator abundance or activity levels. Precipitation during May was more than twice normal (19.1 cm vs. 8.8 cm), and the average temperature was 1.4°C lower than normal. In June, precipitation was nearly three times normal (29.0 cm vs. 10.4 cm), and average temperature was 2.2°C lower than normal (U.S. Environmental Data Service 1993). Cool and wet conditions

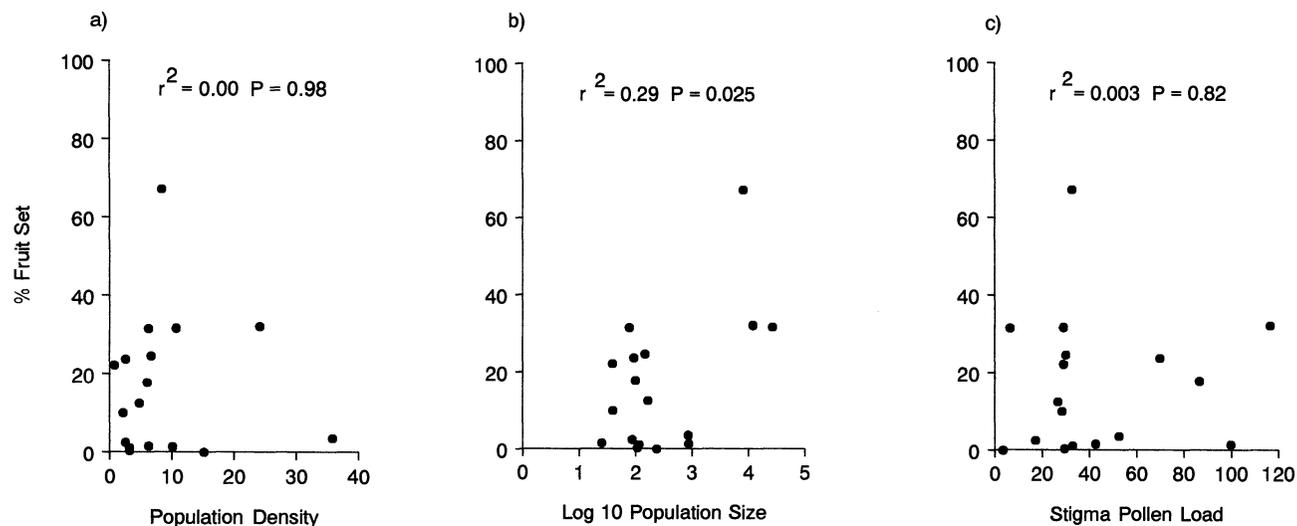


Fig. 5 Relationship between percentage of fruit set and (a) population density, (b) population size, and (c) stigma pollen load in *Anemone canadensis* populations in 1995.

are well known to depress pollinator activity (Cruden 1972; Mogford 1974; Cruden et al. 1976; Baker and Cruden 1991). Similar cool and wet conditions in both May and June had not occurred in the past 30 yr (U.S. Environmental Data Service 1960–1990), indicating that even though these weather conditions may not be the norm, they influenced pollinator activity and thus plant reproduction.

Our study strongly indicates that the relationship between plant reproduction and both density and population size in *A. canadensis* is best thought of as a distribution of outcomes (Thompson 1988) representing a variety of relationships over time, not all of which are statistically or biologically significant. If other species exhibit similar variation between years in the effects of size or density on reproduction, it may be difficult to draw conclusions concerning differences between species from 1-yr studies. In some of these 1-yr studies, no relationship between density and reproduction of a species occurs (Pitelka et al. 1980; Shaw 1987), while in other studies a relationship does occur (Sih and Balthus 1987). Whether reproduction in any given set of *A. canadensis* populations shows a significant relationship with density or size may be highly dependent on whether at least one of the small populations receive large amounts of outcross pollen. In general, small populations usually have reduced per capita reproduction relative to larger ones.

Successful sexual reproduction is only one of many factors affecting viability of *A. canadensis* populations. Recruitment from seeds in experimental plots is poor (<5%) (S. D. Hendrix, B. Molano-Flores, and L. Rigney, unpublished results), indicating that when populations are destroyed by stochastic events, recolonization of sites with more than a few genotypes may be rare. However, once sites are colonized by even one genotype, vigorous vegetative reproduction may permit the population quickly to reach a size that is likely to attract pollinators carrying outcross pollen from other populations. Thus, vegetative reproduction may be necessary to buffer populations against the uncertainties of sexual reproduction resulting from wide variation in density, size, genetic structure, and availability of pollinators.

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Literature Cited

- Ågren J 1996 Population size, pollinator limitation, and seed set in the self incompatible herb *Lythrum salicaria*. *Ecology* 77:1779–1790.
- Aizen MA, P Feinsinger 1994 Forest fragmentation, pollination, and plant reproduction in Chaco dry forest, Argentina. *Ecology* 75:330–351.
- Baker JD, RW Cruden 1991 Thrips-mediated self-pollination of two facultatively xenogamous wetland species. *Am J Bot* 78:959–963.
- Bateman AJ 1956 Cryptic self-incompatibility in the wallflower: *Cheiranthus cheiri* L. *Heredity* 10:257–262.
- Beattie AJ 1976 Plant dispersion, pollination and gene flow in *Viola*. *Oecologia* 25:291–300.
- Byers DL 1995 Pollen quantity and quality as explanations for low seed set in small populations exemplified by *Eupatorium* (Asteraceae). *Am J Bot* 82:1000–1006.
- Byers DL, TR Meagher 1992 Mate availability in small populations of plant species with homomorphic sporophytic self-incompatibility. *Heredity* 68:353–359.
- Cruden RW 1972 Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. *Science* 176:1439–1440.
- Cruden RW, S Kinsman, ER Stockhouse, YB Linhart 1976 Pollination, fecundity, and the distribution of moth-flowering plants. *Biotropica* 8:204–210.
- Douglas KL, RW Cruden 1994 The reproductive biology of *Anemone canadensis* (Ranunculaceae): breeding system and facilitation of sexual selection. *Am J Bot* 81:314–321.
- Ellstrand NC, AM Torres, DA Levin 1978 Density and the rate of apparent outcrossing in *Helianthus annuus* (Asteraceae). *Syst Bot* 3:403–407.
- Feinsinger P, KG Murray, S Kinsman, WH Busby 1986 Floral neighborhood and pollination success in four hummingbird-pollinated Costa Rican plant species. *Ecology* 67:449–464.
- Feinsinger P, HM Tiebout III, BE Young 1991 Do tropical bird-pollinated plants exhibit density-dependent interactions? field experiments. *Ecology* 72:1953–1963.
- Handel SN 1983 Pollination ecology, plant population structure, and gene flow. Pages 163–211 in L Real, ed. *Pollination biology*. Academic Press, Orlando, Fla.
- Harris L 1984 The fragmented forest: island biogeographic theory and the preservation of biotic diversity. University of Chicago Press, Chicago.
- Hendrix SD 1994 Effects of population size on fertilization, seed production, and seed predation in two prairie species. Pages 115–121 in RG Wickett, P Dolan-Lewis, A Woodliffe, P Pratt, eds. *Proceedings of the Thirteenth North American Prairie Conference: spirit of land, our prairie legacy*. Preney Print & Litho, Windsor, Ont.
- Heschel M, KN Paige 1995 Inbreeding depression, environmental stress and population size variation in scarlet gilia (*Pomopsis aggregata*). *Conserv Biol* 9:126–133.
- Jennersten O 1988 Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conserv Biol* 2:359–366.
- Karron JD, NN Thumser, R Tucker, AJ Hessenauer 1995a The influence of population density on outcrossing rates in *Mimulus ringens*. *Heredity* 75:175–180.
- Karron JD, R Tucker, NN Thumser, JA Reinartz 1995b Comparison of pollinator flight movements and gene dispersal patterns in *Mimulus ringens*. *Heredity* 75:612–617.
- Kunin WE 1992 Density and reproductive success in wild populations of *Diplotaxis eruroides* (Brassicaceae). *Oecologia* 91:129–133.
- 1993 Sex and the single mustard: population density and pollinator behavior effects on seed set. *Ecology* 74:2145–2160.
- 1997 Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kuber*. *J Ecol* 85:225–234.
- Kyhl JF 1997 The effects of habitat fragmentation on *Phlox pilosa*. MS thesis. University of Iowa, Iowa City.
- Martin FM 1959 Staining and observing pollen tubes by means of fluorescence. *Stain Tech* 34:436–437.

- Menges ES 1991 Seed germination percentage of increases with population size in a fragmented prairie species. *Conserv Biol* 5:158–164.
- Mogford DJ 1974 Flower colour polymorphism in *Cirsium palustre*. 2. Pollination. *Heredity* 33:257–263.
- Pitelka LF, DS Stanton, MO Peckham 1980 Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). *Am J Bot* 67:942–948.
- Platt WJ, GR Hill, S Clark 1974 Seed production in a prairie legume (*Astragalus canadensis* L.): interactions between pollination, pre-dispersal seed predation, and plant density. *Oecologia* 17:55–63.
- Robertson AW, MR Macnair 1995 The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*. *Oikos* 72:106–114.
- Roll J, RJ Mitchell, RJ Cabin, DL Marshall 1997 Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*). *Conserv Biol* 11:738–746.
- SAS Institute 1989 SAS/STAT user's guide, version 6. 4th ed, vol 1. SAS Institute, Cary, N.C.
- Saunders DA, RJ Hobbs, CR Margules 1991 Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5:18–32.
- Shaw RG 1987 Density-dependence in *Salvia lyrata*: experimental alteration of densities of established plants. *J Ecol* 75:1049–1063.
- Sih A, MS Baltus 1987 Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* 68:1679–1690.
- Spear EE 1987 Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. *J Ecol* 75:351–362.
- Sutherland D 1986 Ranunculaceae Juss., the buttercup family. Pages 87–88 in RL McGregor, TM Barkley, RE Brooks, EK Schofield, eds. *Flora of the Great Plains*. University Press of Kansas, Lawrence.
- Thompson JN 1988 Variation in interspecific interactions. *Annu Rev Ecol Syst* 19:65–87.
- U.S. Environmental Data Service 1960–1994 Climatological data (Iowa). Vols 71–105. National Oceanic and Atmospheric Administration. National Climate Center, Asheville, N.C.
- van Treuren R, R Bijlsma, NJ Ouborg, W van Delden 1993 The effects of population size and density on outcrossing rates in locally endangered *Salvia pratensis*. *Evolution* 47:1094–1104.
- Williams AH 1996 Prairie insect and spider inventory. The prairie enthusiasts: southwest chapter 1996 annual report. Madison, Wis.