males meet the added costs of harem defense on a day-to-day basis by increasing their nightly consumption of fruit. An *A. jamaicensis* utilizes about 30% of the 26 kJ in a 10-g *F. insipida* fruit (Morrison 1980). From previous studies (Morrison 1978a) we know that nonlactating females and nonharem males carry away about seven figs per night, enough to cover the daily costs of resting metabolism (37 kJ) plus 1 h of flying (16 kJ). In contrast, a harem male which fed exclusively from *F. insipida* trees for seven nights took 9–13 figs per night ($\bar{x}$ = 10.9 ± 1.8). These were sufficient to cover his resting metabolism and his 2.9 ± 1.1 h of flying. In addition, the numbers of figs taken per night were significantly correlated with nightly flying times (Spearman r_s = 0.826, P < .05). Harem males apparently adjust their food intake to balance the energy they expend.

Quantitative studies of the economics of defending territories and mates have been limited because of the shortage of natural systems in which one can measure both energy intake and energy expenditures. Such studies to date have focused primarily on territoriality in nectar-feeding birds. Fruit bats provide a valuable new system for developing and testing ideas in this field.

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Literature Cited

Bradbury, J. W., and S. L. Vehrencamp. 1977. Social organization and foraging in emballonurid bats. III. Mating systems. Behavioral Ecology and Sociobiology **2**:1–17.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science **197**:215–223.

Gill, F. B. 1978. Proximate costs of competition for nectar. American Zoologist **18**:753–763.

LeBoeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. American Zoologist **14**:163–176.

McCracken, G. F., and J. W. Bradbury. 1977. Paternity and genetic heterogeneity in the polygynous bat, *Phyllostomus hastatus*. Science **198**:303–306.

McNab, B. K. 1969. The economics of temperature regulation in Neotropical bats. Comparative Biochemistry and Physiology **31**:227–268.

——. 1976. Seasonal fat reserves of bats in two tropical environments. Ecology **57**:332–338.

Morrison, D. W. 1978a. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. Ecology **59**:716–723.

——. 1978b. Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis*. Animal Behaviour **26**:852–856.

——. 1979. Apparent male defense of tree hollows in the fruit bat *Artibeus jamaicensis*. Journal of Mammalogy **60**:11–15.

——. 1980. Efficiency of food utilization by fruit bats. Oecologia **45**:270–273.

Thomas, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. Journal of Experimental Biology **63**:273–293.

Wells, K. D. 1978. Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. Animal Behaviour **26**:1051–1063.

FIXED RATES OF RANDOM OVULE ABORTION IN CRYPTANTHA FLAVA (BORAGINACEAE) AND ITS POSSIBLE RELATION TO SEED DISPERSAL[1]

Brenda Bowers Casper and Delbert Wiens[2]

Flowering plants commonly produce many ovules that do not develop into seeds. A portion of the ovules within an ovary, entire fruits, or even whole inflorescences may fail to mature. Lack of pollination or insufficient resources are often implicated as causal factors. We propose that in some species a percentage of the ovules always abort, regardless of adequate pollination or favorable environmental conditions. We demonstrate that in *Cryptantha flava* (A. Nels.) Payson, embryonic development is generally initiated in at least three of the four ovules of each ovary, although most flowers mature only a single seed. Furthermore, ovule abortion occurs at random with respect to position within the ovary and is not apparently a phenotypic response to environmental factors.

The idea that ovule abortion may function as an adaptive feature in flowering plants has received little attention. In perennial species of *Cryptantha* a reduced seed set per flower is correlated with the retention of the seeds in the calyx which acts as the dispersal unit. Abortion, in this case, may be adaptive for
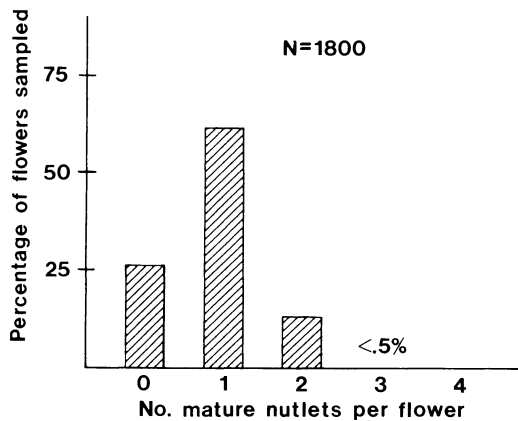
FIG. 1.   Distribution of mature nutlets per flower for *Cryptantha flava*. Three hundred flowers (150 pin, 150 thrum) were collected in 1979 from each of six populations in eastern Utah.
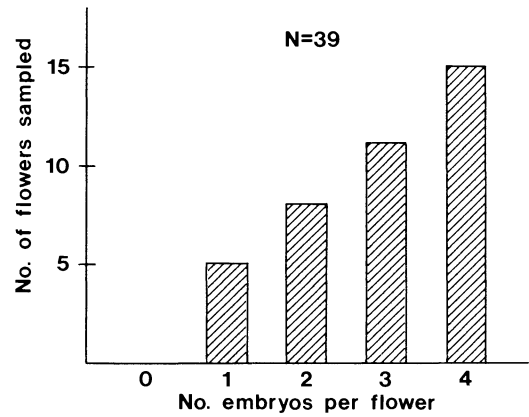

FIG. 2.   Number of embryos initiated per ovary in *Cryptantha flava*.

greater dispersal by wind and thus reduced competition with sibs and parents.

Cryptantha flava is a perennial herb widely distributed throughout the arid Colorado Plateau of eastern Utah, USA, and parts of adjoining states. Seed production data obtained in 1979 from six populations located throughout much of the range of the species (an area approximately 200 × 1100 km) revealed that flowers generally produce one seed (nutlet), sometimes two nutlets, and only rarely three (Fig. 1). Other perennial species of *Cryptantha* occurring sympatrically with *C. flava* (e.g., *C. flavoculata*) generally mature all four nutlets. Although *C. flava* is heterostylous, it is nevertheless self-compatible (B. Casper, *personal observation*), and no difference was found in the distribution of nutlets per flower for pin and thrum individuals (Kolmogorov-Smirnov two-sample test, $D = .028$, $n_1 = 900$, $n_2 = 900$, $P > .10$).

Each ovule within an ovary appears equally likely to develop. This is demonstrable by observing the position of developing ovules in flowers that mature two nutlets. The four nutlets in borages are arranged in a square. Thus if ovules develop at random, pairs of adjacent nutlets should be twice as common as nutlets opposite each other, since there are four combinations of two adjacent nutlets and only two ways of obtaining opposite nutlets. A χ^2 analysis of opposite vs. adjacent positions ($n = 219$) reveals that seed development is random (df = 1, $\chi^2 = 2.49$, $.10 < P < .20$).

To determine whether all the embryo sacs within an ovary are normally fertilized, flowers were collected at random from two populations and enlarged ovaries (about 6–8 d following anthesis) were fixed in FAA, embedded in paraffin, and sectioned longitudinally at 12 μm. Since only enlarging ovaries were exam-

ined, any unpollinated flowers were not included in this sample.

Two-thirds of the ovaries sectioned contained young embryos (usually in the early globular stage) in either three or four of the ovules (Fig. 2). Embryos within a single ovary often varied considerably in size. In some ovules endosperm had disintegrated, and the embryos were obviously collapsed while other developing ovules within the same ovaries appeared normal (Fig. 3). Only a few ovules lacking embryos contained endosperm, which is also evidence of fertilization; most appeared to contain unfertilized embryo sacs. In some ovules that were abnormally shaped, embryo sacs had not formed.

The factors limiting seed maturation in natural species are no doubt numerous and complex. Certainly environmental parameters, including the availability of resources, may be largely responsible for the occasional low seed sets found in many species. The regular reduction in seed number per flower in *C. flava,* however, appears to be genetically controlled. Because the seed set pattern in *C. flava* is consistent throughout the geographic range of the species, it is unlikely that the pattern is a phenotypic response to environmental factors. Furthermore, hand-pollinated plants grown in the greenhouse under regular watering and fertilization regimes typically fail to mature more than two seeds per flower, although all four ovules may initiate development (B. Casper, *personal observation*).

As mentioned previously, abortion may be related to the efficiency of nutlet dispersal in *Cryptantha*. In the nine species that regularly fail to develop all four ovules, the matured nutlets are not deciduous as they are in other perennial members of the genus (A. Cronquist, *personal communication*). Instead the nutlet(s) remains attached to the style, which together with the calyx abscises from the plant. Thus the entire floral
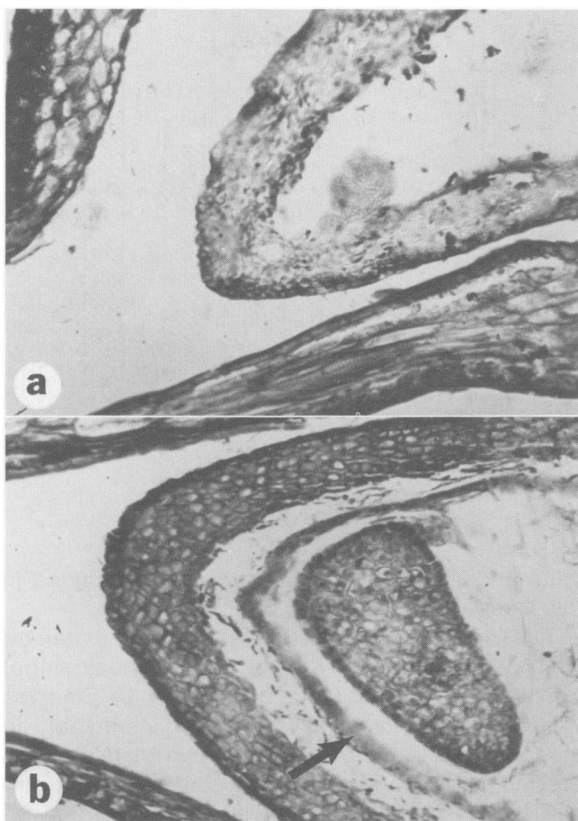
FIG. 3. Longitudinal sections of ovules from the same ovary showing (a) an aborted embryo and (b) a normal embryo in the early heart-shaped stage. The developing embryo is surrounded by endosperm, marked by arrow, which is lacking in (a). 340×.

structure serves as the dispersal unit. If the nutlets of perennial species of *Cryptantha* are wind dispersed as we suspect, the attached calyx may augment the buoyancy of nutlets in air currents and increase the dispersal distance. A difference in the dispersal distance is suggested by the distribution of seedlings within populations. In species producing deciduous nutlets, juvenile individuals are common around the bases of adult plants, but in *C. flava,* seedlings are more widely distributed. The elimination of some nutlets in each flower reduces the total mass of the dispersal unit and thus may allow greater dispersal potential.

Packaging only one or two seeds in each dispersal unit could reduce sibling competition resulting from the dispersal of four nutlets to the same location. In addition, the abortion system provides opportunity for selection at the zygote level, either through competition among embryos or by direct control from the parent plant (Janzen 1977, Charnov 1979).

Parallel examples of ovule abortion related to seed dispersal may exist. For example, *Salazaria mexi-*

cana (Lamiaceae) also produces four ovules per ovary (a feature typical of the mint family). Preliminary data suggest that in *Salazaria,* flowers with a single mature nutlet are approximately twice as common as flowers producing two nutlets, and eight times as prevalent as flowers with three. Four nutlets are produced occasionally, so the system is not fixed as in *C. flava.* After the corolla abscises, the calyx closes, greatly inflates, and serves as the dispersal vehicle for the enclosed seed(s). A reduced seed set per flower may also be important for seed dispersal in *Gilia capitata* Sims. subsp. *capitata* (Polemoniaceae) which matures only 1 to 6 of the 14 ovules per capsule. Unlike other gilias, the fruit of this subspecies remains indehiscent and falls from the plant as a unit (V. Grant 1950 and *personal communication*). In both *G. capitata* subsp. *chamissonis* (Greene) V. Grant and *G. capitata* subsp. *staminea* (Greene) V. Grant, all ovules within the ovary may develop, and seeds are released individually from a typically dehiscing capsule.

Similar postfertilization abortion systems (though not necessarily related to dispersal) could operate in many species for which reduced seed set per flower or extremely low percentage seed sets are noted, including: several other borage genera (Levin 1968, Fabre and Nicoli 1974, Ornduff 1976, S. Weller, *personal communication*), *Calystegia* spp. (Convolvulaceae) (Schlising 1980), *Acer saccharum* Marsh. (Aceraceae) (Gabriel 1967), *Geranium maculatum* L. (Geraniaceae) and *Dalea* spp. (Fabaceae) (R. Cruden, *personal communication*) and possibly *Darwinia fascicularis* Rudge and *D. micropetala* Benth. (Myrtaceae) (Prakash 1969). Fixed abortion of fertilized ovules is also known in some agricultural species: red clover, *Trifolium pratense* L. (Sato 1956), and peas, *Pisum sativum* L. var. Alaska (Linck 1961). In peas, however, a position effect occurs in which ovules toward each end of the pod mostly abort while those closer to the center of the pod generally mature.

In summary, we have demonstrated a pattern of fixed ovule abortion in *C. flava* and speculated on its evolutionary significance. We suggest that in other species, as well, a consistent failure of some ovules to develop in each ovary may not result from ambient environmental conditions or a lack of fertilization, as is often assumed, but could be genetically controlled.

Literature Cited

Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. Proceedings of the National Academy of Science **76**(5):2480–2484.
Fabre, G., and R. M. Nicoli. 1974. Sur la morphologie des

akènes de quelques Boraginacées de la flore de France. Intérêt systématique de cette étude. Societe Botanique de France Bulletin **121**:133–144.

Gabriel, W. J. 1967. Reproductive behavior in sugar maple: self-compatibility, cross-compatibility, agamospermy, and agamocarpy. Silvae Genetica **16**:165–168.

Grant, V. 1950. Genetic and taxonomic studies in *Gilia* I. *Gilia capitata*. El Aliso **2**(3):239–316.

Janzen, D. H. 1977. A note on optimal mate selection in plants. American Naturalist **11**:365–371.

Levin, D. 1968. The breeding system of *Lithospermum caroliniense*: adaptation and counteradaptation. American Naturalist **102**:427–441.

Linck, A. J. 1961. The morphological development of the fruit of *Pisum sativum*, var. Alaska. Phytomorphology **11**:79–84.

Ornduff, R. 1976. The reproductive system of *Amsinckia grandiflora*, a distylous species. Systematic Botany **1**:57–66.

Prakash, N. 1969. Reproductive development in two species of *Darwinia* Rudge (Myrtaceae). Australian Journal of Botany **17**:215–227.

Sato, H. 1956. Morphological and physiological studies on the occurrence of abortive seeds in leguminous forage crops II. Proceedings of the Crop Science Society of Japan **24**:224–226.

Schlising, R. A. 1980. Seed destruction of California morning glories (Convolvulaceae:*Calystegia*) by bruchid beetles. Madroño **27**:1–16.

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