CONSEQUENCES OF PREFORMATION FOR DYNAMIC RESOURCE ALLOCATION BY A CARNIVOROUS HERB, *PINGUICULA VULGARIS* (LENTIBULARIACEAE)¹

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When resource availability changes frequently and unpredictably, natural selection favors flexible resource allocation; however, such versatility may be compromised in perennial plants that differentiate leaves or flowers a year in advance of their development (preformation). We investigated resource allocation by the carnivorous perennial *Pinguicula vulgaris* to determine whether increased resource availability changes within-season allocation to growth, vegetative propagation, and reproduction. In response to resource supplementation (feeding with fruit flies), plants attained a mass 60% greater than that of unfed plants after a single growing season. Feeding also enhanced vegetative propagation, which is closely associated with growth, without modifying relations between these two vegetative functions. In contrast, feeding did not alter the size of vegetative rosettes or the within-season incidence of either flowering or fruiting. This lack of immediate responses occurred because floral and leaf primordia differentiated up to 10 mo before resource supplementation and flower development. However, enhanced resource status likely affected future reproduction indirectly through resource effects on plant size. Large plants produced more floral primordia and between-year changes in fruiting status corresponded to changes in plant size. These results illustrate that preformation can delay responses to enhanced resources by perennial plants.

Key words: growth; Lentibulariaceae; *Pinguicula vulgaris*; preformation; reproduction; supplemental resources; trade-offs; vegetative propagation.

Resource availability often limits seed production by plants, as illustrated by both positive associations between fertility and plant size (Samson and Werk, 1986; Ohlson, 1988; Weiner, 1988; Hanzawa and Kalisz, 1993; Schmid, Bazzaz, and Weiner, 1995) and trade-offs between fruiting success and growth or survival (reviews in Ågren and Willson, 1994; Primack, Miao, and Becker, 1994). Because of resource limitation, supplementation of nutrients and/or water often directly enhances seed production (van Andel and Vera, 1977; Willson and Price, 1980; McCall and Primack, 1985; Boeken, 1989; Vaughton, 1991; Campbell and Halama, 1993). In clonal plants, increased resource availability can also promote a genet's future seed production through increases in both the size of existing ramets (growth and storage) and production of new ramets (vegetative propagation: Harper, 1977; Abrahamson, 1980; Sackville-Hamilton, Schmid, and Harper, 1986; Schmid, 1990).

The benefits of a particular response to increased resources often reflect two size-dependent features of a plant's life history: current vs. future reproductive potential and the likelihood of surviving to reproduce again. Increased allocation to vegetative functions is advanta-

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geous if vegetative growth promotes survival and reproductive output accelerates with increases in plant (genet) size. For example, small plants often allocate proportionately more resources to growth than large plants due to threshold sizes of reproduction (Werner, 1975; Harper, 1977; reviews in Dafni, Cohen, and Noy-Meir, 1981; Mendez and Obeso, 1992). In contrast, uncertain survival or a decelerating relation between reproduction and plant size should promote increased allocation to current reproduction.

Increased proportional allocation to one function need not indicate strategic emphasis on that function, but may merely result if that function is most able to accommodate increased resources. The extreme case occurs when allocation to one function has an upper limit, at least in the short term, so that resources must be allocated to other functions once the limit is reached. Fruit and seed production during a single season may be particularly susceptible to such limitation because of inadequate pollen receipt (reviewed by Burd, 1994), meristem limitation (Watson, 1984; Eriksson, 1985; Geber, 1990; Casper and Neisenbaum, 1993), and/or preformation of floral primordia during the preceding season (Sørenson, 1941; Billings and Mooney, 1968; Mark, 1970; Dafni, Cohen, and Noy-Meir, 1981). These limits on reproductive responsiveness to unusually plentiful resources may often restrict changes in resource allocation (Calvo and Horvitz, 1990; Olivieri, Couvet, and Slatkin, 1994; Diggle, 1997; Geber, de Kroon, and Watson, 1997; Geber, Watson, and de Kroon, 1997).

Preformation of leaves and flowers may commonly limit allocation responses to abundant resources, because many species differentiate primordia many months prior to their development (Geber, Watson, and de Kroon, 1997). Recent studies indicate that preformation may delay the effects of reproductive trade-offs or responses to environmental changes (Aydelotte and Diggle, 1997; Diggle, 1997; Geber, de Kroon, and Watson, 1997). In Podophyllum peltatum, reproductive status and/or shoot size may affect future reproduction and growth for up to 3 yr through both preformation and resource storage (Geber, de Kroon, and Watson, 1997). Given such protracted effects, Diggle (1997) suggested that preforming species maintain flexible reproductive allocation by initiating more floral primordia than they could support during an average growing season and subsequently developing only enough primordia to use the available resources (also see Lloyd, 1980). In contradiction to this hypothesis, Aydelotte and Diggle (1997) found that the mean proportion of flower primordia matured by Caltha leptosepala varied little between years and habitats. However, this constancy could also reflect lack of variation in resource availability. A stronger test of Diggle's hypothesis requires resource supplementation to assess whether extra primordia allow flexibility or whether preformation limits allocation responses to unusually abundant resources.

In this paper we examine reproductive and vegetative responses to resource supplementation by Pinguicula vulgaris L. (common butterwort: Lentibulariaceae), a carnivorous perennial herb that preforms floral and leaf primordia up to 10 mo prior to their development. Previous work indicates that resource allocation by *P. vulgaris* is size dependent. Small (nonreproductive) plants allocate more resources to vegetative functions, whereas larger plants allocate resources to reproduction at the expense of growth (Worley and Harder, 1996). Several lines of evidence indicate that the abundance of insect prey limits both growth and reproduction by P. vulgaris, so that prey supplementation should enhance one of these functions. First, insect prey provide $\sim 25\%$ of the annual nutrient requirements of P. vulgaris (Karlsson, Thorén, and Hanslin, 1994) and may also enhance nitrogen uptake by roots (Hanslin and Karlsson, 1996). Second, reproduction by P. vulgaris seems to be resource limited, as indicated by trade-offs between reproduction and vegetative functions (Thorén, Karlsson, and Tuomi, 1996; Worley and Harder, 1996) and increased investment in flowers and fruit by larger plants (Worley and Harder, 1996). Finally, P. vulgaris self-pollinate autonomously (Molau, 1993; A. C. Worley, University of Toronto, unpublished data), so that pollen limitation of reproduction is much less likely than resource limitation.

Our first question concerns whether supplemental resources increase within-season growth or reproduction by *Pinguicula vulgaris*. Despite resource limitation, preformation of flower primordia may prevent *P. vulgaris* plants from increasing current reproduction in response to enhanced resources, unless they increase the proportion of ovules matured into seeds or mature "extra" flower primordia that would not normally mature. If preformation constrains allocation to current reproduction, plants that capture many insects should immediately increase allocation only to growth and vegetative propagation. In contrast, if preformation imposes no constraints, our prior study (Worley and Harder, 1996) suggests that large plants should increase reproduction, whereas small plants should increase vegetative growth. This prediction raises our second question; do responses to supplemental resources vary with plant size?

Preformation need not affect longer term reproductive responses to resource abundance, because flower and fruit production by *P. vulgaris* increase with plant size (Worley and Harder, 1996). Our third question is whether plant size at the end of a growing season is the primary determinant of future fruit production. Therefore, in addition to examining within-season reproductive responses to prey supplementation, we examined reproductive success in relation to a plant's fruiting status and size during the preceding year.

MATERIALS AND METHODS

Pinguicula vulgaris and study sites—Throughout its holarctic range, *Pinguicula vulgaris* grows in bogs and on damp rocks and ledges (Moss, 1983). Plants grow on diverse soil types, from acidic, nutrientpoor mires to calcareous soils (Karlsson, 1988). The populations that we studied occupied the banks of the Sheep River, in the Sheep River Wildlife Sanctuary, 85 km southwest of Calgary, Alberta (50°36' N, 114°47' W). Our main study site was in a former side channel on the east side of the river and was ~4 × 50 m. The site was bordered by spruce (*Picea glauca* [Moench] Voss) and buffalo berry (*Shepherdia canadensis* [L.] Nutt.), and moss was the main ground cover. Although the Sheep River floods occasionally and the ground was wet for much of the 1992 and 1993 growing seasons, most plants grew at or above the flood line.

Pinguicula vulgaris plants comprise a basal rosette of entire, oblanceolate leaves, annual roots, and not more than six flowers (Fig. 1). The glandular leaves secrete a sticky mucopolysaccharide, which traps small insects and other arthropods (Heslop-Harrison and Knox, 1971). The flowers are borne singly on leafless 5–15 cm scapes (Fig. 1) and develop sequentially. Most plants in Sheep River populations produce one or two flowers per season. These flowers self-pollinate autonomously, which provides reproductive assurance, but full seed set probably requires a combination of self- and insect-pollination (Molau, 1993; A.C. Worley, unpublished data). The ovary of each flower matures into a two-lobed capsule containing 110–140, 24-μg seeds (Karlsson, 1986). At our site, the growing season is from mid-May to late September, with flowering during June or July and fruits maturing during August.

Perennation by *P. vulgaris* involves a single subterranean "winter bud," which develops from the apical meristem during the growing season and contains leaf and floral primordia for the subsequent growing season (Fig. 2). Leaf primordia for the following year begin differentiating by early June from the apical meristem, which lies \sim 5 mm below the soil surface (Fig. 3). By autumn, when the current year's leaves have senesced fully, these leaf primordia have formed a compact bud, which remains dormant in the ground until the following spring (Fig. 2). By late August or early September the full complement of leaves for the next season has differentiated, and flower primordia have formed in the center of the bud (Fig. 4).

Pinguicula vulgaris propagates vegetatively by subsidiary buds (gemmae), which develop in the outer leaf axils of the winter bud (Fig. 2). Gemmae begin developing in the middle of the growing season (July) when the incipient winter bud has seven to ten leaf primordia. By winter, gemmae become independent of the parent bud, and they form roots and leaves during the following season. Both gemmae and the new winter bud continue to develop and grow until the end of the season.

Data collection—In May 1992, we selected groups of four plants at each of 30 locations, which we individually marked and monitored until the end of the 1993 growing season to assess reproductive success and proportional resource allocation. Plants at each location had exposed flower buds and were of similar size, with rosette diameters of at least 3 cm. Locations (blocks) were included in the design to control for



Figs. 1–4. Developmental stages of *Pinguicula vulgaris*. **1.** Flowering plant. In situ, the leaves hug the ground to form a flat rosette. Note the expanding leaf in the center of the rosette and the poorly developed root system. The apical meristem and developing winter bud are at the center of the leaf bases. Scale bar = 1 cm. **2.** Winter bud (wb) and gemmae (g). The dead roots are still attached to the base of the winter bud. Scale bars for Figs. 2-4 = 1 mm. **3.** Close-up of the developing winter bud (wb). The apical meristem is at the center of the bud. A flower stalk (fs) and expanding flower bud (fb) are also present. **4.** Center of a developing winter bud. Three flower primordia (fp) at varying stages of development are visible. The apical meristem (am) is sheathed by a leaf primordium.

small-scale environmental variation and possible genetic structuring resulting from vegetative propagation. The plants were examined every 3-4 d during the 1992 growing season (daily during flowering) to assess flower and fruit production. We recognized three reproductive categories: nonreproductive plants did not flower; flowering plants flowered but did not set fruit; and fruiting plants flowered and set at least one fruit. When plants became fully dormant at the end of the growing season (20 September-3 October 1992), we excavated winter buds and their associated gemmae. We counted the gemmae and measured the wet mass of both winter buds and all their gemmae with a Mettler PM100 digital balance. We then replanted the winter buds in their original locations. Gemmae were not replanted to avoid confusing them with gemmae produced during the following season. By autumn of 1992, 110 of the original 120 marked plants were alive. One hundred and three of these plants at 27 locations survived until the spring of 1993, and 94 plants from 26 locations were alive at the completion of the experiment.

During May 1993, two of the four plants at each location (or one if not all plants at a location had survived) were randomly assigned to a resource supplementation treatment and the remaining plants were left as unfed. Fed plants received two or three freshly killed fruit flies on their leaves twice a week beginning 1 June and continuing throughout the 18-wk growing season. On 14 June we observed ants removing fruit flies from the plants. To prevent further interference by ants, we surrounded all plants in the experiment with 5-cm high wire-mesh exclosures whose bases were covered with Tanglefoot®, a concentrated resin that is commonly used to deter insects from climbing fruit trees. All exclosures were in place by 23 June, by which time the first flower buds of plants that subsequently flowered were visible but flowering had not started.

We also caged 13 pairs of nonexperimental plants to determine whether the ant exclosures affected capture of natural prey. Mean prey capture (± 1 SE) was 8 \pm 1.5 insects (mostly collembola and mites) by control plants and 2 \pm 0.4 insects by caged plants in one week (23–29 June). The rates were 6 \pm 1.1 and 2 \pm 0.8 insects by control and caged plants, respectively, in the following week (30 June–6 July). These differences were significant in both weeks (paired-sample *t* test, week 1: $t_{12} = 4.46$, P < 0.001, week 2: $t_{12} = 2.90$, P < 0.02). Because the cages reduced prey capture, we caged all control and fed plants to maintain a difference in insect availability between treatments in the feeding experiment.

We collected data on sexual reproduction, vegetative propagation, growth, and final plant size (winter-bud mass in 1993). Plants were monitored for flower and fruit production as in 1992. At or close to maturity, fruit were collected and preserved in 70% ethanol. We used a Wild-M5 dissecting microscope to count mature seeds and failed ovules, which were summed to obtain total ovule number. The winter buds and gemmae were weighed as described for 1992 (3-8 October 1993), and the ratio of "final" (1993) bud mass to "initial" (1992) bud mass was calculated as a measure of relative growth. We refer to this ratio as "growth," but it reflects a different process from that usually referred to as growth. In Pinguicula, growth represents size differences between former and current winter buds, rather than the size increments of a persistent structure. Thus, for a new winter bud that is smaller than its progenitor, the growth ratio is less than one. These measures reflect net allocation rather than total allocation to each function because we weighed winter buds and gemmae after leaf senescence. Five of the 94 remaining plants were eliminated from the study at this stage, including three plants that lost flowers to herbivory or accidents, one control plant that had been fed in error, and one plant that experienced fungal infection

We used fresh biomass as a measure of resource allocation because growth responses must be assessed by repeated, nondestructive sampling. Patterns of carbon allocation commonly correlate with the distribution of macronutrients (Abrahamson and Caswell, 1982; Reekie and Bazzaz, 1987). Furthermore, our measures likely assess net carbon allocation to growth and vegetative propagation reliably because dormant winter buds and gemmae have equivalent water content.

Growth responses to feeding may reflect either direct shunting of surplus photosynthates to the perennating bud or increased size of current leaves to provide enhanced photosynthetic capacity. We compared video images of control and fed rosettes to test whether feeding increased current vegetative size. We video-taped the plants on 27 July, when plants were in flower and ~5 wk after effective feeding commenced. By the time they flower, plants have expanded all leaves in the winter bud and leaves have not yet begun to senesce. Thus, plants should have their maximum rosette area at this time. We calibrated each video image with a 1-cm scale and digitized the images to obtain the total area of each rosette.

If preformation delays a reproductive response to resource abundance until the next growing season, feeding should stimulate an immediate growth response, which would increase both winter-bud size and production of flower primordia. The experiment outlined above assessed the growth response, but provided no information on the production of flower primordia, which would require destructive sampling so that plants could not be used in future experiments. Therefore, we quantified the relation of flower primordia production to bud size with 78 separate plants collected in autumn 1992 from four sites, including the site used for all other aspects of this study and three other sites along the banks of the Sheep River, within 2 km of the main study site.

Field observations indicated that *P. vulgaris* plants typically produce more flower primordia than are matured. To investigate the general flexibility of primordia maturation, we removed the first flower bud as soon as it became visible from 16 of 32 plants grown in a growth chamber. If plants compensate for bud removal by maturing a higher proportion of their flower primordia, bud removal should not affect the number of flowers matured.

Statistical analysis—Vegetative functions—We fitted mixed models using restricted maximum likelihood (MIXED procedure; SAS, 1997) to analyze final (1993) bud mass and the total mass of gemmae (vegetative propagules) produced during 1993. Main effects included location (random effect), current-season reproductive category (nonreproductive, flowering, fruiting), and feeding treatment. Initially, fruiting category in 1992 (fruiting, nonfruiting) was also included as a main effect; however, because fruiting in 1992 did not affect growth or vegetative propagation in 1993 and it does not represent an imposed design component, we removed it from the analyses. Covariates included initial (1992) bud mass, 1993 gemmae mass, and 1993 gemmae number. The analysis of gemmae mass included growth, as indicated by the ratio of final (1993) to initial (1992) bud mass. We conducted a similar analysis of 1993 rosette area, but included only initial bud mass as a covariate. All possible two- and three-way interactions, except those involving location, were included in initial models, and nonsignificant terms involving covariates were dropped using backward elimination (α = 0.05). Interactions involving location were not considered because several locations were represented by single plants. Data were logtransformed for both analyses to stabilize variances. To facilitate presentation, we backtransformed descriptive statistics, resulting in asymmetric standard errors, which we report as lower (LSE) and upper (USE) standard errors. We indicate partial regression coefficients with the letter band their standard errors with s_b . These coefficients indicate the response of the dependent variable to one unit change in a specific independent variable, while all other independent variables remain constant.

Several individuals were eliminated from each analysis. First, two plants with incomplete information on initial bud mass and one plant with an extremely low initial bud mass were eliminated from all analyses. Second, we had good video images for 75 of the remaining plants. Before analyzing rosette area, we eliminated five additional plants with senescing flowers. During analysis we eliminated one control plant with an extremely low rosette area that grew next to a plant which died of a fungal infection and one fed plant with an extremely large rosette area

TAI	3le 1.	Mixed models o	f factors	affecting	rosette area,	final bu	ud mass, ar	d vegetative	e propagation.	The in	itial model	included	1992 bud	mass
	for th	e analysis of 199	3 rosette a	area; 1992	2 bud mass,	1993 ge	emmae mas	s, and 1993	gemmae num	ber for	the analysis	of 1993	bud mass;	1992
	bud n	hass, growth duri	ng 1993, i	and 1993	gemmae nur	nber fo	r the analys	is of 1993 g	gemmae mass;	and tw	o- and thre	e-way into	eractions f	for all
	analy	ses. Nonsignificar	it terms in	nvolving o	covariates w	ere drop	oped using	backwards e	limination, an	d only t	terms that w	vere signif	ficant in a	t least
	one a	nalysis are includ	ed in the	table. Th	e random lo	cation e	ffect was to	ested with a	likelihood rat	io test.				

Effect	Rosette area (1993)	Final bud mass (1993)	Gemmae mass (1993)
Location Feeding Current reproduction (1993) Feed × reproduction Initial bud mass (1992)	$G_{23} = 0.29$ $F_{1,52} = 2.39$ $F_{2,61} = 0.59$ $F_{2,58} = 1.24$ $F_{1,59} = 29.45^{***}$	$G_{26} = 0.26$ $F_{1.64} = 40.67^{***}$ $F_{2.75} = 0.98$ $F_{2.70} = 0.66$ $F_{1.76} = 29.50^{***}$	$G_{25} = 0.00$ $F_{1,53} = 4.25*$ $F_{2,53} = 1.47**$ $F_{2,53} = 0.83$ $F_{1,52} = 12.82***$
Growth = $\frac{1992 \text{ bud mass}}{1993 \text{ bud mass}}$			$F_{1,53} = 25.50^{***}$
Gemmae mass (1993) Gemmae number (1993)		$F_{1,76} = 20.38^{***}$ $F_{1,76} = 9.64^{**}$	$F_{1,53} = 89.31^{***}$

*P < 0.05, **P < 0.01, ***P < 0.001.

(final N = 68). Both of these plants were in the same reproductive category (flowering), and their inclusion created interactions that were not supported by the rest of the data. Third, we had measures of final bud mass for 86 plants in the feeding experiment. For analyses of final bud mass and sexual reproduction, we eliminated one plant with an extremely high gemmae mass that created interactions not supported by the rest of the data (final N = 85). The analysis of gemmae mass contained only plants that produced gemmae (final N = 62).

In the analyses of both final bud mass and gemmae mass in 1993, several covariates affected the dependent variable. To illustrate the influence of each covariate most clearly, data presented in the figures were adjusted for the effect of the other covariates as follows. First, a predicted value was calculated for each observation, based on intercepts and partial regression coefficients from the mixed model, the observed value of the covariate of interest, and the means of the other covariates. Then the residual from the mixed model for each observation was added to its predicted value. As a consequence of these adjustments, the data in the figures do not correspond directly to the raw data and cannot be compared between figures.

Sexual reproduction—We analyzed aspects of sexual reproduction with logistic regression (GENMOD procedure; SAS, 1997) because plants produced ≤ 2 flowers and fruits, so we could not analyze flower and fruit production as continuous variables using general linear mod-



Fig. 5. Relation between final (1993) and initial (1992) bud mass for control and fed plants ($b + s_b = 0.48 \pm 0.082$). The solid line indicates no change in bud mass. Data are adjusted for the effects of location, reproduction, gemmae mass, and gemmae number. The overall analysis of the mixed model is in Table 1.

els. We analyzed the proportion of plants with >1 flower primordium in the 1992 destructive sample as a function of mean final (1992) bud mass per location and site. We analyzed both the relative frequency of flowering by all plants and the proportion of flowering plants that produced fruit per location during 1993 as functions of feeding treatment, mean initial (1992) bud mass, 1993 vegetative propagation, and growth. Nonsignificant continuous terms were dropped using backward elimination ($\alpha = 0.05$).

To determine whether previous reproduction influenced current reproduction directly, we performed two analyses. First, we used logistic regression to analyze the proportion of plants per location that changed fruiting status between 1992 and 1993 as a function of fruit production in 1992, bud mass at the end of 1992, 1993 gemmae mass, and 1993 growth. Feeding was not included in this analysis because it did not affect flowering or fruiting in 1993 (see Results). Second, we used Stuart's test (Marascuilo and McSweeney, 1977) to determine whether the proportion of plants in each reproductive category differed significantly between years. Stuart's test compares marginal proportions in square contingency tables when the chi-square assumption of independent observations is violated. Here, categorization of plants at two times introduced a correlation between marginal probabilities. Stuart's test provides 95% confidence intervals for between-year changes in marginal proportions. When the confidence interval does not span zero, the difference between proportions is considered significant.

RESULTS

Growth—Feeding stimulated growth substantially (Table 1, Fig. 5). Fed plants finished the 1993 growing season with a mean bud mass of 105 mg (LSE = 98.6 mg, USE = 112.0 mg, N = 39) compared to 60 mg (LSE = 55.8 mg, USE = 64.3 mg, N = 46) for unfed plants ($F_{1.58} = 67.72$, P < 0.001), even though the two feeding categories had equivalent mean bud masses during the autumn preceding resource supplementation (overall mean bud mass = 55 mg, LSE = 52.2 mg, USE = 57.9 mg, N = 85: $F_{1.58} = 0.14$, P > 0.7: ANOVA with location and feeding treatment as main effects). On average, fed plants grew tenfold more than controls, so that the final size overlapped little (Fig. 5). In contrast to the effects on the perennating bud, feeding did not affect the area of the current year's rosette (Table 1).

Initial (1992) bud mass was an important predictor of both 1993 rosette area and final (1993) bud mass, regardless of feeding treatment. The partial regression coefficient for the effect of bud mass on rosette area did not differ significantly between feeding treatments or from 0.67, the expected allometric relation between volume and area ($b \pm s_b = 0.53 \pm 0.098$: $t_{59} = 1.43$, P >0.05). This suggests that leaf area only depended on the size of the preceding winter bud. The partial regression coefficient for final bud mass was significantly less than one $(b \pm s_b = 0.48 \pm 0.089)$. Thus, small plants had proportionately larger rosettes and grew proportionately more than large plants (Fig. 5). This effect did not depend significantly on either a plant's reproductive status (in contrast to Worley and Harder, 1996), or resource supplementation. As a result of the general enhancement of final bud mass by prey supplementation, all fed plants gained mass during 1993, whereas unfed plants with an initial mass > 60 mg generally lost mass (Fig. 5). Hence, feeding counteracted the tendency for shrinkage by large plants, which seems to be a general feature of the natural size dynamics of P. vulgaris along the Sheep River (Worley and Harder, 1996).

Final bud mass also varied significantly with gemmae production (Table 1). For plants with a given initial (1992) bud mass and 1993 gemmae number, final (1993) bud mass varied positively with total 1993 gemmae mass ($b \pm s_b = 0.42 \pm 0.094$). In contrast, plants allocating a given total mass to gemmae had smaller final buds if that mass was divided among many gemmae than among few gemmae ($b \pm s_b = -0.38 \pm 0.122$). This decrease in winter-bud size indicates a cost to dividing resources among multiple gemmae.

Vegetative propagation—During both years most plants produced at least one gemma (87% and N = 110in 1992, and 73% and N = 89 in 1993). No threshold size for gemmae production was obvious; plants that produced no gemmae were well within the size range of gemmae-producing plants. Only gemmae-producing plants were included in the analysis of 1993 gemmae mass.

Gemmae mass in 1993 varied positively with initial (1992) bud mass, growth, and 1993 gemmae number (Table 1, Fig. 6). The partial regression coefficients of these relations did not differ between unfed and fed plants or among reproductive categories (bud mass: $b \pm s_b = 0.71$ \pm 0.198; growth: $b \pm s_b = 1.02 \pm 0.203$; gemmae number: $b \pm s_b = 1.08 \pm 0.114$). Feeding weakly affected gemmae mass directly (Table 1), but because fed plants grew much more than unfed plants, feeding strongly affected gemmae mass through its effects on growth (Fig. 6). However, for a given initial bud mass, growth and gemmae number, fed plants produced a smaller total gemmae mass (adjusted mean = 2.37 mg, LSE = 2.05 mg, USE = 2.73 mg) than unfed plants (adjusted mean = 3.69 mg, LSE = 3.22 mg, USE = 4.23 mg). Thus, fed plants allocated slightly more supplemental resources to growth than to gemmae production.

Sexual reproduction—Several lines of evidence indicate that single-year reproductive output by *P. vulgaris* depends on a plant's resource history, as represented by its size and reproductive effort during the preceding season, but not on current resource availability (feeding). First consider the production of floral primordia during



Fig. 6. Relation of vegetative propagation (total gemmae mass) by control and fed plants to growth ($b \pm s_b = 1.02 \pm 0.203$). The dashed line indicates no change in bud mass. Data are adjusted for the effects of location, feeding and other significant covariates (see Materials and Methods). See Table 1 for analysis of the mixed model, which considered only plants that produced gemmae.

the preceding growing season. All 78 winter buds examined for floral primordia during autumn 1992 had at least one primordium and 45% produced two or more primordia. The proportion of these plants that produced multiple flower primordia varied positively with 1992 bud mass (Table 2, Fig. 7a). At least one plant produced more than one flower primordium at most locations within study sites where mean bud mass exceeded 60 mg (Fig. 7a). Site also affected production of flower primordia (Table 2), but the site of the resource-supplementation experiment did not differ from two of the three other sites, including the site of our previously reported work (Worley and Harder, 1996).

Even though the results of our study of floral primordia imply that most plants in the feeding experiment produced primordia during 1992, only 42% (N = 85) of these plants flowered during 1993. The probability of flowering varied positively with initial (1992) bud mass (Table 2). For example, at least one plant flowered at all locations where mean initial bud mass exceeded 62 mg, and at least 50% of plants flowered at locations where mean initial bud mass exceeded 78 mg (Fig. 7b). Despite the importance of previous resource history, flowering did not vary significantly with current resource conditions as represented by feeding treatment, 1993 gemmae mass, or growth during 1993 (Table 2). In contrast to the preceding analysis, which considered all plants in the feeding experiment, fruit set by plants that flowered during 1993 was not influenced by either 1992 bud mass (resource history), feeding, 1993 gemmae mass, or 1993 growth (current resource availability; Table 2).

Removal of floral buds from plants maintained in a growth chamber did not stimulate compensatory maturation of extra floral primordia. In particular, plants whose first flower buds had been removed produced fewer flowers (adjusted mean flower number ± 1 SE = 2.14 \pm 0.196) than unmanipulated plants (adjusted mean flower number ± 1 SE = 2.86 \pm 0.196: $F_{1,29}$ = 6.61, P < 0.02; based on an ANCOVA with initial bud mass as a covari-

TABLE 2.	Logistic regression results (means \pm 1 SE) for factors affecting proportions of <i>Pinguicula vulgaris</i> plants that produced multiple flower
prim	ordia, plants that flowered, flowering plants that fruited, and plants that changed fruiting status between 1992 and 1993. We analyzed
flowe	ering and fruiting during 1993 in response to feeding treatment, 1992 bud mass, 1993 gemmae mass, and growth during 1993. Nonsignificant
terms	s were dropped using backwards elimination and with the exception of feeding treatment only terms that were significant in at least one
analy	vsis are in the table. ^a

	>1 flower primordium (1992)		Flowering (1993)		Fruiting by flowering plants (1993)		Δ fruiting status (1992–1993)	
Effect	Estimate (SE)	Wald chi square	Estimate (SE)	Wald chi square	Estimate (SE)	Wald chi square	Estimate (SE)	Wald chi square
Intercept	-4.14 (1.206)	11.78***	-6.12 (1.279)	22.95***	-9.66 (5.801)	2.77	-4.94 (2.013)	6.01*
Site ^b		10.31*	_		_			
Feeding			0.17 (0.606)	0.08	0.62 (0.770)	0.65		ns
1992 bud mass	0.08 (0.020)	17.39***	0.09 (0.019)	22.41***	2.31 (1.314)	3.08	0.06 (0.030)	4.47*
1992 fruiting status ^c			—		—		9.50 (2.290)	17.21***
1992 bud mass × 1992 fruiting ^c			—		—		-0.12 (0.034)	12.96**

^a ns, P > 0.05 and omitted from final model; * P < 0.05; ** P < 0.01; *** P < 0.001.

^b Only the analysis of floral primordia involved more than one study site. Parameter estimates for the site effects are not provided.

^c Only the analysis of change in fruiting status involved a plant's fruiting status during 1992.

ate). If manipulated plants had been allowed to mature the removed flower bud, their mean flower production (3.14 flowers) would not have differed significantly from that of unmanipulated plants ($F_{1,29} = 1.06$, P > 0.3).

Most plants that flowered also set fruit (1992: 78%, N = 81, 1993: 70%, N = 36; however, a significantly smaller percentage of plants produced fruit during 1993 (29%) than during 1992 (73%: $\Delta_{\text{fruit}} \pm 95\%$ CI = -44 ± 16.9%). This decline largely resulted from an increase in the percentage of nonreproductive plants ($\Delta_{nonreproductive} =$ $53 \pm 13.8\%$), as the same percentage of plants flowered but did not set fruit during both years ($\Delta_{\rm flower} = -8 \pm$ 15%). The probability of changing fruiting status between 1992 and 1993 depended on whether a plant had fruited during 1992 and its size at the end of 1992 (Table 2: 1992 fruit \times 1992 bud mass interaction). Plants that did not fruit in 1992 were most likely to produce fruit in 1993 if they had a large perennating bud at the end of 1992 (Table 2, Fig. 8a). In contrast, among plants that fruited in 1992, primarily small individuals changed to a nonfruiting status in 1993 (Table 2, Fig. 8b). These results indicate a strong influence of plant size on the dynamics of sexual reproduction in this Pinguicula vulgaris population.

Feeding could increase the number of seeds per fruit, so we also analyzed the effects of feeding on seed production. However, low fruit numbers in 1993 (only 25 plants set fruit) coupled with losses due to herbivory or accidents limited our sample of mature fruit to only 15 plants. Although fed plants set slightly more seeds (mean \pm 1 SE = 134 \pm 22.8 seeds, N = 5) than control plants (122 \pm 15.8 seeds, N = 10), this difference was not significant ($t_{13} = 0.44$, P > 0.6) and the sample was too small for more detailed analysis.

DISCUSSION

Preformation seems to limit within-season allocation responses to abundant resources by *Pinguicula vulgaris*.

Supplemental feeding greatly stimulated growth of the winter bud (Fig. 5: also see Aldenius, Carlsson, and Karlsson, 1983; Karlsson et al., 1991; Karlsson, Thorén, and Hanslin, 1994; Hanslin and Karlsson, 1996) and vegetative propagation by *P. vulgaris* plants of all sizes (Fig. 6). In contrast, feeding did not alter either within-season vegetative size (Table 1) or reproductive effort (Table 2).

Vegetative responses to variation in resource availability-Feeding enhanced growth sufficiently that the size distribution of fed plants did not overlap the distribution of unfed plants that started the experiment at an equivalent size (Fig. 5). This large response indicates that insect availability severely limits growth by P. vulgaris at our study site, as it does in other *Pinguicula* spp. and other carnivorous genera (e.g., Darwin, 1878; Harder and Zemlin, 1967; Aldenius, Carlsson, and Karlsson, 1983; Karlsson et al., 1991; Karlsson and Pate, 1992; Thorén and Karlsson, 1998). The extent of this growth response probably does not reflect strategic emphasis on vegetative functions. Rather, it likely arises from the limited alternatives for allocating abundant resources caused by the inability of P. vulgaris to increase current reproductive effort. This conclusion draws support from the observation that small and large plants exhibited equivalent relative growth responses to feeding (i.e., no significant interaction between feeding and initial bud mass), even though more large plants expended effort in reproduction (Table 2; Figs. 7, 8).

This species' preformation of leaf primordia and its growth form may also have constrained vegetative responses to feeding. In unbranching plants with preformation, such as *P. vulgaris*, initiation of leaf primordia for a given year is terminated by the onset of floral differentiation. Thus the maximum number of leaves is determined prior to the growing season. Such plants cannot respond vegetatively to abundant resources by initiating new leaves and, if feeding commences after leaf expan-



Fig. 7. (a) The proportion of plants producing more than one flower primordium in 1992 in relation to mean 1992 bud mass per location. These data represent the destructive sample described in the text and include plants from four sites along the Sheep River, including the site on which all other aspects of this study are based. (b) The proportion of plants flowering in 1993 as a function of mean initial (1992) bud mass per location. The predicted relations in both panels are based on logistic regression (Table 2).

sion, are not likely to increase leaf size. These limitations may explain why feeding did not affect rosette area and suggest that a large fraction of surplus resources is consigned to future potential through growth of the perennating bud and the associated development of vegetative propagules (also see Diggle, 1997). In accordance with these ideas, a long-term feeding experiment showed a 1–



Fig. 8. The proportion of plants changing fruiting status per location between 1992 and 1993 in relation to fruiting status and mean final bud mass in 1992. The relation for plants that did not fruit in 1992 is shown in (a) and the relation for plants that fruited in 1992 in (b). The predicted relations are based on logistic regression (Table 2).

2 yr delay before rosettes of *P. vulgaris* increased in size following supplemental feeding (Thorén and Karlsson, 1998).

The effects of feeding on gemmae production indicate relatively little influence of resource abundance on sizedependent allocation to vegetative propagation by *P. vulgaris.* In particular, feeding did not alter the relation between gemmae mass and initial plant size or growth. Thus, feeding largely affected vegetative propagation indirectly through enhanced growth (Fig. 6). Surprisingly, fed plants had slightly lower gemmae masses (0.04 < P< 0.05) than control plants of equivalent initial size and growth. This suggests that plants convert resources gained through feeding to growth of the perennating bud slightly more readily than to gemmae.

Reproductive responses to variation in resource availability-The observed lack of reproductive responses by P. vulgaris to either resource abundance or removal of flower buds could reflect either experimental difficulties or constraints imposed by preformation. In this context, two experimental conditions warrant mention. First, our experimental feeding may have been insufficient to support increases in flower number, because by caging plants to exclude ant thievery we may have reduced natural prey capture by unfed plants, rather than supplementing prey capture by fed plants. This explanation seems unlikely because unfed plants in this study exhibited a similar relation between growth and initial bud mass to that found at a nearby site for uncaged plants (Worley and Harder, 1996), whereas fed plants exhibited significantly elevated growth (Fig. 5a).

Second, our addition of prey and removal of flower buds may have occurred too late during the growing season to provide the environmental cues that increase flowering. In several arctic and alpine species, maturation of flowers from flower primordia depends on early-season temperatures and photoperiod (Billings and Mooney, 1968). However, other feeding experiments with *P. vulgaris*, which involved longer within-season feeding periods, similarly found no reproductive responses to enhanced resources (Aldenius, Carlsson, and Karlsson, 1983; Karlsson et al., 1991; Thorén, Karlsson, and Tuomi, 1996). In addition, although Svensson et al. (1993) found that the proportion of flowering *P. vulgaris* and *P. villosa* plants varied positively with precipitation early during the current season, mean summer temperature during the previous year had the strongest effect on flowering. Hence, *P. vulgaris* seems unable to allocate abundant resources directly to reproductive effort.

Species with preformation may maintain the capacity to take advantage of plentiful resources by producing more floral primordia than can normally develop into flowers (Lloyd, 1980; Diggle, 1997). Our results show that this production of extra flower primordia occurs in *P. vulgaris*, and it may be common in species with preformation (e.g., Mark, 1970). However, *P. vulgaris* plants that we fed or from which we removed floral buds did not mature more flowers than unmanipulated plants, even though they likely had additional floral primordia and the growth response of fed plants confirms that they assimilated the supplemental resources. The explanation for this reproductive unresponsiveness remains unclear.

The lack of immediate reproductive response does not imply that preforming species, such as P. vulgaris, cannot capitalize reproductively on unusually plentiful resources. Instead, preformation delays responses to resource abundance by constraining them to occur indirectly through changes in plant size. In particular, increases in the size of the perennating bud induced by resource abundance likely enhance production of floral primordia (Fig. 7a), thereby raising the chance of a plant flowering (Fig. 7b) and fruiting (Fig. 8). For example, Thorén and Karlsson (1998) recently reported that six seasons of feeding increased rosette and winter-bud size in P. vulgaris. Extended feeding also increased flowering frequency, but not until the establishment of clear differences in rosette size, and presumably in the size of the preceding season's winter bud. Probably as a result of such delays, seed production by many species depends on temperature, rainfall, or nutrient availability during the previous, rather than the current, year (Mark, 1965; Hill-Cottingham and Williams, 1967; Billings and Mooney, 1968; Mark, 1968; Boeken, 1990; Svensson et al., 1993; Geber, Watson and de Kroon, 1997). Hence, preformation delays, rather than precludes, reproductive responses to resource abundance. In contrast, preformation should not limit immediate reproductive responses to resource shortage, resulting in asymmetrical allocation responses to enrichment and deprivation. Consideration of preformation should clarify the dynamics of resource allocation in perennial species.

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