

# Unifying Life History Analyses for Inference of Fitness and Population Growth

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## ABSTRACT

The lifetime fitnesses of individuals comprising a population determine its numerical dynamics, and genetic variation in fitness results in evolutionary change. The dual importance of individual fitness is well understood, but empirical fitness records generally violate the assumptions of standard statistical approaches. This problem has plagued comprehensive study of fitness and impeded empirical study of the link between numerical and genetic dynamics of populations. Recently developed aster models address this problem by explicitly modeling the dependence of later expressed components of fitness (e.g. fecundity) on those expressed earlier (e.g. survival to reproduce). Moreover, aster models employ different sampling distributions for components of fitness, as appropriate (e.g. binomial for survival over a given interval and Poisson for fecundity). The analysis is conducted by maximum likelihood, and the resulting compound distributions for lifetime fitness closely approximate the observed data. We illustrate the breadth of aster’s utility with three examples demonstrating estimation of the finite rate of increase, comparison of mean fitness among genotypic groups, and phenotypic selection analysis. Aster models offer a unified approach to address the breadth of questions in evolution and ecology for which life history data are gathered.

*Subject headings:* *Chamaecrista fasciculata*, community genetics, demography, *Echinacea angustifolia*, fitness components, *Uroleucon rudbeckiae*

26 The fitness of an individual is well understood as its contribution, in offspring, to the  
population. Fitness has both evolutionary significance, as an individual’s contribution to a  
28 population’s subsequent genetic composition, and ecological importance, as an individual’s  
numerical contribution to a population’s growth. The simplicity of these closely linked  
30 ideas belies serious complications that arise in empirical studies. Lifetime fitness comprises  
multiple components of fitness expressed over one to many intervals. As a result, the  
32 distribution of fitness, even for a synchronized cohort in the absence of systematic sources  
of variation, is typically multimodal and highly skewed in shape and thus corresponds to no  
34 known parametric distribution. This problem has long been acknowledged (Mitchell-Olds  
and Shaw 1987; Stanton and Thiede 2005), yet to date there is no single, rigorously justified  
36 approach for jointly analyzing components of fitness measured sequentially throughout  
the lives of individuals. This limitation severely undermines efforts to link ecological and  
38 evolutionary inference.

Here we present applications of a new statistical approach, aster, for analyzing  
40 life-history data with the goal of making inferences about lifetime fitness or population  
growth. Aster modeling generates the overall likelihood for a set of components of fitness  
42 expressed through the lives of individuals. Within a single analysis, aster permits different  
fitness components to be modeled with different statistical distributions, as appropriate.  
44 It also accounts for the dependence of fitness components expressed later in the life-span  
on those expressed earlier. The statistical theory for aster models is presented in Geyer  
46 et al. (2007). Here, we first review the limitations of previous approaches to analysis  
of life-histories. Second, we describe aster models. Finally, we present three empirical  
48 examples to illustrate the utility of aster modeling as a comprehensive approach to analysis  
of life-history data.

## 1. The problem and previous efforts to address it

Individual fitness realized over a lifespan typically does not conform to any well known distribution that is amenable to parametric statistical analysis. In contrast, individual components of fitness, such as survival to age  $x$ , reproduction at that age, and the number of young produced by a reproductive individual of that age, generally conform much more closely to simple parametric distributions. For this reason, components of fitness are sometimes analyzed separately to obviate the problem of the distribution of lifetime fitness. For example, in a study of genetic variation in response to conspecific density of a population of *Salvia lyrata*, Shaw (1986) provided separate analyses of two components of fitness, survival over two time intervals and size of the survivors, as a proxy for future reproductive capacity in this perennial plant. Implicitly, this approach considers size, or in other cases fecundity, conditional on survival. Though the statistical assumptions underlying the analyses tend to be satisfied, it offers no way to combine the analyses to yield inferences about overall fitness.

A common method for analyzing fitness as survival and reproduction jointly is to use fecundity as the index of fitness, assigning values of zero for fecundity of individuals that died prior to reproduction. When observations are available for replicate individuals, a variant of this method is to use as the measure of fitness the product of the proportion surviving and the mean fecundity of survivors (e.g. Belaoussoff and Shore 1995; Galloway and Etterson 2007). In both cases, the resulting distribution is actually a mixture of underlying discrete and (quasi)continuous distributions, yet analyses have generally treated it as a single, continuous response, despite its skewness and multimodality, such that no transformation yields a distribution suitable for parametric statistical analysis. Authors frequently remark on the awkwardness of these distributions in their studies (e.g. Etterson 2004), but rarely publish fitness distributions. Antonovics and Ellstrand (1984), however,

presented the extremely skewed distribution of lifetime reproductive output (their Fig. 2)  
76 from their experimental studies of frequency-dependent selection in the perennial grass,  
*Anthoxanthum odoratum*. Finding no transformation that yielded a normal distribution  
78 suitable for analysis of variance, they assessed the robustness of their inferences by applying  
three distinct analyses (categorical analysis of discrete fecundity classes, ANOVA of means,  
80 and nonparametric analysis). In this study, results of the three analyses were largely  
consistent, but, in general, results are likely to differ.

82 Others have noted the importance of complete accounting of life-history in inferring  
fitness or population growth rate, as well as evaluation of its sampling variation, and have  
84 presented methods to accomplish this. Caswell (2001) and Morris and Doak (2002) explain  
how to obtain population projection matrices from life-history records and, from them, to  
86 estimate population growth rate. They also describe methods for evaluating its sampling  
variation and acknowledge statistically problematic aspects of these methods. Specifically,  
88 Caswell (2001) notes (p.304) that the delta method and other series approximations assume  
both that variances of the elements of a population projection matrix are small and that  
90 the population growth rate is normally distributed. It is often further assumed that all  
the parameters are independent (Caswell (2001), p.302). These assumptions are likely  
92 to be violated in many cases. To avoid these assumptions, Caswell (2001) recommended  
resampling approaches, first applied in this context by Lenski and Service (1982), who  
94 emphasized that the complete life-history record of each individual is the unit of observation.

Recent efforts to evaluate the nature of selection have likewise taken a comprehensive  
96 demographic approach. McGraw and Caswell (1996) considered individual life-histories but  
chose the maximum eigenvalue of an individual's Leslie matrix ( $\lambda$ ) as its fitness measure.  
98 They regressed  $\lambda$  on the fitness components, age at reproduction and lifetime reproductive  
output to estimate selection on them, but noted violation of the assumption of normality

100 of residuals required for statistical testing. Van Tienderen (2000) advocated an alternative  
approach involving evaluation of the relationships between each component of fitness and  
102 the phenotypic traits of interest via separate multiple regression analyses to obtain the  
selection gradients in different episodes of selection (Lande and Arnold 1983). These  
104 selection gradients are then weighted by the elasticities (Caswell 2001) of each component of  
fitness obtained from analysis of the appropriate population projection matrix. Using this  
106 method, Coulson et al. (2003) also noted violation of the usual distributional assumption.  
Moreover, because the method combines results from multiple analyses, it does not fully  
108 account for sampling variation. Beyond these approaches, methods targeting the problem  
of “zero-inflated” data (i.e. many observations of zero distorting a distribution) have also  
110 been proposed (Cheng et al. 2000; Dagne 2004; Martin, et al. 2005). However, like the  
other methods, this method does not generalize readily for inference in the wide range of  
112 contexts that life-history data can, in principle, address.

## 2. Inference of individual fitness with aster

114 We present aster models (Geyer et al. 2007) for analysis of life-history records as  
a general, statistically sound approach to address diverse questions in evolution and  
116 ecology. As noted above, two standard properties of life-history data are central to  
the statistical challenges that aster addresses. First, the expression of an individual’s  
118 life-history at one stage depends on its status at earlier stages. For example, observation of  
an individual’s fecundity at one stage is contingent on its survival to that stage. Second,  
120 no single parametric distribution is generally suitable for modeling all components of  
fitness, e.g. survival and fecundity. The aster approach jointly models the components of  
122 fitness using distributions suitable for each and explicitly taking into account the inherent  
dependence of each stage on previous stages. We represent the life-history and, in particular,

124 the dependence of one life-history component on another, with graphical models as in Fig. 1  
with arrows pointing from a *predecessor* variable to its *successor*.

126 EDITOR: PLACE FIGURE 1 HERE.

The theory underlying the aster approach requires modeling the conditional distribution  
128 of each variable given its predecessor variable as an exponential family of distributions  
(Lehmann and Casella 1998; Barndorff-Nielsen 1978; Geyer et al. 2007) with the predecessor  
130 variable providing the sample size for its successors. This requirement retains considerable  
flexibility, because many well-known distributions are exponential families, including  
132 Bernoulli, Poisson, geometric, normal, and negative binomial (Mood, et al. 1974, p. 312  
ff.). When questions arise about the applicability of aster models, some diagnostic tools are  
134 available, as demonstrated in our Example 3.

A predecessor variable  $n$  must be nonnegative integer valued. If  $n > 0$ , then the  
136 successor is the sum of  $n$  independent and identically distributed variables having the  
named distribution. If  $n = 0$ , then the successor is zero. This accommodates much of the  
138 dependence in life history data. In a graph like Fig. 1A, where each of the variables  $Sx$   
models survival (zero-or-one with one indicating alive), a dead individual stays dead and  
140 does not reproduce.

Aster is a general approach, suited to analyzing complicated life-histories (e.g. Fig. 1).  
142 Approaches commonly used for particular data structures are special cases of aster. The  
simplest possible aster models have graphs with only one arrow per individual  $1 \rightarrow X$ . If  
144  $X$  is normal, this is a linear model (LM) as in multiple regression or analysis of variance.  
If  $X$  is Bernoulli or Poisson, this is a generalized linear model (GLM) as in logistic or  
146 Poisson regression (McCullagh and Nelder 1989). The next simplest models have graphs  
 $1 \rightarrow X \rightarrow Y$  with  $X$  Bernoulli and  $Y$  zero-truncated Poisson (like Fig. 1D); here the



148 marginal distribution of  $Y$  is zero-inflated Poisson (Martin, et al. 2005). An aster model  
with graph  $1 \rightarrow X_1 \rightarrow X_2 \rightarrow \dots \rightarrow X_n$  with all  $X_i$  Bernoulli corresponds to survival  
150 analysis. We note that, in all these cases, multiple parameterizations arise. The parameters  
that are directly interpretable, the *mean-value parameters*, are different from those that  
152 are modeled linearly, the *canonical parameters*. In Bernoulli (logistic) regression, the  
mean value parameter is the proportion  $p = E(X)$ , whereas the canonical parameter is  
154  $\theta = \text{logit}(p) = \log(p) - \log(1 - p)$ . In Poisson regression, the mean value parameter is  
 $\mu = E(X)$  whereas the canonical parameter is  $\theta = \log(\mu)$ .

In all aster models, a transition between life-history stages, i. e. each arrow in  
the graph, corresponds to the conditional distribution of one fitness component, which  
contributes one term to the log likelihood

$$l(\theta) = \sum_j [x_j \theta_j - x_{p(j)} c_j(\theta_j)], \quad (1)$$

where  $x_j$  is the canonical statistic and  $\theta_j$  the canonical parameter for the  $j$ -th conditional  
distribution and  $x_{p(j)}$  is the predecessor of  $x_j$ . Each term of (1) has exponential family  
form, but the sum does not. It can, however, be put in exponential family form

$$l(\varphi) = \left[ \sum_j x_j \varphi_j \right] - c(\varphi) \quad (2)$$

156 by a change of parameter. Either (1) or (2) is a log likelihood for the full model with one  
parameter per variable, and the canonical statistic vector  $x$  is the same for both, but the  
158 linearly modeled canonical parameters,  $\theta$  and  $\varphi$ , differ. To distinguish the two canonical  
parameter vectors, we call  $\theta$  *conditional* and  $\varphi$  *unconditional*.

Unconditional aster models are submodels of the full model determined by the change  
of parameter  $\varphi = M\beta$ . The submodel is also an exponential family with log likelihood

$$l(\beta) = \left[ \sum_k y_k \beta_k \right] - d(\beta) \quad (3)$$

where  $y = M^T x$ . The matrix  $M$  is called the *model* or *design* matrix. For this submodel  $y$  is the canonical statistic and  $\beta$  is the canonical parameter whose maximum likelihood estimate (MLE) solves the equations

$$y_k = E_\beta(Y_k). \tag{4}$$

160 Both  $y$  and the MLE of  $\beta$  are minimal sufficient (contain all of the information in the data about the parameter). The expectation of the canonical statistic  $E_\beta(Y)$  is the mean value  
 162 parameter. The relationship between canonical and mean value parameter is monotone  $\partial E_\beta(Y_k)/\partial \beta_k > 0$ ; increasing one  $\beta$  while holding the rest fixed increases the corresponding  
 164 mean value parameter. Moreover, hypothesis tests and confidence intervals concerning the corresponding canonical parameters directly evaluate the statistical significance of these  
 166 canonical statistics. Unconditional aster models share all of these properties with GLM.

In contrast, none of these properties are shared with conditional aster models, i. e. when the conditional canonical parameter is modeled linearly  $\theta = T\gamma$ , where  $T$  is a model matrix. The resulting submodel is *not* itself an exponential family. The MLE is the  $\gamma$  that solves the equations

$$y_k = \sum_j E_\gamma(X_j | x_{p(j)})t_{jk}, \tag{5}$$

where  $t_{jk}$  are the components of  $T$ , but it has no simple properties. The MLE is not a  
 168 sufficient statistic and has no monotone relationship with expectations.

Either kind of aster model (conditional or unconditional) is a model for the joint  
 170 distribution of all the data. Whereas either may be useful for some particular data, only unconditional models have simple interpretations in terms of unconditional mean values  
 172 (of the canonical statistics), like those familiar from LM and GLM. We recommend them because, when lifetime fitness is a canonical statistic, these tests and confidence intervals  
 174 directly address fitness. The unconditional parameterization is not readily understood intuitively because terms in  $\beta$  that nominally refer to a single component of fitness (affect

176 its  $\varphi_i$  only) directly influence the unconditional expectation of overall fitness by affecting  
not only the distribution of the specified component, but also the distributions of its  
178 predecessor, predecessor of predecessor, etc. Consequently, it is difficult (but not impossible,  
see our Example 2), to see the role played by a single component of fitness. This is an  
180 unavoidable consequence of being able to address overall fitness.

We demonstrate the value and versatility of the aster approach with three examples. In  
182 the first, we illustrate inference of population growth rate. We consider a small dataset that  
Lenski and Service (1982) used to demonstrate their nonparametric method for inferring  
184 population growth rate from a set of individual life-histories of the aphid, *Uroleucon*  
*rudbeckiae*. In this case, we illustrate the use of a conditional model, though either form of  
186 model could be used. In our second example, we apply aster to compare mean fitness among  
groups. Specifically, we quantify effects of inbreeding on fitness of *Echinacea angustifolia*, a  
188 long-lived plant, showing confidence intervals for mean fitness (Fig. 2). In the last example,  
we reanalyze data of Etterson (2004) to evaluate phenotypic selection on the annual legume,  
190 *Chamaecrista fasciculata*, to estimate the fitness surface in relation to phenotypic traits. In  
this case, we show how much simpler aster analysis is when fitness is a canonical statistic  
192 of an unconditional model and also how to proceed when, due to the experimental design,  
it is not. A contributed package “aster” for the R statistical language (R Development  
194 Core Team 2006) does all calculations related to aster models, contains the datasets for our  
examples, and is freely available (<http://www.r-project.org>). Two technical reports (Shaw,  
196 et al. 2007a,b) give more extensive analyses, which are reproducible (see Chapter 1 of Shaw,  
et al. 2007a).

### 3. Example 1: Estimation of population growth rate, $\lambda$

198

Lenski and Service (1982) recognized the need for a valid statistical approach to  
200 inferring rates of population growth ( $\lambda$ ) from life-history records via the stable age equation  
(Fisher 1930). They emphasized the importance of accounting for individual variation in  
202 survivorship and fecundity and of treating the full life-history record of an individual as the  
unit of observation. Lenski and Service (1982) presented a nonparametric approach that  
204 resamples complete records of individual life histories via the jackknife procedure. Using the  
properties of the jackknife, they showed how to obtain estimates and sampling variances of  
206  $\lambda$ . They illustrated the approach with a small dataset sampled from the aphid, *Uroleucon*  
*rudbeckiae*. The survival and fecundity in each of fourteen age intervals were recorded for  
208 18 individuals in a cohort (see Fig. 1A), and these data served as the basis for estimating  $\lambda$   
and its sampling variance.

210 Applying aster to these data, we modeled the binomial parameter governing survival  
probability,  $\text{logit}(\sigma_x)$ , as a quadratic function of age,  $x$ . Survivorship declined significantly  
212 with age ( $P = 0.001$ ), significantly ( $P = 0.028$ ) nonlinearly. Expected fecundities,  $\beta_x$ ,  
modeled according to a Poisson distribution, were estimated for each age class,  $x$ , given  
214 survival to that age.

Interest focuses primarily on estimating  $\lambda$ , but also on its sampling variance, as noted  
216 by Alvarez-Buylla and Slatkin (1994), because of its importance in assessing whether  
a population is growing or declining. The stable age equation implicitly defines  $\lambda$  as a  
218 nonlinear function of the unconditional expectations  $\mu_x = \sigma_x \beta_x$ , which are estimated by  
aster; from these,  $\lambda$  is determined by solving the stable age equation, and standard errors  
220 are obtained using the delta method (Shaw, et al. 2007a, give details). From these data, we  
estimated  $\lambda = 1.677$  with a standard error of 0.056. Our estimate agrees closely with that  
222 of Lenski and Service (1982) (1.688), and 95% confidence intervals are also similar (aster:

1.57, 1.79; jackknife: 1.52, 1.85). We emphasize, however, that the aster approach can be  
224 used in more complicated situations where resampling methods would not be valid.

#### 4. Example 2: Comparison of fitness among groups

226 In this example, we illustrate use of aster models to compare mean fitnesses of groups.  
Specifically, we investigate how relatedness of parents affects progeny fitness in a perennial  
228 plant, *Echinacea angustifolia* (narrow-leaved purple coneflower), a widespread species in  
the N. American prairie and Great Plains. Following the conversion of land to agriculture  
230 and urbanization that began about a century ago, the formerly extensive populations  
now persist in typically small patches of remnant prairie. The plant is self-incompatible,  
232 and Wagenius (2000) detected no deviation from random mating in a large population in  
western Minnesota. In the context of fragmented habitat, matings between close relatives  
234 in the same remnant, and perhaps also long distance matings, may have become more  
common.

236 To evaluate the effects of different mating regimes on the fitness of the progeny, formal  
crosses were conducted between pairs of plants a) from different remnants, b) chosen at  
238 random from the same remnant, and c) known to share maternal parent. The parental  
plants had been growing for 3–4 years in randomized arrays in a common experimental  
240 field. From the resulting seeds, 557 seedlings were germinated. After three months in  
a growth chamber, the surviving 508 individuals were transplanted back into the same  
242 experimental field. Survival of each seedling was assessed in the growth chamber on three  
dates and, after transplanting into the field, annually, 2001–2005. The number of rosettes  
244 (basal leaf clusters, 1–7) per plant was also counted annually 2003–2005. Here, individual  
size is considered a component of fitness during the juvenile period; the typically strong  
246 positive relationship between size and eventual fecundity justifies this here, as elsewhere.

Mortality of many plants ( $\sim 30\%$ ) resulted in a distribution of rosette count in 2005  
248 having many zeros. We modeled survival through each of eight observation intervals as  
Bernoulli, conditional on surviving through the preceding stage; we modeled rosette count  
250 in each of three field seasons, given survival to that season, as zero-truncated Poisson  
(Fig. 1B). To account for spatial and temporal heterogeneity, we also included in the models  
252 as fixed effects a) year of crossing (1999 or 2000), b) planting tray during the period in the  
growth chamber, c) spatial location (row and position within row) in the field.

254 Our primary focus is on evaluating the effects of mating treatments on overall progeny  
fitness, taken as expected rosette count in 2005 for a seed obtained in 2001. In addition, we  
256 investigated the timing and duration of the effects of mating treatment on fitness. These  
effects could be slight during the early stages but, cumulatively, could strongly influence  
258 overall fitness. Alternatively, it may be that the effects of mating treatment at the early  
stages largely account for their overall effects on fitness. These scenarios differ in their  
260 implications concerning the inbreeding load expected in standing populations (Husband  
and Schemske 1996). To evaluate these scenarios, we developed four aster models, named  
262 “chamber,” “field,” “sub,” and “super.” Each was a joint aster analysis of all 11 fitness  
components (survival over eight intervals, rosette count at three times). The “field”  
264 model, corresponding to the first scenario, includes explicit mating treatment effects only  
on the final rosette count (variable `r05` in Fig. 1B), but because of the unconditional  
266 parameterization of aster models, these effects propagate back to earlier stages as well.  
The “chamber” model, referring to the second scenario, includes explicit mating treatment  
268 effects only on the final survival before transplanting (variable `lds3` in Fig. 1B), but, again,  
these effects propagate back through the two preceding bouts of survival. The remaining  
270 two models are required to test the above scenarios of timing of effects; the “sub” model is  
the greatest common submodel of “chamber” and “field,” and the “super” model is their  
272 least common supermodel (i. e. “sub” includes no effects of mating treatment on any aspect

of fitness, whereas “super” includes separate effects of mating treatment on survival up to  
274 transplanting and on final rosette count).

The aster analysis revealed clear differences among the mating treatments in mean  
276 fitness (model “field” compared to “sub”, ( $P = 1.1 \times 10^{-5}$ ). The fitness disadvantage of  
progeny resulting from sib-mating relative to the other treatments is a 35%–42% reduction  
278 in rosette count (Fig. 2 B).

EDITOR: PLACE FIGURE 2 HERE.

280 Because of the propagation of effects back to earlier stages, the effects of mating treatment  
on r05 in the “field” model directly account for expression of fitness at all earlier stages.  
282 Thus, this analysis suffices for inferring the overall effects of mating treatment on fitness.

Our further investigation of the timing and duration of these effects detects differences  
284 among mating treatments in survival up to transplanting (comparison of “sub” and  
“chamber” models  $P = 0.012$ ). Beyond this, the comparison of the “chamber” and “field”  
286 models with the “super” model shows that the “field” model accounts well for differences  
in expressed fitness; “super” fits no better than “field” ( $P = 0.34$ ) but does fit better than  
288 “chamber” ( $P = 3.1 \times 10^{-4}$ ). The terms in the “super” model that quantify the effect of  
mating treatment on survival up to transplanting are not needed to fit the data, because the  
290 back propagation of effects subsumes the effects of mating treatment in the growth chamber.  
This does not mean there are no effects of mating treatment on fitness before transplanting.  
292 The comparison of “sub” and “chamber” confirms they exist, and Fig. 2 clearly shows  
them. The fitness disadvantage of progeny resulting from sib-mating relative to the other  
294 treatments is clear in the 7%–10% reduced survival up to the time of transplanting but the  
overall fitness disadvantage of inbreds is considerably greater (Fig. 2A).

### 5. Example 3: Phenotypic selection analysis

296

Lande and Arnold (1983) proposed multiple linear and quadratic regression of fitness  
298 on a set of quantitative traits as a method for quantifying natural selection directly on  
each trait. In practice, these analyses have generally employed measures of components of  
300 fitness as the response variable, rather than overall fitness (e.g. Lande and Arnold 1983;  
Kingsolver et al. 2002). As a result, the estimated selection gradients (the partial regression  
302 coefficients) reflect selection on a trait through a single episode of selection, rather than  
selection over multiple episodes or over a cohort’s lifespan, as needed for evolutionary  
304 prediction. Focusing on this limitation, Arnold and Wade (1984a) considered partitioning  
the overall selection gradient into parts attributable to distinct episodes of selection, and  
306 Arnold and Wade (1984b) illustrated the approach with examples. Wade and Kalisz (1989)  
modified this approach to allow for change in phenotypic variance among selection episodes.  
308 Whereas these developments were intended to accommodate the multiple stages of selection,  
they do not directly account for the dependence of later components of fitness on ones  
310 expressed earlier, because they entail multiple separate analyses.

Further, Mitchell-Olds and Shaw (1987), among others, have noted that statistical  
312 testing of the selection gradients is often compromised by the failure of the analysis to satisfy  
the assumption of normality of the fitness measure, given the predictors. This concern  
314 applies to McGraw and Caswell’s (1996) approach, which integrates observations from the  
full life-history. To address this problem for the case of dichotomous fitness outcomes,  
316 such as survival, Janzen and Stern (1998) recommended the use of logistic regression for  
testing selection on traits and showed how the resulting estimates could be transformed to  
318 obtain selection gradients. To allow for shapes of the fitness function more general than  
quadratic, Schluter (1988) and Schluter and Nychka (1994) suggested estimation of the  
320 relationship between fitness and traits as a cubic spline, but this also requires a parametric



error distribution, whether normal, binomial, or Poisson.

322        Unconditional aster analysis estimates the relationship between overall fitness and  
traits directly in a single, unified analysis. We illustrate this use of aster with a reanalysis  
324 of Etterson’s (2004) study of phenotypic selection on three traits in three populations of  
the annual legume, *Chamaecrista fasciculata*, reciprocally transplanted into three sites.  
326 The three traits, measured when the plants were 8–9 weeks old, are leaf number (LN, log  
transformed), leaf thickness (measured as specific leaf area, SLA, the ratio of a leaf’s area  
328 to its dry weight, log transformed) and reproductive stage (RS, scored in 6 categories,  
increasing values denote greater reproductive advancement). Here, for simplicity, we  
330 consider a subset of the data for the three populations grown in the Minnesota site,  
comprising records on 2235 individuals.

332        In this experiment, individuals were planted as seedlings, and fitness was assessed as  
1) survival to flowering, 2) flowering, given that the plant survived, 3) the number of fruits  
334 a plant produced, and 4) the number of seeds per fruit in a sample of three fruits, the last  
two contingent on the plant having flowered. For simplicity, we collapsed survival, flowering  
336 and fruiting to a single component of fitness, modeled as Bernoulli (**reprod**). Plants that  
produced fruit were assigned 1 for **reprod**, and those that didn’t, regardless of the reason,  
338 0. Consequently, overall fitness was modeled jointly as reproduction, number of fruits,  
and number of seeds in 3 fruits, (termed **reprod**, **fruit**, and **seed**, Fig. 1C). Preliminary  
340 analyses assessed the fit of truncated Poisson and truncated negative binomial distributions  
to the data for both fecundity components; on this basis the latter distribution was used  
342 for **fruit** and **seed**. In addition to the traits of interest, the model included as fixed effects  
the spatial blocks in which individuals were planted.

344        To illustrate phenotypic selection analysis most straightforwardly, we begin by  
analyzing two of the fitness components, **reprod** and **fruit** with graph Fig. 1D, in relation

346 to the traits LN, SLA, and RS. We use an unconditional aster model, in which overall  
fitness is the number of fruits an individual seedling produced. This model detected  
348 strong dependence of fitness on all three traits such that selection is toward more leaves  
( $P < 10^{-6}$ ), thinner leaves ( $P = 0.006$ ) and earlier ( $P < 10^{-6}$ ) reproductive stage.

350 We detected highly significant negative curvature for LN and SLA suggestive of  
stabilizing selection, ( $P < 10^{-6}$ ); because RS is categorical, we did not consider models  
352 quadratic in it. The plot of the fitness function together with the observed phenotypes  
(Fig. 3, solid contours) reveals that the fitness optimum lies very near the edge of the  
354 distribution of leaf number.

EDITOR: PLACE FIGURE 3 HERE.

356 Thus, for this trait, despite significant negative curvature, selection against both extremes  
of the standing variation in the trait (i.e. stabilizing selection) is not observed. The aster  
358 analysis fits the data well, as reflected by the scatter plots of Pearson residuals which show  
very little trend and only a few extreme outliers for fruit number (Fig. 4A).

360 EDITOR: PLACE FIGURE 4 HERE.

The assumptions for the aster model appear satisfied, and the estimated fitness surface is  
362 both biologically plausible and fits the data well. These points reinforce our confidence in  
the aster model  $P$ -values and estimated fitness surface.

364 We compare the result from aster modeling with that obtained by the approach of  
(Lande and Arnold 1983), which has become standard, ordinary least squares regression  
366 (OLS) of fruit count on traits. The bivariate fitness function inferred via OLS has positive  
curvature for LN, suggesting disruptive selection. This contrasts with the negative curvature  
368 obtained by aster. Fig. 3 reveals why OLS is misled. The fitness surface fitted by aster

(solid contours) has a peak on the right side (large LN) and is fairly flat on the left  
370 (small LN). The quadratic approximation (dotted contours) cannot have flat regions; its  
best approximation is a saddle. Further, a quadratic function cannot have both a saddle  
372 and a peak; thus OLS misses the peak. Another problematic feature of the quadratic  
approximation is that it goes negative. Thus, the main problem with OLS is the bias due to  
374 using a quadratic approximation to a highly non-quadratic surface. The aster model is also  
quadratic, but it is quadratic on the *canonical* parameter scale. The corresponding fitness  
376 estimates, which are mean value parameters, are necessarily positive.

The nominal  $P$ -values produced by OLS regression indicate that the positive curvature  
378 of the quadratic approximation in the LN direction is statistically significant ( $P < 10^{-6}$ ),  
but the homoscedasticity and normality assumptions required for OLS regression to give  
380 meaningful  $P$ -values are seriously violated (Fig. 4B). Such violations of assumptions for an  
OLS regression analysis are expected, given that 3% of plants have fitness of zero and that  
382 the distributions of numbers of fruits per plant is heavily skewed. These violations make  
the nominal  $P$ -value from the OLS invalid.

384 We extend the above phenotypic selection analysis to include the additional fitness  
component, **seed**, using the graph Fig. 1C. In this case, fitness is no longer a canonical  
386 statistic, i.e. there is no linear combination of the variables corresponding to fitness.  
The two fecundity components, **fruit** and **seed**, are modeled as separately dependent  
388 on **reprod**. This analysis detected dependence of **fruit** on LN ( $P < 10^{-6}$ ) and on SLA  
( $P = 0.046$ ) and of **seed** on both LN ( $P < 10^{-6}$ ) and RS ( $P < 10^{-6}$ ). It also found  
390 significant curvature in the relationship between **fruit** and both LN ( $P < 10^{-6}$ ) and SLA  
( $P = 0.035$ ) and between **seed** and LN ( $P = 0.0008$ ). Here again, we did not attempt to fit  
392 quadratic dependence on RS. Use of an unconditional aster model in these analyses yields  
an estimate of the relationship between each fitness component and each trait that takes

394 into account pre-reproductive mortality.

The above analysis does not, however, satisfy the goal of evaluating the relationship  
396 between overall fitness and the traits; because fitness is not a canonical statistic, its  
expectation is not produced directly by aster methods. However, it can be approximated  
398 by averaging simulations. In detail, we use the estimated parameter values to simulate  
fitness records for individuals representing each trait combination, and from these, we  
400 calculate `fruit * seed / 3`. The average over the simulated fitness values for each trait  
combination approximates its expected fitness. The resulting fitness surface (Fig. 5, solid  
402 contours) resembles that estimated using only `fruit` as the fecundity measure, though it  
provides more compelling evidence of true stabilizing selection on LN. The best quadratic  
404 approximation fitted by OLS has a saddle also in this case.

EDITOR: PLACE FIGURE 5 HERE.

406 There are two alternative data structures in which a simple aster analysis, needing  
no simulation, would directly analyze fitness. The graph  $1 \rightarrow \text{reprod} \rightarrow \text{fruit} \rightarrow \text{seed}$   
408 would be appropriate if all seeds (from all fruits) had been counted for each individual.  
Then, in an unconditional aster model, fitness would be `seed`, a canonical statistic, and  
410 the analysis would automatically take the contribution of `reprod` and `fruit` to fitness into  
account. However, it is often impractical, as in this case, to count all seeds. Subsampling  
412 is a common practice in studies of animals (e.g. Howard 1979), as well as plants. An  
alternative to exhaustive enumeration that facilitates aster analysis is to obtain for each  
414 individual the seed count for a random number of fruits, corresponding to the graph  
 $1 \rightarrow \text{reprod} \rightarrow \text{fruit} \rightarrow \text{samp} \rightarrow \text{seed}$ , where `samp` is the number of fruits sampled for  
416 the individual, a  $\text{binomial}(\text{fruit}, p)$  random variable, where  $p$  is fixed and known (the  
fraction of fruit sampled). In this sampling scheme, fitness would be proportional to `seed`,  
418 a canonical statistic, and aster analysis would be simplified.

For our actual data, it might seem natural to use the product of fruit count  
420 and number of seeds per fruit as one variable in an aster analysis, so the graph is  
 $1 \rightarrow \text{reprod} \rightarrow \text{fruit} * \text{seed} / 3$  but this would not be valid, because this product is not  
422 distributed according to an exponential family. Alternatively, it might seem natural to use  
the preceding graph with `samp` replaced by the constant 3, but this is also invalid because  
424 the constant 3 is not distributed according to an exponential family. Thus, the structure  
of this aster model precluded inference of overall selection via a simple aster analysis.  
426 Nevertheless, simulation yielded the expected fitness surface.

In this section, we have illustrated how aster can conduct phenotypic selection analysis  
428 on complete life-history records to yield more biologically interpretable estimates of the  
fitness surface. Moreover, even for analysis of an annual life-history, commonly considered  
430 relatively straightforward, aster greatly improves over OLS in its adherence to statistical  
assumptions and, accordingly, in the validity of the inferences. We have also shown that,  
432 even when the available data preclude modeling total reproductive output as sequentially  
dependent on all earlier expressed fitness components, aster estimates the parameters of  
434 a fitness model that can be used (with simulation, if necessary) to produce a statistically  
sound phenotypic selection analysis.

## 436 **6. Discussion**

Both the numerical and genetic dynamics of a population depend fundamentally  
438 on individuals' contributions of offspring, their fitness. Extensive theoretical work (e.g.  
Fisher 1930; Charlesworth 1980) has formalized and extended this insight of Darwin, yet  
440 statistical challenges have continued to compromise the empirical evaluation of fitness.  
The aster approach addresses these challenges and takes full advantage of available  
442 data to yield comprehensive assessments of fitness that are as precise as possible. The

precision of aster modeling not only offers statistical power for tests of hypotheses; it also  
444 promotes quantitative comparison of fitnesses. Most important, as a general framework for  
analyzing life-history data, aster can address questions that arise in diverse evolutionary  
446 and ecological contexts. The examples presented here illustrate the breadth of aster’s  
applicability, including estimation of population growth rate, comparison of mean fitness  
448 among groups, and inference of phenotypic selection. Even beyond analysis of life-history  
data, aster modeling is appropriate for any set of responses in which there are dependencies  
450 analogous to those characteristic of life-histories. In an experimental study of foraging  
behavior, for example, individual subjects may forage in a given interval or not and, given  
452 that they forage, may take varying numbers of prey. In a medical context, aster can expand  
on survival analysis by incorporating measures of patients’ well-being in evaluating the  
454 relative benefits of different procedures. We emphasize that aster obviates the common  
practice of multi-step analysis, which cannot provide valid statistical tests or sound  
456 estimates of sampling error. A single aster model can encompass the real complexities not  
only of life-histories, but also of discrete and continuous predictors, and thus provide a full  
458 analysis to yield direct inferences about fitness and population growth.

Lifetime fitness rarely, if ever, conforms to any distribution amenable to parametric  
460 statistical analysis less complex than aster analysis. This pathology of fitness distributions  
has plagued empirical studies of fitness. Resampling approaches are sometimes used, but  
462 this is not a general solution, because *valid resampling schemes are not generally available  
for complex data structures*. Moreover, resampling methods sacrifice statistical precision  
464 relative to parametric analysis. As an alternative, transformations are often attempted, but  
the prevalence of mortality before reproduction typically results in fitness distributions with  
466 many individuals at zero, such that no transformation produces a well known distribution.  
Moreover, even if such a transformation could be found, analyses of fitness on an alternative  
468 scale can mislead (Stanton and Thiede 2005). Aster addresses these problems by directly

modeling each distinct component of fitness with a suitable parametric distribution and  
470 accounting for the dependence of each fitness component on those expressed earlier. As  
a consequence, it models the sampling variation appropriately and yields results on the  
472 biologically natural scale of expected number of individuals produced per individual. Even  
when life-history records are available for only a portion of the life-span of a cohort, as in  
474 our Example 2, joint analysis via an unconditional aster model provides comparisons based  
on the most comprehensive fitness records at hand.

476 Studies of variation in fitness often focus on a single component of fitness (e.g. Arnold  
and Lande 1983). These are less subject to distributional problems and can yield insight  
478 into the nature of fitness variation during a particular episode of selection. However, the  
resulting understanding of fitness and its variation is fragmentary and can be misleading  
480 when the relationship between components of fitness, on the one hand, and traits or  
genotypes, on the other, varies over the lifespan (Prout 1971). Whereas Arnold and Wade  
482 (1984a) proposed an approach to evaluate phenotypic selection over multiple episodes  
(modified by Wade and Kalisz 1989), this approach uses separate analyses of each episode,  
484 ignoring the dependence structure of fitness components. Consequently, the sampling  
variance of the resulting estimates of selection cannot readily be determined.

486 Our first example illustrates use of aster to infer population growth rate. Lenski and  
Service (1982) first noted the importance of sound statistical modeling for population  
488 growth. Our use of aster in this context builds on their work by employing parametric  
models for each life-history event. The resulting estimate of growth rate is similar to that  
490 obtained by Lenski and Service’s (1982) method using the jackknife, as are the confidence  
intervals from the two approaches. The key point is that aster analysis provides a sound  
492 parametric basis for inferences about population growth even for data structures that are  
not suited to resampling. Though we have emphasized the utility of unconditional aster

494 models for inferences about lifetime fitness, conditional aster models also offer the capability  
of obtaining estimates of expected values of a life-history component, conditional on earlier  
496 life-history status (e.g. fecundity at a given age, given survival to that age), as we have  
done in this example.

498 In the example of Lenski and Service (1982), complete records are available for each  
individual in a single cohort, so the life table can be based on age. Life histories are  
500 often tabulated in relation to size or stage categories instead of age, because size or stage  
often predicts survival and fecundity better than age does (Caswell 2001, chap. 2); this  
502 is especially useful when ages of individuals are unknown, for example, in censuses of  
populations in nature, as in the examples of Alvarez-Buylla and Slatkin (1994). Though  
504 our examples include only cases based on age, aster analysis is also suitable for analyzing  
life-history data according to stage or size.

506 Our second example demonstrates the use of unconditional aster models to estimate  
and compare mean fitness for groups produced by different mating schemes and, thus,  
508 differing in genetic composition. This analysis reveals that the remnant populations of  
*E. angustifolia* are subject to severe inbreeding depression of at least 70% overall, when  
510 extrapolated linearly to inbreeding arising from one generation of selfing. In a similar  
application of aster, Geyer et al. (2007) have analyzed survival and annual production of  
512 flower heads jointly for samples of these remnant populations grown in the common field.  
This analysis revealed greater than twofold differences in mean fitness among remnants  
514 ( $P < 0.01$ ). In the case we provide here, we further demonstrate how the likelihood  
framework of aster permits straightforward tests of several hypotheses. We show that the  
516 significant early disadvantage in size and survival of inbred plants does not adequately  
account for the fitness differences at the end of the period of observation. Rather, inbreeding  
518 depression in growth and survival exacerbates the fitness disparity beyond the first three



months. Thus, in addition to providing statistically rigorous comparisons of overall fitness  
520 among groups, aster yields insights into the timing of fitness effects.

Aster readily extends further to accomplish phenotypic selection analysis, by  
522 establishing the relationship between individuals' overall demographic-genetic contribution  
to the next generation and the traits they express. For this, the aster model includes the  
524 traits under consideration as predictors of cumulative fitness; inference of quadratic and  
correlational selection is also straightforward. Our Example 3 shows aster's estimation of  
526 the fitness surface when fitness is a linear function of the components of fitness and also  
demonstrates how to obtain such an estimate even when it is not. Van Tienderen (2000)  
528 presented a method with a similar goal, but it does not take into account the dependence  
relationships of the fitness components and is subject to the usual distributional problems  
530 (e.g. Coulson et al. 2003). Further, it cannot validly represent the statistical uncertainty of  
inferred parameters because it involves separate analyses to estimate selection gradients for  
532 each fitness component. In our examples 2 and 3 and the example in Geyer et al. (2007),  
use of an unconditional model was essential to obtain results that are interpretable as  
534 comparisons of overall fitness. In our examples  $P$ -values and confidence intervals reported  
are asymptotic, but we do not need to rely on asymptotic normality of MLE because  
536 the parametric bootstrap is easily done with the aster software and does not require this  
assumption.

538 The centrality of fitness to many evolutionary and ecological questions demands  
a statistical approach that rigorously models the inevitable, complex dependencies of  
540 life-history data. Our examples provide only a glimpse of the range of possible uses of aster  
models. Conceivably, all the issues in all our examples and more besides, could arise in a  
542 single analysis, as could more extensive dependence. The aster approach addresses these  
challenges. Its versatility suits it to answer the full breadth of questions that life-history

544 data can address. Aster can play a key role in linking ecological and evolutionary study of  
populations.

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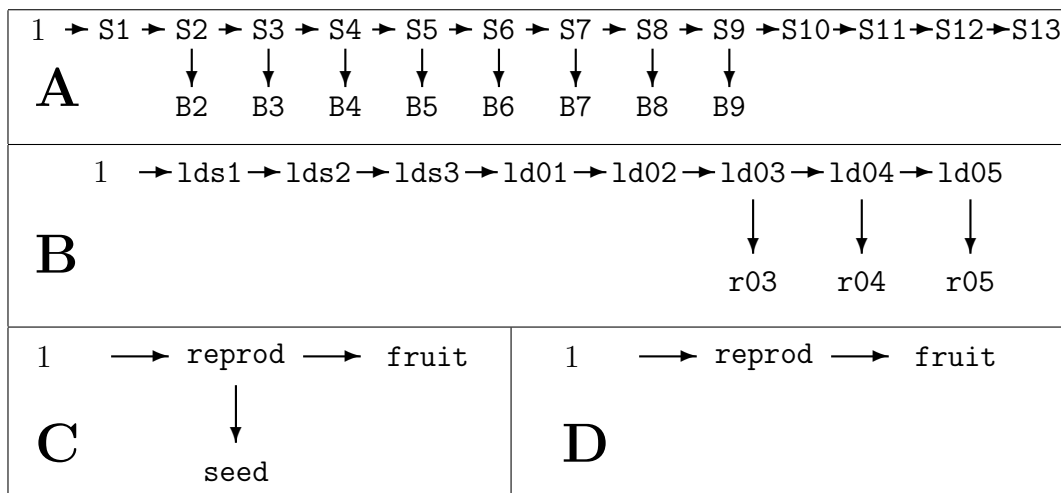


Fig. 1.— Graphical models for our three empirical examples. Each node of a graph is associated with a variable, root nodes with the constant variable 1, indicating presence of an individual at the outset. Arrows lead from one life history component to another that immediately depends on it (from predecessor node to successor node of the graph). If a predecessor variable is nonzero, then a particular conditional distribution of the successor variable is assumed. If a predecessor variable is zero for a given individual, for example due to mortality, then its successor variables are also zero. A: Example 1: *Uroleucon rudbeckiae*, an aphid. An individual’s fitness is determined by its survival to each age,  $S_i$ , modeled as (conditionally) Bernoulli and the number of young it produces at each age,  $B_i$  modeled as (conditionally) zero-truncated Poisson B: Example 2: *Echinacea angustifolia*, a perennial plant. Fitness comprises juvenile survival at three times up to transplanting into the field ( $lds_i$ ) and subsequent survival through five years ( $ld0_i$ ), as well as the plant’s number of rosettes ( $r0_i$ ) in three years. The survival variables are modeled as (conditionally) Bernoulli (zero indicates mortality, one indicates survival), and  $r0_i$  is (conditionally) zero-truncated Poisson (i.e. a Poisson random variable conditioned on being greater than 0). C and D: Example 3: *Chamaecrista fasciculata*, an annual plant. Success or failure of reproduction (here, including survival to reproduction) is given by **reprod**, modeled as Bernoulli (zero indicates no seeds, one indicates survival to reproduction). Given that a plant reproduces, the components of its fecundity are its number of fruits (**fruit**) and, in C its and number of seeds per fruit in a sample of three fruits (**seed**). Each are modeled as negative binomial, respectively, two-truncated and zero-truncated.



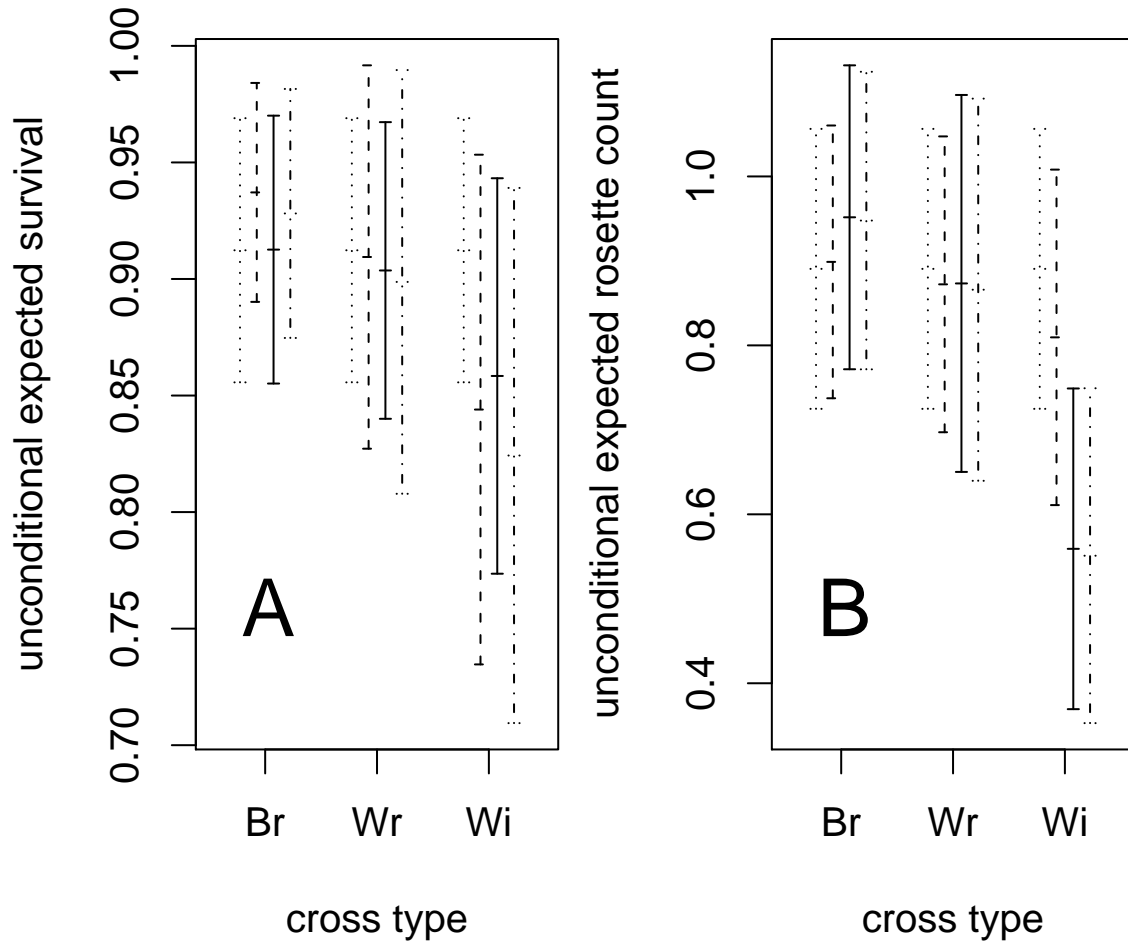


Fig. 2.— Predicted values and 95% confidence intervals for the unconditional mean value parameter for (A) survival up to transplanting and (B) rosette count in the last year recorded (i.e. overall fitness over the study period) for a “typical” individual for each cross type. The experimentally imposed crossing treatments are Br, between remnant populations; Wr, within remnant populations; and Wi, inbred within remnants (i.e. between sibs). Lines indicate model: dotted, “sub” model; dashed, “chamber” model; solid, “field” model; dot-dash, “super” model.

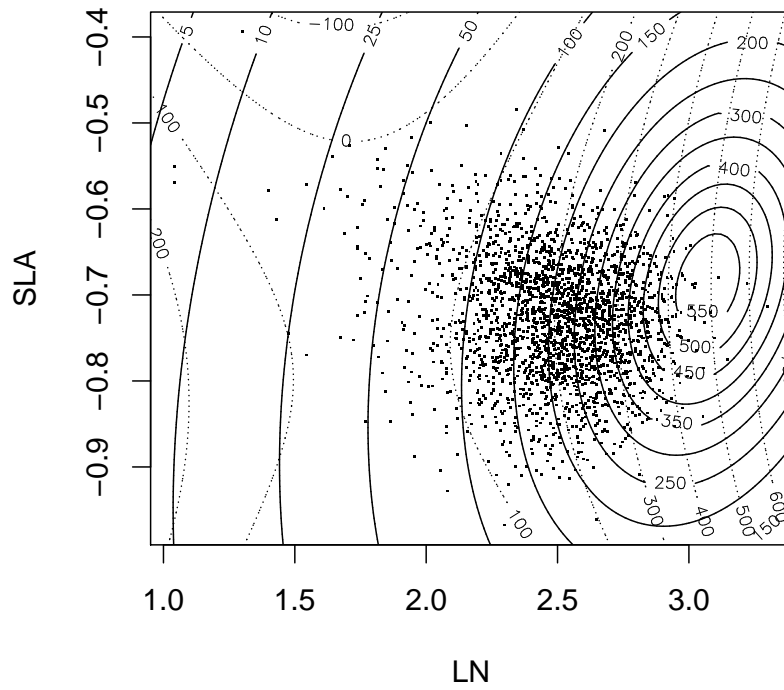


Fig. 3.— Scatterplot of SLA (specific leaf area, ln transformed) versus LN (leaf number, ln transformed) with contours of the fitness function (expected fruit count) estimated by aster (solid) and its quadratic approximation via Ordinary Least Squares (dotted). Cf. Fig. 5.

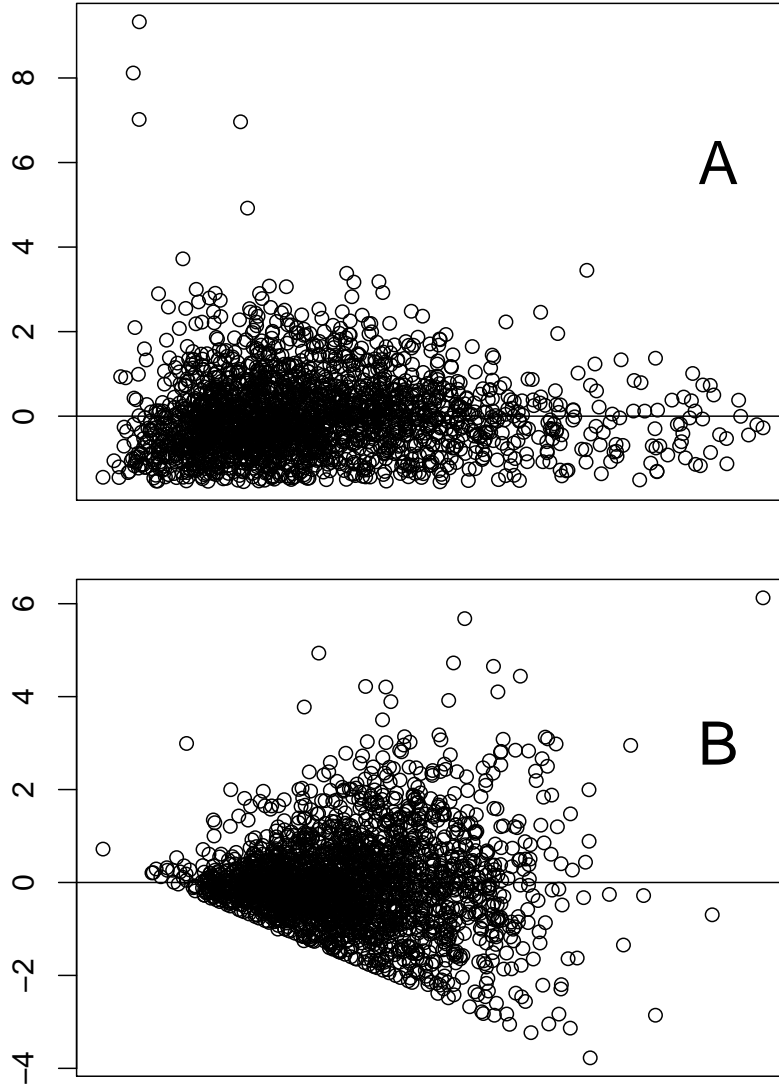


Fig. 4.— Residual plots from phenotypic selection analyses for *Chamaecrista fasciculata*. A. Pearson residuals for fruit count conditional on reproduction plotted against values fitted from the aster model quadratic in leaf number (LN) and specific leaf area (SLA) and also containing reproductive stage (RS) and spatial block. B. Similar except standardized residuals fitted by ordinary least squares (same response and predictors as in A).

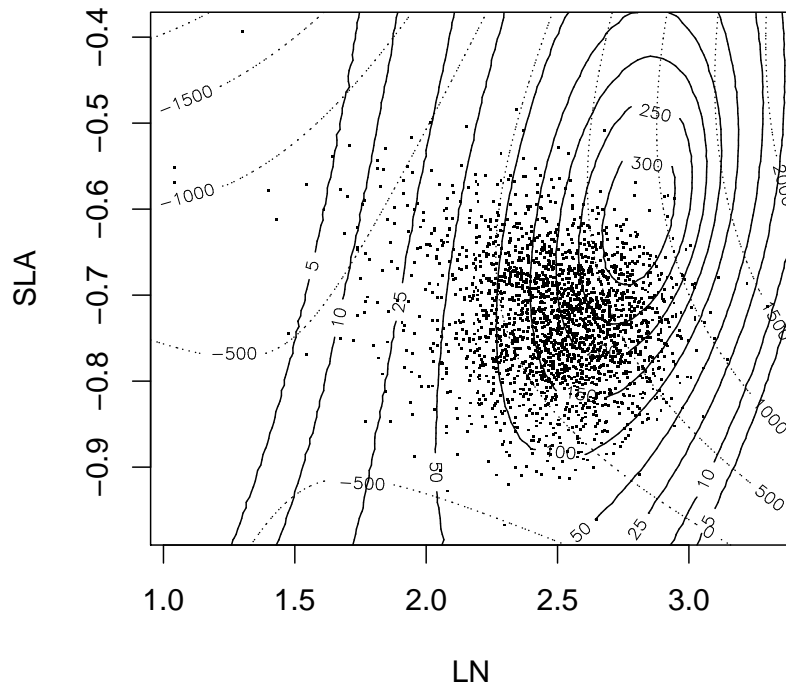


Fig. 5.— Scatterplot of SLA (specific leaf area,  $\ln$  transformed) versus LN (leaf number,  $\ln$  transformed) with contours of the fitness function (expectation of fruit times seed divided by three) estimated by aster (solid) and the quadratic approximation via Ordinary Least Squares (dotted). Cf. Fig. 3.