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THE EFFECTS OF HERBIVORY ON PATERNAL FITNESS IN SCARLET GILIA: BETTER MOMS ALSO MAKE BETTER POPS

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Abstract.—Whether plants can benefit from the direct effects of herbivory has been contentious among ecologists and evolutionary biologists. Although previous studies have provided experimental evidence of enhanced maternal fitness following herbivory in a natural system, an accurate depiction of plant-herbivore interactions must include the effects of herbivory on male as well as female fitness. Here we show that ungulate herbivory on scarlet gilia results in an increase in paternal as well as maternal fitness. This study represents the first evidence of overcompensation in a natural system where both paternal and maternal components of fitness have been assessed.

Over the past decade there has been a heated debate as to whether or not plants can benefit from being eaten (Belsky 1986, 1987; McNaughton 1986; Bergelson and Crawley 1992*a*, 1992*b*). The basis of this controversy has focused on whether the direct effects of herbivory can enhance plant fitness. Until recently, resolution has been hampered by a lack of supportive evidence (Belsky 1986; Verkaar 1986). Several studies (Paige and Whitham 1987; Paige 1992, 1994, unpublished data) have provided experimental evidence of enhanced fitness following herbivory in a natural system. However, these studies, and for that matter the majority of studies that consider the effects of herbivory on plant reproductive success, have been limited to the seed-bearing success achieved through maternal function (Snow and Lewis 1993; Schlichting and Delesalle 1997). Thus, an accurate picture of plant-herbivore interactions must also include the effects of herbivory on male fitness (Mutikainen and Delph 1996; Strauss et al. 1996). Using a combination of experimental and genetic approaches we show that ungulate herbivory on scarlet gilia, *Ipomopsis aggregata* (Polemoniaceae), results in an increase in paternal, as well as maternal, fitness. This study represents the first evidence of overcompensation in a natural system where both paternal and maternal components of fitness have been assessed.

MATERIAL AND METHODS

Study Sites and Organisms

Field studies were conducted during the summer of 1994 in a large population (>150,000 individuals) of scarlet gilia in the San Francisco Peaks near Flag-

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staff, Ariz. Scarlet gilia is a monocarpic, hermaphroditic, biennial/perennial herb that flowers from early July through late September (Paige 1992). Following germination, scarlet gilia develops eventually into a leafy rosette approximately 12 cm in diameter. After 1–8 yr in a vegetative state, it sends up a single stalk that flowers, reproduces once, and then dies. Hence it is reproductive for only 1 yr making it ideal for acquiring measures of lifetime fitness. Scarlet gilia is self-incompatible and pollinated by two species of hummingbird—the rufous hummingbird, *Selasphorus rufus,* and the broad-tailed hummingbird, *Selasphorus platycercus*—and a single species of hawkmoth, the white-lined sphinx, *Hyles lineata.*

Previous studies (Paige and Whitham 1987; Paige 1992, 1994, unpublished data) in Arizona have shown that during the period of stem elongation, on the average 77% (range 64%–91%) of all plants are browsed by mule deer, *Odocoileus hemionus,* and elk, *Cervus elaphus.* Of these, 80% have approximately 95% of their aboveground biomass consumed, being browsed down to a height of 1–2 cm. Removal of the single inflorescence stimulates the production of, on the average, five new flowering stalks from dormant lateral buds along the remaining portion of the plant's stem. This change in plant architecture results in an increase in flower and fruit production. Because there are no significant differences between browsed and unbrowsed individuals in the number of seeds produced per fruit, seed mass, germination success, or subsequent seedling survival, an increase in total fruits produced by browsed plants results in an increase in maternal fitness (Paige and Whitham 1987; Paige 1992, 1994, unpublished data).

Effects of Ungulate Herbivory on Paternal Fitness

To assess the effects of ungulate herbivory on paternal fitness, the following three experiments were conducted: a hand-pollination experiment, a simulated hummingbird-pollination experiment, and a natural pollination experiment followed by a paternity analysis. In addition, the following floral traits were measured to assess potential herbivore-induced changes in floral morphology that could affect pollen transport: corolla length, stigma and style length at receptivity, width of the corolla opening, and placement of the anthers (insertion, exsertion, and maximum distance between the anthers). Measurements were taken on two flowers from each of 25 randomly selected browsed and 26 randomly selected unbrowsed plants.

The hand-pollination experiment was designed to assess the effects of pollen quality (as measured by the number of seeds sired per fruit, seed size, and germination success) between browsed and unbrowsed ''males.'' This experiment, by design, ignores potential differences in pollen production and floral morphology between browsed (B) and unbrowsed (U) fathers that could affect pollen transport. For this experiment, 40 focal ''female'' plants were selected within a 100 × 50 m grid covering approximately two-thirds of the entire population. The grid was divided into 10 columns spaced 10 m apart. Within each column, four focal females (two browsed and two unbrowsed), spaced 10 m apart, were selected; female order was shifted by one in each column (e.g., BBUU in col. 1 to UBBU in col. 2 to UUBB in col. 3, and so on). Two ''male'' plants (i.e., one browsed and one unbrowsed) were selected approximately 10 m from each focal

female in a randomly determined direction. All plants were selected prior to bud break and were covered with nylon tricot–covered wire cages to exclude pollinators and herbivores. Following bud break, receptive stigmas on focal females were hand-saturated with pollen using the two to three outermost dehiscing anthers from a single flower from each paired male. Flowers were bagged with nylon tricot mesh, and fruits were collected at the time of dehiscence. Complete data sets where two fruits were sired by both browsed and unbrowsed males were retrieved from 29 of the 40 plants for analysis (the remaining plants either did not set fruit or one of the treatments was missing and thus excluded from the analysis).

The hummingbird-pollination experiment was designed primarily to assess the effects of potential differences in floral morphology on pollen transport by hummingbirds and consequent numbers and qualities of seeds sired by browsed versus unbrowsed males. The design of the hummingbird experiment was identical to the hand-pollination experiment described above with the following two exceptions. Twenty focal females were used instead of 40, and pollinations from males to focal females were carried out using a stuffed hummingbird. Pollinations were accomplished by probing the hummingbird's bill into the corolla of a donor flower with dehiscing anthers and then into the corolla of a receptive recipient flower. The number of probes were standardized to two, the mean number of hummingbird probes per flower observed in the field, with each lasting approximately 1 s. The hummingbird's bill was cleansed with 70% ethyl alcohol (ETOH) following each cross and dried prior to performing the next cross. Flowers were bagged with nylon tricot mesh, and fruits were collected on dehiscence. Complete data sets where fruits were sired by both browsed and unbrowsed males were retrieved from 10 of the 20 plants for analysis (as in the experiment above, the remaining plants either did not set fruit or one of the treatments was missing and thus excluded from the analysis). For both experiments, numbers of seeds per fruit were counted, and seeds were individually weighed. For the hand-pollination experiment seeds were germinated on #1 Whatman filter paper in moist petri plates to assess germination success. In both experiments a split-plot design was conducted on number of seeds produced per fruit and seed weight.

The natural pollination experiment and genetic analysis was designed to assess the effects of herbivory on paternal fitness under more natural conditions. This experiment was conducted in a $24 \times 12 \times 6$ ft screen flight cage. Ten plants, five browsed and five unbrowsed, were transplanted from the study population into 1-gal pots and placed in the flight cage prior to flowering. Translocated plants were growing at least 10 m apart to minimize genetic similarities (Campbell 1991) and were matched for size (using stem diameter; Paige 1992, 1994). On flowering, one rufous hummingbird and later two white-lined sphinx moths were released into the flight cage and allowed to feed and pollinate freely for approximately 3 wk. Both the hummingbird and moths appeared to feed normally on scarlet gilia, although the hummingbird spent a portion of its first day trying to escape the flight cage before settling down to feed. A hummingbird feeder was also available to supplement pollinators. Fruits were bagged with ny-

lon tricot mesh. On dehiscence 44 fruits (approximately four per plant) and maternal tissues were collected for paternity analysis.

Following collection, parental leaf material was placed on dry ice, shipped to the University of Illinois at Urbana-Champaign, and stored at $-70°C$ until extraction. We extracted DNA from each of the 10 maternal plants and 44 offspring (an average of four per plant) grown from collected seed, using cetrimonium bromide (CTAB) (Weising et al. 1995). Following extraction, each DNA sample was quantified and diluted to a concentration of 25 ng/µL for polymerase chain reaction (PCR). Each reaction contained 0.5U of Taq polymerase, 0.1 mM of each deoxyribonucleoside triphosphate (dNTP), 0.2 µM of an Operon 10 base-primer (from kits A & C), 1× PCR buffer (20 mM Tris-HCl, 50 mM KCl), 2 mM $MgCl_2$, 25 ng of DNA, and sterile water to a final volume of 25 µL. The DNA, PCR buffer, primer, $MgCl_2$, and water were combined to a volume of 15 µL, capped with 10 µL of liquid wax, placed in a thermal cycler, and subjected to a ''hot start'' (Chou et al. 1992). Following the hot start, Taq polymerase, dNTPs and water were added to a final volume of 25 µL. The samples were then subjected to the following RAPD-PCR program: (1) 3 min at 94°C, (2) 30 s at 94°C to denature the DNA, (3) 30 s at 36°C to anneal the primer, (4) 1.5 min at 72°C for primer extension, and (5) a final extension for 10 min at 75°C (Williams et al. 1990). Steps 2–4 were repeated 44 times. The end product was run on a 1% agarose gel stained with ethidium bromide and visualized under UV light. To assign parentage, gels were then photographed and scored for parental bands unique to either browsed or unbrowsed individuals.

To assess potential confounding effects of differences in pollen production and/or pollen viability, 40 flowers, two from each of 10 randomly selected browsed plants and two from each of 10 randomly selected unbrowsed plants, were collected at the initiation of anther dehiscence for pollen counts and viability assessments. Pollen counts were conducted using a Coulter Counter (Harder et al. 1985). Pollen viability was assessed using a nitro blue tetrazolium stain (Hauser and Morrison 1964).

Effects of Ungulate Herbivory on Maternal Fitness

An assessment of maternal fitness was also made to confirm previous results (Paige and Whitham 1987; Paige 1992, 1994, unpublished data) that browsed plants have higher fitness. To accomplish this, 25 plants—10 browsed once, five secondarily browsed (i.e., browsed more than once), and 10 uneaten controls—were randomly selected and matched for size (stem diameter). These plants were compared in terms of numbers of flowers and fruits produced at the end of the flowering season.

RESULTS AND DISCUSSION

Among the floral traits measured, two showed significant differences between browsed and unbrowsed plants (MANOVA, $F = 2.83$, df = 6, 43, $P = .021$). Browsed plants produced significantly narrower corolla openings (3.01 ± 0.09 mm vs. 3.39 ± 0.09 mm, $F = 5.73$, df = 1, 48, $P = .021$) with shorter styles

(30.9 $\pm$ 1.03 mm vs. 34.5 $\pm$ 1.00 mm, $F = 3.95$, df $= 1$, 48, $P = .053$) than plants that were not browsed. No significant differences were found for corolla length (33.00 $\pm$ 0.87 mm vs. 33.04 $\pm$ 0.85 mm, $F = 0.00$, df $= 1$, 48, $P = .983$), anther insertion (-3.31 ± 0.34 mm vs. -3.79 ± 0.34 mm, $F = 0.616$, df $= 1$, 48, $P = .436$), anther exsertion (0.28 $\pm$ 0.23 mm vs. 0.42 $\pm$ 0.22 mm, $F = 0.113$, df $= 1$, 48, $P = .738$), or maximum distance between the inner- and outermost anthers (3.67$\pm$ 0.35 mm vs. 4.21 $\pm$ 0.34 mm, $F = 0.751$, df $= 1$, 48, $P = .391$) for browsed versus unbrowsed plants, respectively. It is possible that the observed morphological differences could alter both the amount of pollen transported and the amount of pollen received. For example, narrower corollas could result in a decrease in the amount of pollen transported on the crown and chin of a hummingbird, the ultimate effect being a decrease in the number of seeds sired by browsed fathers. Shorter styles could result in either an increase in the amount of pollen received, funneling more onto the stigma, or a decrease if more self-pollen is carried to the more-inserted stigma from the relatively more-exserted anthers. (In spite of being a protandrous plant there is usually some residual pollen remaining and/or occasional overlap between the expression of male and female traits.)

Results of both the first and second experiments (i.e., the hand-pollination experiment and the hummingbird experiment) gave virtually identical results. In both experiments there were no significant differences between seeds sired by browsed or unbrowsed males in terms of the number of seeds produced per fruit ($F = 0.52$, df $= 1$, 27, $P = .48$; $F = 0.05$, df $= 1$, 8, $P = .82$, for hand-pollination and hummingbird experiments, respectively) or seed mass ($F = 1.74$, df $= 1$, 27, $P = .19$; $F = 0.82$, df $= 1$, 8, $P = .38$, for hand-pollination and hummingbird experiments, respectively; table 1). This was true whether browsed or unbrowsed males were crossed with browsed or unbrowsed females ($F = 0.12$, df $= 1$, 27, $P = .74$; $F = 0.00$, df $= 1$, 8, $P = .99$ for number of seeds produced per fruit and $F = 0.02$, df $= 1$, 27, $P = .89$; $F = 0.12$, df $= 1$, 8, $P = .74$ for seed weight for hand-pollination and hummingbird experiments, respectively). In addition, there were no significant interactions between browsed and unbrowsed females and browsed and unbrowsed males for either number of seeds per fruit or seed mass in either experiment ($P > .12$). Furthermore, there were no significant differences between seeds sired by browsed or unbrowsed males in terms of percentage germination (data were collected only from the hand-pollination experiment). This was true whether browsed and unbrowsed males were crossed with browsed females (78% vs. 79% germination for browsed vs. unbrowsed males, $\chi^2 = 0.0006$, df $= 1$, $P = .95$) or unbrowsed females (75% vs. 69% germination for browsed vs. unbrowsed males, $\chi^2 = 0.199$, df $= 1$, $P = .70$; table 1). There were also no significant differences among treatments ($\chi^2 = 4.28$, df $= 3$, $P > .20$). Thus, results of the hand-pollination experiment indicated that there were no significant differences in pollen viability. This result was further substantiated from pollen counts and viability analyses, which showed no significant differences between browsed and unbrowsed plants ($t = 0.04$, df $= 39$, $P = .66$ and $t = 0.84$, df $= 16$, $P = .41$, for pollen counts and viability analyses, respectively; table 1). Similarly, results

TABLE 1

THREE EXPERIMENTS CONDUCTED TO ASSESS THE EFFECTS OF UNGULATE HERBIVORY
ON PATERNAL FITNESS TRAITS OF SCARLET GILIA

	Browsed Males	Unbrowsed Males	P^*
Experiment 1—hand-pollination:			
Seeds/fruit:			
Browsed females	$8.48 \pm .89$	$7.21 \pm .78$	N.S.
Unbrowsed females	$7.10 \pm .89$	$7.20 \pm .88$	N.S.
Seed mass (mg):			
Browsed females	$1.76 \pm .13$	$1.49 \pm .11$	N.S.
Unbrowsed females	$1.55 \pm .13$	$1.55 \pm .12$	N.S.
% germination:			
Browsed females	78	79	N.S.
Unbrowsed females	75	69	N.S.
No. pollen grains/flower†	$17,738 \pm 2,026$	$16,680 \pm 1,262$	N.S.
Pollen viability/flower† (%)	61.4 ± 4.6	68.9 ± 1.9	N.S.
Experiment 2—simulated hummingbird pollination:			
Seeds/fruit:			
Browsed females	5.63 ± 1.67	3.63 ± 1.67	N.S.
Unbrowsed females	4.57 ± 1.79	5.57 ± 1.79	N.S.
Seed mass (mg):			
Browsed females	$1.54 \pm .20$	$1.70 \pm .20$	N.S.
Unbrowsed females	$1.45 \pm .22$	$1.72 \pm .22$	N.S.
Experiment 3—paternity analysis:			
Predicted offspring sired	19.1	8.9	
Observed offspring sired	19.0	9.0	N.S.

NOTE.—In experiments 1 and 2, browsed and unbrowsed males were crossed with browsed and un-browsed females to assess components of male fitness. Browsed and unbrowsed males were paired with single browsed or unbrowsed females (see text for details). Means ± 1 SE of the mean are shown.
* See text for statistical tests.
† Pollen counts and viability analyses were conducted on a separate set of browsed and unbrowsed plants than those used for the remaining measures in experiment 1.

of the hummingbird-pollination experiment indicated that observed differences in floral morphologies between browsed and unbrowsed plants did not translate into differences in paternal success as measured by the number and quality of seeds sired (table 1).

As in previous studies (Paige and Whitham 1987; Paige 1992, 1994, unpublished data), browsed plants, even when secondarily browsed, produced significantly more flowers than unbrowsed plants (222.4 ± 23.8 and 209.7 ± 34.9 vs. 94.3 ± 23.8 flowers for browsed plants and secondarily browsed plants vs. unbrowsed plants, $F = 8.19$, df = 2, 21, $P = .002$) and fruits (97.7 ± 9.07 and 77.1 ± 13.3 vs. 42.9 ± 9.07 fruits for browsed plants and secondarily browsed plants vs. unbrowsed plants, $F = 9.32$, df = 2, 21, $P = .001$; fig. 1). It is also important to note that as in previous years (Paige and Whitham 1987; Paige 1992, 1994), there were no significant differences in the number of seeds/fruit, seed weights, or germination success between browsed and unbrowsed plants, consistent with the paternal experiments above (see table 1). These results are not due to biased size selection, given that roots have consistently been larger in browsed and experimentally clipped plants (in which 95% of the aboveground
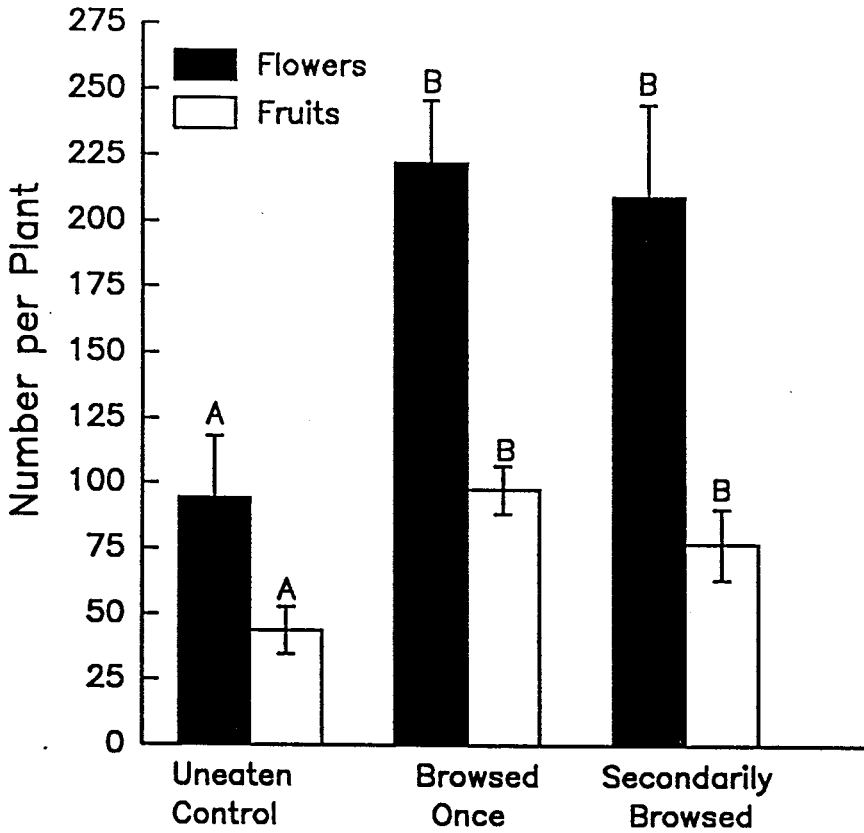
FIG. 1.—Comparison of two components of maternal fitness—flower production and fruit set—for plants that were browsed once, more than once (i.e., secondarily browsed), and uneaten controls. Means with the same letters for flowers and for fruits show no significant differences at the .05 level, least significant difference multiple-range test.

biomass has been removed) when measured at the end of the flowering season (Paige and Whitham 1987; Paige 1992, 1994), as argued by Bergelson et al. (1996). Previous studies have clearly shown that the roots (diameter, biomass) of browsed plants significantly increase through time following herbivory, but stem diameters do not (see Paige 1994). For example, experiments in which root diameters were measured on the same individual plants, early and late in the flowering season, showed significant increases in root diameter when naturally browsed or experimentally clipped down to a height of 1 cm (removing approximately 95% of the aboveground biomass, simulating the most common level of herbivory), while there was no significant change in root diameters of undamaged controls (fig. 2; ANCOVA, using stem diameter as a covariate, $F = 4.37$, df $= 5, 55$, $P = .002$; ANOVA, without a covariate, $F = 4.19$, df $= 5, 56$, $P = .0026$).

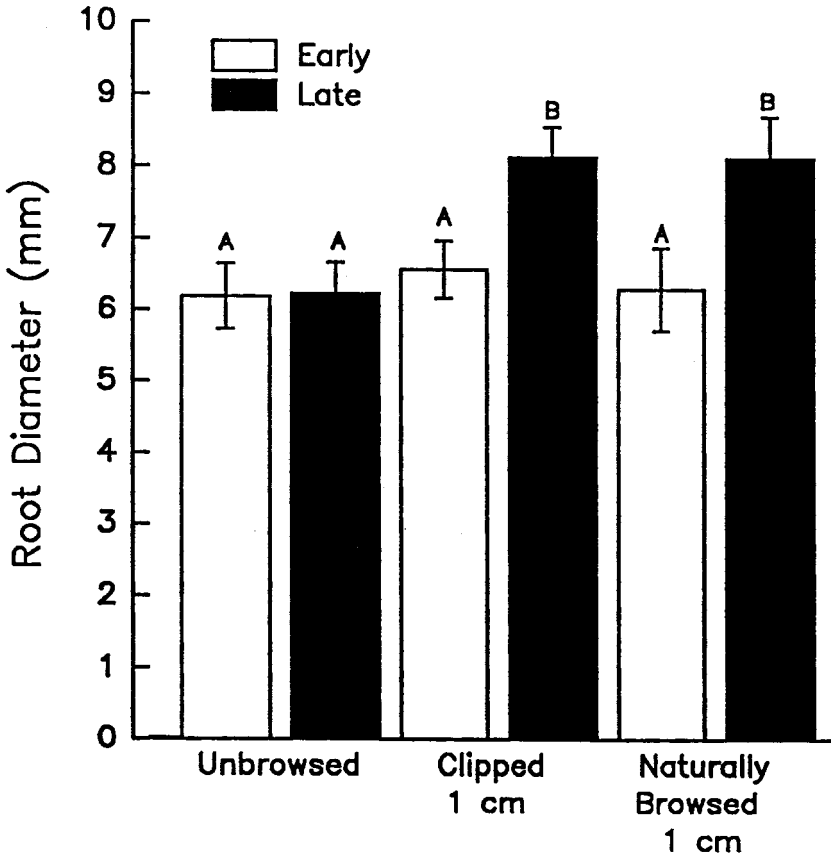Using the above data we calculated the number of viable pollen grains pro-

Fig. 2.—Comparison of root diameters early (late May) and late (early October) in the 1996 Arizona flowering season for plants that were naturally browsed, experimentally clipped, and uneaten controls. Means with the same letters show no significant differences at the .05 level, least significant difference multiple-range test.

duced per plant with the potential to sire offspring for both browsed and unbrowsed plants. We multiplied the mean number of flowers produced per plant by the mean number of viable pollen grains produced per flower (table 1) by the minimum visitation rate by pollinators (percentage of fruit set). Results showed that, at the individual plant level, browsed plants produced 2.16-fold as much viable pollen as plants that were not browsed (1,063,382 vs. 493,103 viable pollen grains per plant for browsed vs. unbrowsed plants, respectively). The increase in pollen production by browsed plants is due to an increase in the number of flowers produced per plant, given that there were no significant differences in the number of viable pollen grains produced per flower and in the minimum visitation rate, as measured by the percentage fruit set per plant ($48.5\% \pm 2.9\%$ vs. $45.8\% \pm 4.3\%$ and $38.8\% \pm 3.6\%$ for unbrowsed plants,

plants browsed once, and plants secondarily browsed, respectively; $F = 1.29$, df $= 2, 22$, $P = .30$).

   The third experiment (i.e., the genetic analysis), which was designed to assess naturally the paternal contribution of browsed versus unbrowsed individuals, confirmed that higher flower and, hence, higher pollen production by browsed plants translates into an increase in paternal fitness. Among 19 RAPD primers screened, eight were polymorphic, allowing us to categorize (to browsed or unbrowsed sires) or definitively assign the paternity of 28 of the 44 offspring reared from equal numbers of browsed and unbrowsed parents. As an internal control on the reliability of the technique, we blindly assigned or categorized 32 of the 44 offspring back to known mothers or to a group of dams (either browsed or unbrowsed). In all 32 cases 100% of the offspring were correctly assigned to known mothers or categorized to browsed or unbrowsed dams giving us confidence in assigning or categorizing paternity. Among the 28 paternally assigned offspring, 19 were sired by browsed fathers and only nine were sired by unbrowsed fathers. This represents an approximate 2.11-fold increase in paternal fitness by browsed over unbrowsed individuals. This is in accord with the 2.16-fold higher pollen production by plants that were browsed, with no significant difference in either the ratio of browsed and unbrowsed flower production to the number of browsed and unbrowsed offspring produced ($\chi^2 = 0.068$, df $= 1$, $P > .80$) or the number of predicted (based on the 2.16-fold increase in pollen production) to observed browsed and unbrowsed offspring produced ($\chi^2 = 0.0008$, df $= 1$, $P > .95$, table 1). Thus, these results indicate that an increase in flower and pollen production directly translates into an increase in paternal fitness. In addition, as in previous years (Paige 1992), the majority of plants were ungulate browsed during the flowering season (83% in this study). Thus, not only was there an approximate twofold advantage at the individual plant level in terms of pollen production, but there were also 4.9 times as many browsed plants as unbrowsed plants in the population, giving browsed plants an even greater advantage in contributing pollen (a calculated 8.7-fold advantage).

   Overall, the results of this study show that ungulate herbivory on scarlet gilia results in an increase in paternal, as well as maternal, fitness. Although browsed plants produced approximately two times as many flowers per plant as plants that were not browsed, no reductions in either the number of pollen grains produced per flower or pollen viability were found. In addition, even though browsed plants produced narrower corollas and shorter styles than plants that were not browsed, our experiments demonstrated that these differences did not impede the transport of pollen, such that browsed and unbrowsed plants sired and set equal numbers and qualities of seed. Furthermore, given that visitation rates on a per flower basis were not significantly different and that browsed plants produced twice as many flowers and, as a result, twice as much pollen as unbrowsed plants, we conclude that browsing in scarlet gilia increases the paternal component of fitness.

   These results represent the first study showing evidence of overcompensation where both paternal and maternal components of fitness have been assessed.

Furthermore, these results are of general importance in that the paternal component of fitness is rarely examined in studies of plant-herbivore interactions (Bertin 1982; Ennos and Dodson 1987; Schlichting and Devlin 1989; Broyles and Wyatt 1990; Devlin and Ellstrand 1990) and could alter the interpretation of herbivore impacts (Strauss et al. 1996). For example, there are many cases where plants produce more flowers following apical damage but where fruit set is unaffected or reduced (Hendrix 1979; Inouye 1982; Maschinski and Whitham 1989; Reichman and Smith 1991). In such cases the paternal component of fitness could be enhanced, ultimately resulting in an overall increase in total fitness.

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