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HERBIVORY AND *IPOMOPSIS AGGREGATA:*
DIFFERENCES IN RESPONSE, DIFFERENCES IN EXPERIMENTAL PROTOCOL: A REPLY TO BERGELSON AND CRAWLEY

Recent studies have shown that, when mule deer and elk remove 95% or more of the aboveground biomass of the monocarpic biennial scarlet gilia, *Ipomopsis aggregata,* seed production and subsequent seedling survival averaged 2.4 times that of the uneaten controls (Paige and Whitham 1987; Mopper et al. 1991; Whitham et al. 1991; Paige 1992a, 1992b). The increase in relative fitness was largely because of an architectural change in the plant; ungulate removal of scarlet gilia's single inflorescence resulted in the production of multiple flowering stalks due to the release of apical dominance.

Studies by Bergelson and Crawley (1992a, 1992b) extend these results by looking at the generality of scarlet gilia's response to ungulate herbivory over a substantial portion of its geographical range. From the results of their work they conclude, first, that over much of its range, scarlet gilia does not overcompensate for grazing in the way that experiments conducted in Flagstaff, Arizona, demonstrated (Paige and Whitham 1987). Second, the presence of ungulate grazers leads to a substantial decrease in plant density despite the fact that grazing on young bolting shoots had very little influence on fruit production.

Although Bergelson and Crawley (1992a, 1992b) claim that their experimental protocol matched that used elsewhere (Paige and Whitham 1987), there were a number of differences in the design of their experiments that altered the outcome and interpretation of their results. Here I wish to address issues of design and contribute further to the discussion by presenting additional data.

CLIPPING REGIME AND INDIVIDUAL FITNESS

In both of their studies, Bergelson and Crawley (1992a, 1992b) incorporated an experimental clipping regime different from that of a previous study (Paige and Whitham 1987). They removed only 10%–75% of the aboveground biomass, leaving approximately 8 cm of the main shoot, whereas we removed 95% of the aboveground biomass, leaving approximately 1 cm of the main shoot (Paige and Whitham 1987). Bergelson and Crawley stated that the removal of less tissue per plant represents a more rigorous test of the growth compensation hypothesis, which biases their results toward finding evidence of overcompensation. Here I show that the removal of more tissue results in greater relative fitness than the removal of less tissue, contrary to the reasoning of Bergelson and Crawley.

To test Bergelson and Crawley's assumption, I took relative fitness measures

TABLE 1

ANCOVA FOR THE EFFECTS OF DIFFERENTIAL HERBIVORY ON FLOWER PRODUCTION, FRUIT
PRODUCTION, AND STEM DIAMETER IN SCARLET GILIA, *IPOMOPSIS AGGREGATA*,
IN 1988 AT THE MUSEUM OF NORTHERN ARIZONA IN FLAGSTAFF

Fitness Measure	95% Biomass Removed ($N = 10$)	62% (11%–81%) Biomass Removed ($N = 13$)	Uneaten Control ($N = 10$)	F	df	P
No. of flowers	302.3 ± 46.8^a	195.6 ± 28.1^b	124.7 ± 16.6^c	7.34	2,29	.003
No. of fruits	102.8 ± 15.9^a	66.3 ± 9.5^b	54.9 ± 7.3^b	4.50	2,29	.019
Stem diameter (mm)	$6.2 \pm .68^a$	$7.1 \pm .70^a$	$5.2 \pm .42^a$	1.80	2,30	.183

NOTE.—Means ($\pm$ 1 SE) with the same letters show no significant differences at the .05 level: Student-Newman-Keuls multiple-range test. Stem diameter was used as a covariate to further adjust for plant size differences. Tests were run on log-transformed or log(Y + 1)-transformed data to equalize variance.

from 33 plants matched for size in late September 1988 at the Museum of Northern Arizona (MNA) in Flagstaff. Because stem diameter is a relatively accurate measure of plant size (positively correlated, e.g., with plant height, $R^2 = 0.571$, $N = 60$, $P < .0001$; biomass, $R^2 = 0.535$, $N = 25$, $P < .0001$; and flower production, $R^2 = 0.655$, $N = 25$, $P < .0001$), plants were matched on the basis of stem diameter (basal stem diameters covered the full range of sizes within the population, from 3 to 10 mm, with no significant differences between treatments; see table 1). Plants were selected along random transects through the population. When a plant was encountered it was measured, and the next two plants of similar size from the two remaining treatment groups along the transect were incorporated. Thirteen plants had 62% (range 11%–81%; see below) of their aboveground biomass removed (with 8 or more cm of stem tissue remaining) by ungulate herbivores, 10 plants had approximately 95% of their aboveground biomass removed (leaving about 1 cm of stem tissue), and 10 uneaten plants served as controls.

In a second, more controlled comparison, 45 plants were matched for size (stem diameter range 5–10 mm) along randomly chosen transects (as above) in late September 1992 at MNA; 15 plants had been browsed 8 cm above the ground (removing approximately 69%, range 11%–85%, of the aboveground tissue; see below), 15 plants had been browsed 1 cm above the ground (removing approximately 96% of the aboveground tissue), and another 15 plants served as uneaten controls. No size differences existed among the three treatment groups (table 2). Previous studies (Paige and Whitham 1987; Paige 1992a) have failed to show significant differences in relative fitness between naturally browsed and experimentally clipped plants (which were chosen from the pool of uneaten individuals following natural herbivory), arguing that plant selectivity by herbivores had no effect on *Ipomopsis aggregata*'s ability to compensate or, alternatively, that herbivores were not selective. Thus, the treatment plants represent unbiased samples of all plants, which makes clipping experiments unnecessary.

Although no direct prebrowsing measures were made in either of the aforemen-

TABLE 2

ANCOVA FOR THE EFFECTS OF DIFFERENTIAL HERBIVORY ON FLOWER PRODUCTION,
FRUIT PRODUCTION, ROOTSTOCK DIAMETER, AND STEM DIAMETER IN SCARLET GILIA,
IPOMOPSIS AGGREGATA, IN 1992 AT THE MUSEUM OF NORTHERN ARIZONA IN FLAGSTAFF

Fitness Measure	96% Biomass Removed ($N = 15$)	69% (11%–85%) Biomass Removed ($N = 15$)	Uneaten Control ($N = 15$)	F	df	P
No. of flowers	460.6 ± 45.4^a	327.2 ± 23.1^b	202.7 ± 20.2^c	17.3	2,41	.0001
No. of fruits	229.7 ± 33.1^a	$180.1 \pm 14.8^{a,b}$	117.6 ± 16.1^b	5.96	2,41	.005
Rootstock diameter (mm)	$10.5 \pm .58^a$	8.2 ± 0.33^b	7.5 ± 0.39^b	17.6	2,41	.0001
Stem diameter (mm)	$7.3 \pm .35^a$	7.8 ± 0.38^a	6.9 ± 0.40^a	.97	2,42	.38

NOTE.—See note in table 1 for explanation.

tioned experiments, plants were similar in height and phenology at the time of browsing (K. N. Paige, personal observation). The following data support these observations. In 1988 and 1992, 92% and 100%, respectively, of all herbivory occurred early (mid- to late May) in the flowering season on this site. No herbivory has been observed prior to mid-May. Estimates were obtained by comparing levels of herbivory on 100 randomly selected plants in late May/early June to the levels of herbivory on 100 randomly selected plants at the end of the flowering season in late August/mid-September in 1988 and 1992, respectively. In addition, height measures on 87 randomly selected plants in mid- to late May 1988 and 45 plants selected in late May 1992 showed that plants averaged 21 cm (29%, 9–14 cm; 46%, 15–24 cm; 20%, 25–33 cm; 5% 40–43 cm) and 26 cm (2%, 9–14 cm; 49%, 15–24 cm; 38%, 25–34 cm; 9%, 35–44 cm; 2%, 45–52 cm) in height, respectively, during the time of browsing. Thus, plants with approximately 1 cm of stem tissue remaining had, on the average, 95% (range 89%–98%) and 96% (range 88%–98%) of their aboveground biomass removed by ungulate herbivores, whereas plants with approximately 8 cm of tissue remaining had, on the average, 62% (range 11%–81%) and 69% (11%–85%) of their aboveground biomass removed in 1988 and 1992, respectively.

Results from the MNA comparisons indicate that the removal of more tissue results in greater relative fitness than the removal of less tissue. Plants that had only 11%–85% of their aboveground biomass removed (with 8 or more cm of stem tissue remaining) were found to compensate equally, similar to Bergelson and Crawley's findings (tables 1, 2). But, when approximately 95% of the aboveground biomass was removed (leaving about 1 cm of stem tissue), plants produced significantly more flowers and fruits than either plants that had less (11%–85%) stem tissue removed or uneaten controls (tables 1, 2).

LEVEL OF CLIPPING AND NATURAL HERBIVORY

In addition, the level of clipping chosen by Bergelson and Crawley (1992*a*, 1992*b*) may not accurately reflect natural levels of browsing by ungulate herbivores. Censuses conducted along designated transects at the end of the flowering

season in four different populations (on Fern Mountain in 1985–1987 and 1992, MNA in 1992, and two populations along Highway 151 in 1992) to assess natural levels of browsing in Arizona showed that, on the average, 80% of all browsed plants had 95% or more of their aboveground biomass removed by ungulate herbivores each year (on Fern Mountain: 73% in 1985, $N = 168$; 75% in 1986, $N = 146$; 87% in 1987, $N = 151$; 92% in 1992, $N = 71$; at MNA: 71% in 1992, $N = 42$; two populations along Highway 151: 76%, $N = 54$ and 84%, $N = 49$, in 1992).

Because differences in fitness can occur because of the amount of tissue removed (see above), it is particularly important to simulate as closely as possible the levels of herbivory that naturally occur in the field. If the levels of ungulate herbivory from Arizona are indicative of the levels of ungulate herbivory within the sites Bergelson and Crawley studied, then their clipping regime was not an accurate depiction of natural levels of compensation, which thereby biases their results against finding evidence of overcompensation. Although Bergelson and Crawley (1992a, 1992b) did not assess or discuss natural levels of ungulate herbivory on any of their study sites, personal observation of sites in Wyoming indicate similar high levels of ungulate herbivory.

THE EFFECTS OF TIMING

Another difference deals with the timing of Bergelson and Crawley's (1992a) clipping experiments. They applied clipping treatments anywhere from May 18 to June 26, decreasing the period for growth compensation by as much as 6 wk, or one-half (specific clipping dates are not given for any of the 14 populations studied by Bergelson and Crawley). They reasoned that, because there was "little or no bud development" on any of the experimental plants, clipping was completed within 2–3 wk of the initiation of stem elongation. If plants had any sign of bud development at all, plants were likely clipped 5–6 wk (the time it takes for flower bud formation) following the initiation of stem elongation (which would correspond to clipping dates of mid- to late June; K. N. Paige, unpublished data). This is likely a conservative estimate since phenologically scarlet gilia is more advanced at this northerly latitude (J. Bergelson and M. J. Crawley, personal communication), elongating as early as mid-April (K. N. Paige, personal observation). Furthermore, on the average, in Bergelson and Crawley's experiments, plants were clipped after achieving 58% of their final height, whereas in our studies, plants were naturally browsed or experimentally clipped after achieving only 36% of their final height (Paige and Whitham 1987; Paige 1992a). These differences also suggest substantial phenological differences between our experiments. Because the timing of damage is important in terms of growth compensation and ultimate plant fitness (Maschinski and Whitham 1989; Whitham et al. 1991; Paige 1992a) and the majority (91%) of plants are naturally browsed early (mid- to late May) in the season (Paige and Whitham 1987; Paige 1992a, 1992b), clipping late (mid- to late June) will bias results toward decreased fitness.

To assess the effects of timing of herbivory on the reproductive success of scarlet gilia, I randomly selected 37 plants early in the flowering season at North-

TABLE 3

ANCOVA FOR THE EFFECTS OF CLIPPING ON THREE DIFFERENT DATES IN 1986 ON FLOWER AND
FRUIT PRODUCTION IN SCARLET GILIA, *IPOMOPSIS AGGREGATA*,
AT NORTHLAND PRESS IN FLAGSTAFF, ARIZONA

	CLIPPING DATE					
FITNESS MEASURE	May 18 ($N = 7$)	June 17 ($N = 15$)	July 1 ($N = 15$)	F	df	P
No. of flowers	239.4 ± 45.8^a	$151.1 \pm 24.6^{a,b}$	89.3 ± 10.5^b	3.17	2,33	.05
No. of fruits	207.3 ± 38.4^a	102.7 ± 18.0^b	44.2 ± 6.0^c	6.71	2,33	.004

NOTE.—Means ($\pm$ 1 SE) with the same letters show no significant differences at the .05 level: Student-Newman-Keuls multiple-range test. Stem diameter was used as a covariate to adjust for plant size differences. Tests were run on log-transformed or $\log(Y + 1)$-transformed data to equalize variance.

land Press in Flagstaff and experimentally clipped them on one of three dates. Seven plants were clipped on May 18, 1986, 15 plants were clipped on June 17, 1986, and 15 plants were clipped on July 1, 1986, with 95% or more of the aboveground biomass removed (plants were clipped down to approximately 1 cm in height). At the end of the flowering season (late August), plants were compared in terms of the numbers of flowers and fruits produced.

Results of these studies showed that plants clipped in May produced significantly more flowers than plants clipped in July and significantly more fruits than plants clipped in June or July (table 3). Because Bergelson and Crawley (1992*a*) did not include naturally browsed plants (correctly adjusted for size; see below) for comparison, it is difficult to assess the effects of clipping date on fitness compensation. Overall, such staggered clipping likely decreased their chances of determining the actual degree to which populations of scarlet gilia can compensate.

Bergelson and Crawley (1992*a*) also show, for all response variables (maximal reproductive output, fruits, weight, root weight, phenology, and branch number), a significant interaction between the effect of site and the effect of clipping. They suggest that such an interaction is indicative of site-specific effects of browsing on the performance of individuals. Although this may be true, variation in clipping date alone would give similar results, with later clipping resulting in a decrease in fitness, a reduction in weight, and a delay in phenology.

NATURAL HERBIVORY AND INDIVIDUAL FITNESS: MATCHING PLANTS FOR SIZE

Bergelson and Crawley (1992*b*) also compared plants that were naturally browsed to those that were not browsed in 14 populations across the geographical range of scarlet gilia. Browsed and unbrowsed plants were matched for size on the basis of rootstock diameter, measured at the top of the root. M. J. Crawley (personal communication) felt that rootstock diameter was a better measure of plant size than stem diameter as used in our studies (stem diameter measures were taken at the base of the stem above the top of the rootstock). Their justification for

using rootstock diameter comes from a clipping experiment in which they re-
moved 10%–75% of the aboveground biomass, leaving approximately 8 cm of the
main shoot. The results of their experiment were unquestionably clear: rootstocks
did not increase in size as a result of their chosen level of clipping. Using con-
trolled comparisons, however, I show that rootstock diameter does increase when
95% or more of the aboveground biomass is removed by ungulate herbivores,
which from all indications is the most common level of ungulate herbivory (with
an average of 80% of all browsed plants having 95% of their aboveground biomass
removed). Thus, use of rootstock diameter as a measure of plant size could have
seriously biased their results.

For example, results obtained from the previously described comparison (see
Clipping Regime and Individual Fitness, above) in which 15 plants were naturally
browsed 1 cm above the ground (removing an average of 96% of the aboveground
biomass), 15 plants were browsed 8 cm above the ground (removing an average
of 69% of the aboveground biomass), and 15 uneaten plants served as controls
showed that plants in which 96% of the aboveground biomass was removed had
significantly larger final rootstock diameters than plants in which an average of
69% of the aboveground biomass was removed or uneaten control plants (table
2). No significant differences in stem diameter were found between the three
treatment groups (table 2). Previous studies (K. N. Paige, unpublished data) have
shown that stem diameters do not significantly change over time (5.21 ± 0.23
early versus 5.61 ± 0.16 late, paired $t = 1.58$, df $= 32$, $P > .13$), whereas
rootstock widths do (see experimental clipping results below).

Additional comparisons in mid-July 1992 at MNA, among 30 plants that were
naturally browsed (15 having approximately 96% and 15 having approximately
60% of their aboveground biomass removed) and 15 uneaten controls, matched
for size (stem diameter), showed that both root width and root biomass became
significantly larger following the removal of 96% of the aboveground biomass
(table 4). However, plants with 60% of their aboveground biomass removed (aver-
age height at the time of browsing $= 26$ cm; average browse height $= 10.4$ cm)
did not show a significant increase in either root diameter or mass. Furthermore,
on another site in Flagstaff, Arizona (Fern Mountain), comparisons between 15
naturally browsed (having approximately 95% of their aboveground biomass re-
moved) and 12 unbrowsed plants, matched for size (stem diameters $= 4.2 \pm 0.28$
and 4.1 ± 0.47 mm, respectively, $t = 0.22$, df $= 25$, $P > .82$), showed that
browsed plants had significantly larger rootstock widths than uneaten control
plants (6.6 ± 0.36 versus 3.8 ± 0.24 mm, respectively, $t = 6.01$, df $= 25$, $P <$
.0001).

Changes in rootstock width and biomass were also monitored through time.
On May 27, 1986, 115 bolting individuals of scarlet gilia were matched for size
(stem diameter and height) at MNA. Plants were randomly assigned to one of
two groups: a treatment group in which approximately 95% of the aboveground
biomass was experimentally clipped or an uneaten control group. Twenty-five
plants, 15 treatment plants, and 10 control plants (except on May 27 there were
eight treatment and seven control plants measured) were destructively sampled
over a 5-wk period on May 27 and July 1, 9, 15, and 22. Basal stem diameter was

TABLE 4

ANCOVA FOR THE EFFECTS OF DIFFERENTIAL HERBIVORY ON ROOTSTOCK DIAMETER, ROOT BIOMASS,
AND STEM DIAMETER IN SCARLET GILIA, *IPOMOPSIS AGGREGATA*, IN 1992
AT THE MUSEUM OF NORTHERN ARIZONA IN FLAGSTAFF

Fitness Measure	96% Biomass Removed (N = 15)	60% Biomass Removed (N = 15)	Uneaten Control (N = 15)	F	df	P
Rootstock diameter (mm)	10.3 ± .49[a]	7.5 ± .60[b]	7.3 ± .49[b]	19.1	2,41	.0001
Root biomass (g)	4.6 ± .40[a]	2.9 ± .40[b]	3.3 ± .40[b]	5.02	2,41	.01
Stem diameter (mm)	6.5 ± .38[a]	6.7 ± .48[a]	6.5 ± .43[a]	.10	2,42	.90

NOTE.—See note in table 1 for explanation.

used as a covariate to adjust for the effects of plant size differences on rootstock widths and biomass. Results showed that both the widths and biomass of roots increased significantly in plants that were experimentally clipped (7.35 ± 0.33 versus 9.33 ± 0.51 mm, $F = 4.11$, df = 9, 104, $P < .0002$, for root diameter; 2.63 ± 0.24 versus 4.40 ± 0.38 g, $F = 4.68$, df = 9, 104, $P < .0001$, for root biomass, Student-Newman-Keuls multiple-range test, $P < .05$).

These results indicate that Bergelson and Crawley unknowingly mismatched plants for size in their survey of 14 naturally browsed populations, thus biasing their results toward finding equal or undercompensation. Using an ANCOVA and rootstock diameter as the covariate, they adjusted grazed and ungrazed plants for size (plants were measured late in the flowering season). As they point out, use of rootstock diameter requires that it is not itself affected by grazing. Results here, however, show that high levels of ungulate herbivory (in which 95% or more of the aboveground biomass is removed) result in an approximate 1.6-fold increase in rootstock diameter, whereas the removal of 75% or less does not result in an increase in rootstock diameter (consistent with the findings of Bergelson and Crawley). Therefore, the validity of their results are dependent on the amount of tissue removed by ungulate herbivores and the number of plants included in their analyses that had 95% or more of their aboveground biomass removed (i.e., plants that had 95% or more of their aboveground biomass removed would have been mistakenly mismatched with larger uneaten control plants as a result, which would have biased results toward equal or undercompensation). As noted above, from my own studies high levels of ungulate herbivory (in which 95% or more of the aboveground biomass is removed) appear to be the most common (similar levels were also noted in Wyoming).

When browsed and unbrowsed plants were correctly matched for size (using stem diameter as a covariate instead of root diameter) from Teton site 2, results were similar to those of a previous study (Paige and Whitham 1987). To demonstrate this, 20 plants were randomly selected from within the Teton population in early August 1990. Ten plants had been browsed 1 cm above the ground (having removed approximately 95% of the aboveground biomass), and 10 uneaten plants served as controls. Plants that were naturally browsed produced 2.4 times as many flowers (217.9 ± 57.5 [± 1 SE] versus 89.3 ± 15.7, $F = 9.09$, df = 2,17,

$P < .008$) and 1.9 times as many fruits (104.1 ± 20.8 versus 56.0 ± 9.3, $F = 4.45$, df = 2,17, $P < .05$) as plants that were not browsed. Tests were run on log-transformed data to equalize variance.

UNGULATE EXCLOSURES AND HERBIVORY

Bergelson and Crawley (1992*b*) also compared scarlet gilia populations inside and outside seven deer and elk exclosures found throughout the Rocky Mountains to determine whether gilia populations were benefiting from the presence of ungulate browsers outside the fence. They found consistently higher plant population densities inside the exclosure fences. Therefore, they concluded that the presence of ungulate herbivores led to a substantial decrease in plant density by increasing death rates at some stage in the plants' life cycle.

In the summer of 1990 I visited three of their sites (the Card Canyon exclosure in Logan, Utah, and Teton sites 1 and 2 in Grand Teton National Park, Wyoming). Both of the Teton sites (sewage treatment plants) contained sandy, highly disturbed soils within and dense pine/grassland outside the exclosures. Because scarlet gilia is a disturbance plant, it is not surprising that it is most abundant within the exclosures, particularly because of the fact that there were few sites for seedling establishment outside the exclosures. In fact, for four of the seven exclosures (Prairie City, Oregon; Cle Elum, Washington; Logan Canyon, Utah; and Teton site 1, Wyoming) scarlet gilia was virtually absent (zero to three plants) immediately outside the fence. This situation could result from ungulate herbivory or, alternatively, differences in disturbance regime (as is apparent for the two Teton sites visited) and/or the historical absence of scarlet gilia outside the fence. There is the possibility that during the construction of the exclosures higher disturbance inside the fence allowed the establishment of scarlet gilia. Unfortunately, Bergelson and Crawley (1992*b*) do not discuss methods used in establishing exclosures.

Overall, Bergelson and Crawley (1992*b*) conclude with the notion that ungulates decrease the survival rate of scarlet gilia by eating or trampling rosettes. However, our long-term studies on the interactions between ungulate browsers and scarlet gilia populations do not support such an idea; ungulate browsers do not feed on rosettes, and there is rarely mortality from ungulate trampling (Paige and Whitham 1987; Paige 1992*a*, 1992*b*; K. N. Paige unpublished data). Thus, the results of Bergelson and Crawley (1992*b*) do not unequivocally demonstrate that exposure to browsing by large ungulate herbivores brings about a marked reduction in the population density of scarlet gilia.

The results of these uncontrolled experiments of Bergelson and Crawley (1992*b*) contrast with findings from controlled experiments conducted in Flagstaff, Arizona. To examine the long-term effects of ungulate herbivory, five paired plots were established in 1989 at Northland Press, approximately 1 km south of MNA. Individuals of scarlet gilia were transplanted into 15-m^2 plots previously devoid of conspecifics early in the flowering season during the period of stem elongation (early June). All vegetation within the plots was left undisturbed so that seedling establishment could occur within normal competitive regimes. Five plots con-

TABLE 5

Fitness Effects of Ungulate Herbivores on *Ipomopsis aggregata* in Flagstaff, Arizona, from 1989–1991

Paired Plot Treatment	No. of Parents	Fruit Set of Parents*	Seedling Establishment†	Overwinter Survival of Seedlings‡
Browsed	5	18	14	2
Unbrowsed	5	4	4	0
Browsed	5	403	14	0
Unbrowsed	5	143	4	0
Browsed	8	433	73	22
Unbrowsed	8	152	11	3
Browsed	10	361	159	40
Unbrowsed	10	179	32	9
Browsed	20	286	140	36
Unbrowsed	20	146	85	20

* Paired $t = 8.66$, df $= 4$, $P < .001$.
† Paired $t = 5.03$, df $= 4$, $P < .007$.
‡ Paired $t = 2.72$, df $= 4$, $P < .053$.

tained 48 (5, 5, 8, 10, and 20) elongating plants that had been naturally browsed, and five additional plots contained 48 (5, 5, 8, 10, and 20) unbrowsed elongating plants. Plants were matched for stem diameter so that no size differences existed between the two treatment groups ($t = 0.187$, df $= 95$, $P = .855$). Browsed and unbrowsed plots were paired according to aspect, soil, and vegetation type. Plants were not protected from subsequent herbivory, and no additional herbivory occurred on the parental transplants. Transplants responded in a fashion similar to plants that were not transplanted (e.g., on the average fruit set of browsed plants was 2.4 times that of uneaten controls for both transplants and plants that were not transplanted; Paige 1992*a*; this article); thus the effects of transplanting are negligible.

The results of these experiments showed significantly higher parental fruit set (paired $t = 8.66$, df $= 4$, $P < .001$), seedling establishment (paired $t = 5.03$, df $= 4$, $P < .007$), and overwinter survival of rosettes (paired $t = 2.72$, df $= 4$, $P < .053$) for browsed individuals in comparison to unbrowsed individuals of scarlet gilia (table 5). Although Bergelson and Crawley (1992*a*) correctly pointed out that seeds produced by browsed individuals of *Ipomopsis aggregata* (and *Ipomopsis arizonica*; J. Maschinski and K. N. Paige, unpublished data) suffered a delay in maturation, what they failed to point out was that increased seed production and seedling establishment in browsed plots more than compensated for delayed maturation, which ultimately resulted in an increase in plant population size (for both *I. aggregata* and *I. arizonica*).

CONCLUSIONS

The results presented here indicate that the experimental protocol used by Bergelson and Crawley (1992*a*, 1992*b*) did not match that which I and my associ-

ates used. They incorporated a different clipping regime, clipped plants late in the flowering season, failed to note accurately and match the natural sequence of events (the natural timing and levels of ungulate herbivory), incorrectly matched plants for size when comparing naturally browsed plants to uneaten controls, and failed to use adequate or appropriate controls in a number of experiments, which biased their results toward reporting decreased fitness.

Although I would agree with Bergelson and Crawley that scarlet gilia does not overcompensate (i.e., does not gain a fitness advantage from being eaten) across its entire geographical range (K. N. Paige, unpublished data), I would disagree, based on results presented here (e.g., results from their Teton site 2 in Wyoming), that scarlet gilia shows evidence of overcompensation only in Flagstaff. Results presented here clearly suggest that additional experiments will be necessary before drawing any generalizations concerning the geographical effects of ungulate browsers on scarlet gilia.

Furthermore, the idea that the presence of ungulate browsers unequivocally leads to a considerable decrease in plant density is unsubstantiated. On-site visits, long-term replicated experiments, and long-term observations on the interactions between ungulate browsers and populations of scarlet gilia fail to lend support to such a supposition.

Last, I would like to comment on Bergelson and Crawley's (1992a, p. 881) contention that, "before much more energy is devoted to explaining the adaptive significance of overcompensation and to exploring mutualistic interactions between plants and their herbivores, we ought to find at least one clear case in which a species consistently and unambiguously benefits from being grazed." Overall, I think it is naive to think that different populations of any species will respond in the same fashion to the same selection pressure(s). I would argue that even a single case in which plants benefit from being eaten is worthy of explanation and provides a unique opportunity for deciphering the ecological conditions that favor selection toward mutualism rather than toward escalation of defenses. It is time to look beyond biases and preconceived notions that herbivory is always, unquestionably, detrimental to the plant.

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