

Riding across the selection landscape: fitness consequences of annual variation in reproductive characteristics

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Evolutionary models estimating phenotypic selection in character size usually assume that the character is invariant across reproductive bouts. We show that variation in the size of reproductive traits may be large over multiple events and can influence fitness in organisms where these traits are produced anew each season. With data from populations of two orchid species, *Caladenia valida* and *Tolumnia variegata*, we used Bayesian statistics to investigate the effect on the distribution in fitness of individuals when the fitness landscape is not flat and when characters vary across reproductive bouts. Inconsistency in character size across reproductive periods within an individual increases the uncertainty of mean fitness and, consequently, the uncertainty in individual fitness. The trajectory of selection is likely to be muddled as a consequence of variation in morphology of individuals across reproductive bouts. The frequency and amplitude of such changes will certainly affect the dynamics between selection and genetic drift.

Keywords: fitness; morphological variation; orchids; natural selection; variation in selection; plasticity

1. INTRODUCTION

Darwin described the great diversity of floral forms as adaptations to enhance the probability of cross-pollination. He elaborated this idea in his first post-Origin treatise, *The various contrivances by which orchids are fertilized by insects* and in a later book, *Effects of cross- and self-fertilization in the vegetable kingdom*; he provided ample evidence for the driver of such a remarkable array of adaptations: the fitness advantage of cross-pollination (Darwin 1862, 1877). He concludes the second edition of his ‘Contrivances’ book by saying, ‘It is hardly an exaggeration to say that Nature tells us, in the most emphatic manner, that she abhors perpetual self-fertilisation’ (Darwin 1885). These books, of course, supported his theory of natural selection and launched the field of pollination biology. For nearly 150 years, we have been gathering evidence and creating models to elucidate the patterns and processes involved in the evolution of flowers. Our efforts have revealed a remarkable complexity of context-dependent processes that continue to be refined. We now consider natural

selection to be based on three conditions: presence of variation, a genetic basis for the variation and fitness differences among variants. From these we can predict the outcome of natural selection (Endler 1986).

Most selection models assume that fitness remains constant (Endler 1986; Gavrillets 2004) and, more importantly, that morphological characteristics of iteroparous individuals are invariant within and among reproductive bouts. However, floral traits can vary by temporal environmental variation within a season as well as by flower position on the inflorescence (Tremblay 2006; Herrera 2009). Annual variation in floral traits of an individual is another source of variation, and this is what we address here. Sexual organs and associated structures of perennial flowering plants are produced anew every reproductive bout and probably as a response to environmental conditions change constantly. Plants respond to environmental fluctuations in a variety of ways (Bradshaw 1965; Fowler & Antonovics 1981; Schlichting 1986; Sultan 1987; Price *et al.* 2003; Zhang & Hill 2005; Paenke *et al.* 2007). Interestingly, variability in floral characteristics among reproductive events in iteroparous individuals has seldom been studied, particularly in the context of year-to-year fluctuation in environmental conditions. Not surprisingly, such variation among reproductive bouts has yet to be evaluated with respect

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Figure 1. *Caladenia (Arachnorchis) valida*. Plant habit and flower at Raymond Island, Victoria, Australia. Photos by Andrew Bould.

to individual fitness landscapes, although other components of variance have been evaluated (Wilson & Harder 2003; Lande 2007, 2008, 2009; Rice 2008).

Natural selection models are anchored in the notion that variation in phenotypic expression probably leads to fitness differences among individuals (Lande & Arnold 1983; Endler 1986; Gavrillets 2004 and references therein). If morphological variation in an individual varies little among reproductive bouts, then measuring selection at one specific time may represent a value close to that individual's true fitness. However, if traits of individuals fluctuate substantially from year to year, then an individual may occupy different parts of the fitness landscape over time. Estimating lifetime reproductive success for such individuals and calculating selection coefficients become complex. The models can be even more complicated if the fitness landscape also varies among reproductive periods (DeWitt & Scheiner 2004; Gavrillets 2004; Harder & Johnson 2009).

From this perspective, evolutionary processes can be grouped in three general patterns:

- when fitness landscapes are flat, genetic drift will dominate evolutionary processes;
- when fitness landscapes are not flat and selection gradients are steep, then
 - (i) selection should dominate and be rapid when individual characters vary little among periods, or
 - (ii) selection should be slow, or inconsistent and perhaps indistinguishable from a random process of evolution when individual characters vary extensively among periods.

Morphological variation among reproductive periods can influence fitness. The traditional assumption, that individual phenotypes are invariant, would result in a precise measure of individual fitness. On the other end of the spectrum, an individual may express

considerable phenotypic variation among reproductive bouts. If individuals are very long lived, their lifetime fitness should be close to their mean. However, an individual that lives briefly has fewer opportunities to sample the fitness landscape for a given phenotype. The consequence is that predicting selection advantage for an individual with large morphological variance on a varying fitness landscape becomes more complicated. More importantly the fluctuations among years in floral traits and selection landscapes may result in an evolutionary process indistinguishable from drift.

Here, we return to Darwin's original model system, the orchids, to describe individual variation in size of floral characteristics among reproductive bouts. We ask whether such variation influences patterns of reproductive success.

2. MATERIAL AND METHODS

(a) *Study species*

We studied the spider orchid *Caladenia valida* (Nichols) M. A. Clem. & D. L. Jones on Raymond Island, Victoria, Australia. Flowering individuals of this species produce a single flower (figure 1). We measured flower size (from the top of the dorsal sepal club to the bottom two clubs on the lateral sepals) annually for 50 plants from 2003 to 2007. *Caladenia valida* plants have an underground dormancy stage of several months, but frequently some individuals remain below ground until a subsequent flowering season (Tremblay *et al.* 2009a,b), so resampling of individuals varied from 2 to 4 years. Our measure of fitness is fruit set, and fruits of *Caladenia* species contain 30–30 000 dust like seeds (Dixon & Tremblay 2009). Typical of deceptively pollinated orchids, *C. valida* fruit set is variable among years (2.5–87.8%; 2000–2007) and attributed to pollinator limitation (Tremblay 2005; Tremblay *et al.* 2005).

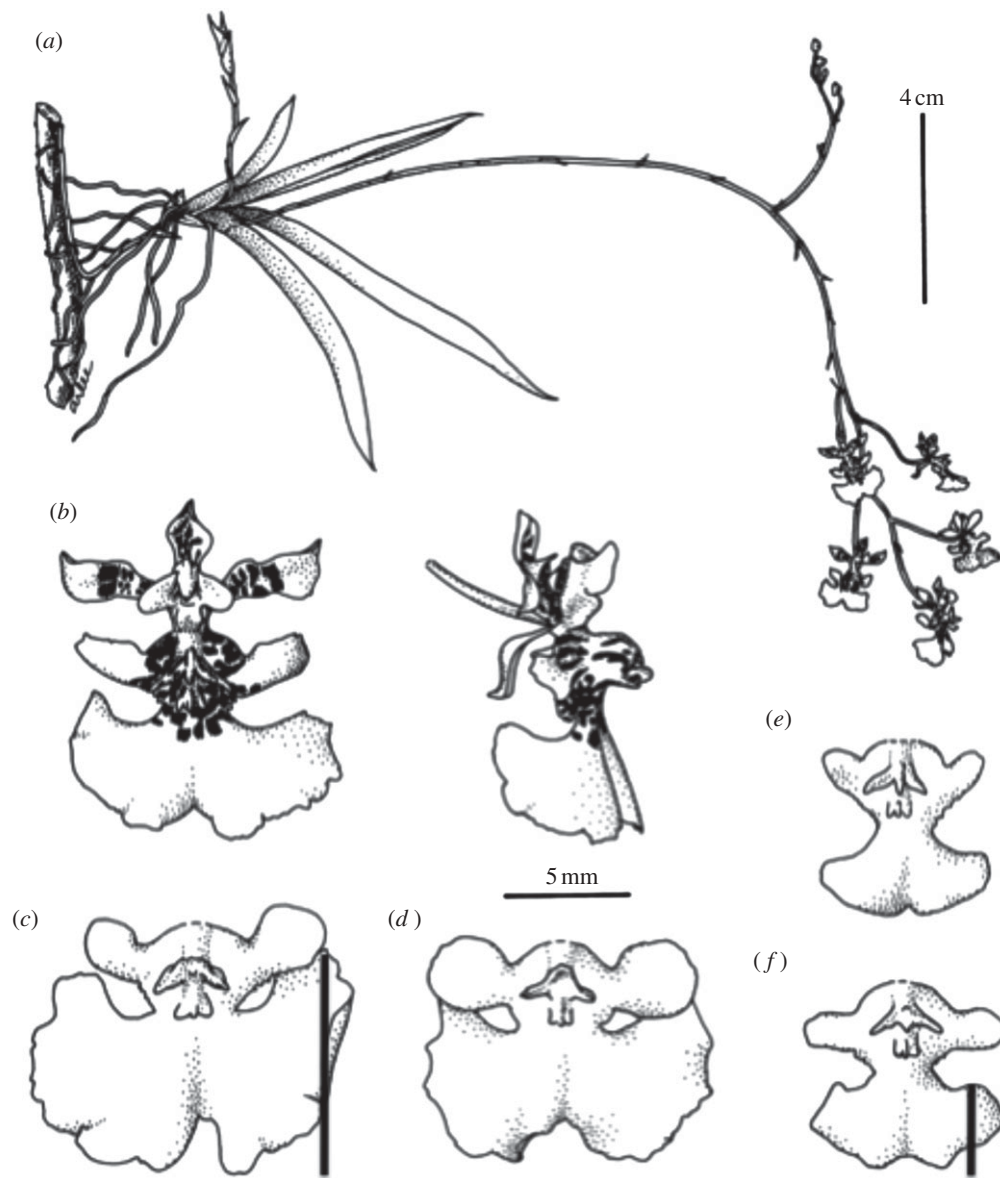


Figure 2. *Tolumnia variegata*. (a) Plant habit. (b) Flowers, front and lateral views. (c–f) Variation in the mid-lobe of the lip morphology (black line) from flowers collected from a single population in one season. Adapted from the American Society of Plant Taxonomists. Illustrated by Arlee M. Montalvo.

We also quantified the relation of fruit set to the length of the mid-lobe of the lip in a population of angelitos, *Tolumnia variegata* (Sw.) Braem (figure 2), from Laguna Tortuguero, Puerto Rico ($18^{\circ}27'05.44''$ N, $66^{\circ}26'34.82''$ W). This species is a common twig epiphyte on shrubs and small trees, primarily in secondary habitats (Ackerman 1995). Plants are relatively short lived. At a nearby site, some individuals lived up to 10 years, but the average expected lifespan of an adult plant was only 2.7 years (Meléndez & Ackerman 1993). Populations of *T. variegata* show substantial genetic and morphological variation within populations (Ackerman & Galarza-Pérez 1991; Ackerman & Ward 1999). Flowers are self-incompatible and offer no pollinator rewards (Ackerman & Montero Oliver 1985; Calvo 1993; Sabat & Ackerman 1996): pollination involves deceit of female *Centris decolorata* Lepeletier (Apidae) presumably seeking oils offered by Malpighiaceae flowers (Roubik 1989; Sabat &

Ackerman 1996; Ackerman *et al.* 1997 (as *C. versicolor*)). Fruits contain several thousand seeds (Calvo 1993), but plants are severely pollination limited as are many orchid species (Calvo 1993; Meléndez & Ackerman 1993; Tremblay *et al.* 2005). We monitored 99 plants in sunny and shady sites during 1999 and 2000. The former year was wetter than average, and the latter was a drought year.

(b) Statistical analysis

We assessed phenotypic selection with Bayesian regression models relating fruit set to morphological variation. Models that accounted for within-plant variability considered

$$Y_{ij} \sim N(\mu_i, \sigma_W^2),$$

$$n_i \sim N(M, \sigma_B^2),$$

where Y_{ij} is the morphological character of interest, μ_i

is the mean morphology for individual i , M is the population mean, σ_W^2 and σ_B^2 are the within- and among-plant variances. Vague priors were assigned to all parameters, except σ_W , which was assigned a uniform prior between 0 and $\sigma_B/2$. This selection is based on a biological assumption: variability between individuals should be greater than variability within a given individual. Our selection of the upper bound for the variance within individuals can be seen as arbitrary, and other possibilities could be explored; nevertheless, it allows us to see the effect of including individual variation in the analysis. Also, in one of the analyses an informative prior was assigned to M ; this prior is based on prior knowledge of the authors with respect to the species. For both studied species, models were fitted using WinBUGS 1.4 (Lunn *et al.* 2000). For each model, two parallel chains of 20 000 iterations were generated, with a burn-in period of 5000 iterations. Convergence was tested graphically and using Brooks & Gelman's (1998) modification of Gelman–Rubin convergence statistic.

For *C. valida*, we analysed logistic models for relating flower size, FS, with presence or absence of fruits. Let $F_{ij} = 1$ if the individual i had a fruit in year j , and $F_{ij} = 0$ if not with a Bernoulli distribution. Then

$$F_{ij} \sim \text{Bernoulli}(p_{ij}),$$

where p_{ij} , the probability that individual i produced a fruit during year j , is related to flower size, FS_{ij} , through a logistic model of the form

$$\log\left(\frac{p_{ij}}{1-p_{ij}}\right) = f(FS_{ij}),$$

where f is a linear model on flower size. Three different models were fitted: constant, linear and quadratic, and they were compared using the deviance information criterion (DIC) (Spiegelhalter *et al.* 2002) (table 1). The model associated with the smallest DIC provides the best fit to the data. Models with DIC differences of less than 2 units of the minimum are considered to be given strong support. Models with DIC values within 4–7 units of the minimum receive considerably less support, and those models with DIC values more than 10 units away from the minimum DIC value can be ruled out (McCarthy 2007).

To compare both models, we calculated predictive posterior distributions for the probability of fruit for different values of flower size (considering or not variability in the fitness landscape).

For *T. variegata* we considered the linear and quadratic influences of lip length and whether a plant grew in sun or shade on fruit number; fruit production was assumed to be a Poisson variable. Alternative models that considered different combinations of these influences (table 2) were compared using the DIC.

The following models were considered (the explanatory variable was centred in order to reduce correlation between regression coefficients):

- (i) Constant model

$$\log(\lambda_{ij}) = \alpha.$$

Table 1. DIC and p_D (effective number of parameters) and Δ DIC (difference between DIC value for the model and lowest DIC value in the model set) values for log-linear models relating fruit set and flower size for *C. valida*. The model in bold receives the strongest support from the DIC.

model	p_D	DIC	Δ DIC
1 constant	1	199.35	3.76
2 linear model	2.02	199.94	4.35
3 quadratic model	3	195.59	0

- (ii) Constant model in shade and in sun

$$\log(\lambda_{ij}) = \alpha(1 - S_i) + \alpha_1 S_i.$$

- (iii) Linear model

$$\log(\lambda_{ij}) = \alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}).$$

- (iv) Linear model in sun, constant model in shade

$$\log(\lambda_{ij}) = \alpha(1 - S_i) + (\alpha_1 + \beta_1(\text{LL}_{ij} - \bar{\text{LL}}))S_i.$$

- (v) Constant model in sun, linear model in shade

$$\log(\lambda_{ij}) = (\alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}))(1 - S_i) + \alpha_1 S_i.$$

- (vi) Linear model in sun and in shade

$$\log(\lambda_{ij}) = (\alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}))(1 - S_i) + (\alpha_1 + \beta_1(\text{LL}_{ij} - \bar{\text{LL}}))S_i.$$

- (vii) Quadratic model

$$\log(\lambda_{ij}) = \alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma(\text{LL}_{ij} - \bar{\text{LL}})^2.$$

- (viii) Quadratic model in sun, constant model in shade

$$\log(\lambda_{ij}) = \alpha(1 - S_i) + (\alpha_1 + \beta_1(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma_1(\text{LL}_{ij} - \bar{\text{LL}})^2)S_i.$$

- (ix) Quadratic model in sun, linear model in shade

$$\log(\lambda_{ij}) = (\alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}))(1 - S_i) + (\alpha_1 + \beta_1(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma_1(\text{LL}_{ij} - \bar{\text{LL}})^2)S_i.$$

- (x) Constant model in sun, quadratic model in shade

$$\log(\lambda_{ij}) = (\alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma(\text{LL}_{ij} - \bar{\text{LL}})^2) \times (1 - S_i) + \alpha_1 S_i.$$

- (xi) Linear model in sun, quadratic model in shade

$$\log(\lambda_{ij}) = (\alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma(\text{LL}_{ij} - \bar{\text{LL}})^2) \times (1 - S_i) + (\alpha_1 + \beta_1(\text{LL}_{ij} - \bar{\text{LL}}))S_i.$$

Table 2. DIC and p_D (effective number of parameters) and Δ DIC (difference between DIC value for the model and lowest DIC value in the model set) values for log-linear models relating fruit set, lip length and site (sunny or shady) for *T. variegata*. Models in bold receive stronger support from the DIC.

model		p_D	DIC	Δ DIC
1	constant model	1	481.19	3.17
2	constant model in shade and in sun	2	478.93	0.90
3	linear model	1.98	480.91	2.88
4	linear model in sun, constant model in shade	3	478.02	0
5	constant model in sun, linear model in shade	2.98	480.84	2.82
6	linear model in sun and in shade	3.97	479.91	1.89
7	quadratic model	2.97	482.90	4.88
8	quadratic model in sun, constant model in shade	3.94	478.24	0.22
9	quadratic model in sun, linear model in shade	4.93	480.17	2.15
10	constant model in sun, quadratic model in shade	3.96	482.71	4.69
11	linear model in sun, quadratic model in shade	4.94	481.77	3.75
12	quadratic model in sun and in shade	5.90	482.03	4.01

(xii) Quadratic model in sun, quadratic model in shade

$$\log(\lambda_{ij}) = (\alpha + \beta(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma(\text{LL}_{ij} - \bar{\text{LL}})^2) \times (1 - S_i) + (\alpha_1 + \beta_1(\text{LL}_{ij} - \bar{\text{LL}}) + \gamma_1(\text{LL}_{ij} - \bar{\text{LL}})^2)S_i.$$

An informative $N(1.5, (1/6))$ prior was assigned to M , the overall mean for lip length. Predictive posterior distributions for the probability of fruit were calculated for different values of lip length for both models (considering or not variability in the fitness landscape) in order to compare these distributions.

3. RESULTS

(a) Magnitude of variation

For *Caladenia*, the standard deviation of flower size between individuals, σ_B , has a posterior mean of 8.99 and a 95 per cent posterior probability interval of (7.93, 10.29), while the posterior mean for the standard deviation of flower size within individuals, σ_W , is 4.35 and its 95 per cent posterior probability interval is (3.87, 4.90). In the case of *Tolumnia*, the standard deviation of lip length between individuals has a posterior mean of 0.175 with a 95 per cent posterior probability interval of (0.16, 0.19), while the posterior mean for the standard deviation of lip length within a given individual has mean 0.086 and 95 per cent posterior interval of (0.078, 0.095). In both cases, the mean and the extremes of the intervals for the within-individuals standard deviation are half the values for the between individuals standard deviation.

(b) Effects of varying morphology

The probability of fruit set by *Caladenia* suggests disruptive selection, where small and large flowers have a fitness advantage, regardless of whether the regressions accounted for within-plant variation (figure 3). Within-plant variation affected the width of the credibility interval at both ends of the spectrum (figure 3). The standard deviation for size among years for an individual exceeded that of the population simply because the population sample size was much

larger than the number of years sampled for an individual. We therefore constrained our statistical model so that the expected standard deviation could not be larger than half the variation of the whole population. If we accept this range of size as realistic, then fitness varies among size classes. Given this biological assumption, the posterior distribution of the fitness landscape for an individual with a mean size of 30 cm is platykurtic (producing wide credible intervals). By contrast, an individual with a mean size of 60 cm with a smaller credible interval of fitness and relatively invariant fitness across its range of size would have a range of fitness more concentrated around the mean (figure 4). The variation in size is likely to be influenced in part by environmental conditions, evaluation of the relationship between a related size character (maximum flower size) and total annual rainfall during 2001–2007 which showed a positive correlation ($F_{1,341} = 16.22$, $p < 0.0001$, $r_{\text{adj}}^2 = 0.04$).

The alternative models considered for *Tolumnia* fit the data similarly (table 2), providing equivocal evidence for phenotypic selection or the effects of light environment. Models that consider variation among plants in the sun and shade are given stronger support than those that ignored this effect (table 2). Models receiving stronger and equivalent support are models 2 (constant model in shade and sun), 4 (linear model in sun, constant model in shade) and 8 (quadratic model in sun, constant model in shade) (table 2). For further analysis, we used model 4 that had the smallest DIC, but results obtained with this model are not very different from the other two models above.

In *Tolumnia*, the standard deviation for within-individual variation across years exceeded that for variation among individuals. Consequently, we also constrained this model so that the expected standard deviation could not be larger than half the variation of the whole population.

Plants that flower in the sun or shade have different fitness advantages across the size of lip lengths (figure 5). Plants in the shade have constant fitness across all sizes, whereas plants with shorter lips grown in the sun have higher fitness than those with

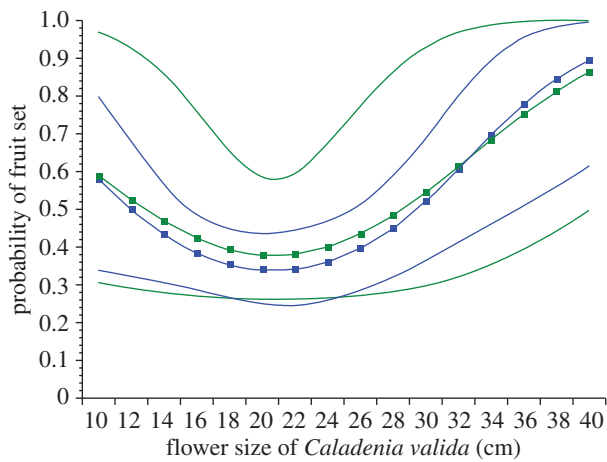


Figure 3. Phenotypic selection landscape of a variable selection surface in *C. valida* for flower size ($n = 50$). There appears to be a selection disadvantage for plants with sizes in the middle of the range. Blue lines represent the mean and the 95% credible intervals of the fitness landscape for the traditional model of no variance in size of individuals across lifespan. The green lines are the mean and 95% credible intervals of fitness landscape of individuals with variation in size.

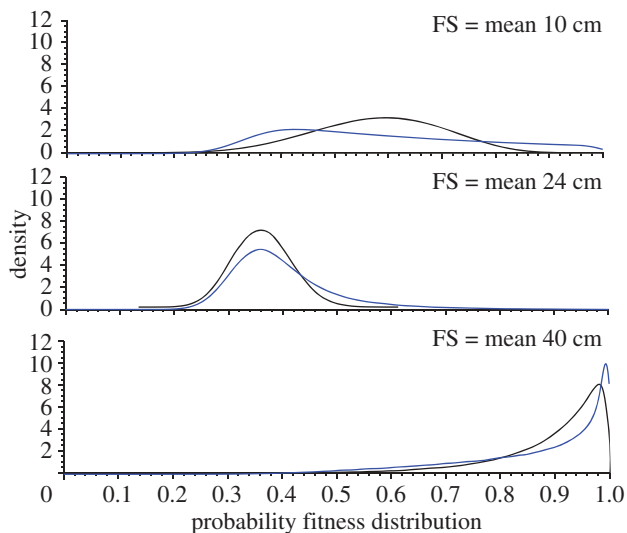


Figure 4. Probability distribution of fitness within individuals with mean size of *Caladenia* flowers at 10, 24 and 40 cm. The sum of the density below each curve equals 1. Black lines show the probability distribution of fitness of individuals that are invariant and blue lines consider variation in size across reproductive bouts.

a longer lip. Inclusion of individual variation in the model increases the 95 per cent credible intervals around the mean, greater fitness variation for a specific floral size. The distribution of fitness within individuals with a mean of 0.80, 1.00 and 1.15 cm shows a skewed distribution when variation in lip length is taken into consideration (figure 6). The effect of variation in lip length on fitness is dramatically shown, not in the general shape of the distribution but on the range of possible fitness for an individual with a lip of 0.80 cm. The density distribution of fitness extends to nine fruits (albeit with a low probability), and that the probability of individuals having five or more

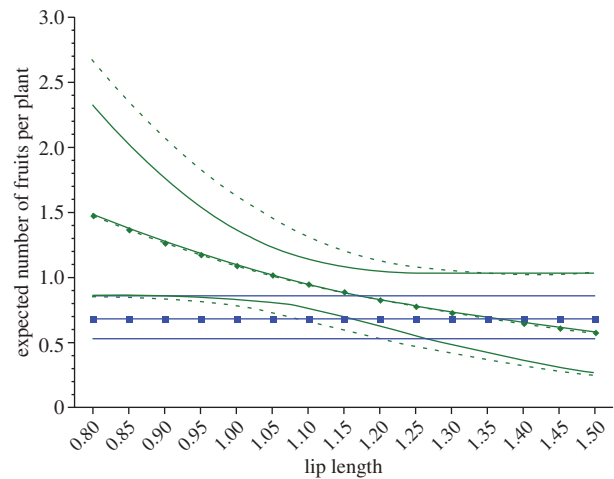


Figure 5. Phenotypic selection landscape of a variable selection surfaces in *T. variegata* for the length of the mid-lobe of the lip (lip length; cm). Green lines represent plants grown in the sun, blue lines are for plants grown in the shade; continuous line models exclude individual variation across reproductive bouts and the stipple line model includes such variation. There is a selection advantage for a shorter lip length in plants grown in the sun. The 95% credible intervals of the fitness landscape are shown. FS, flower size.

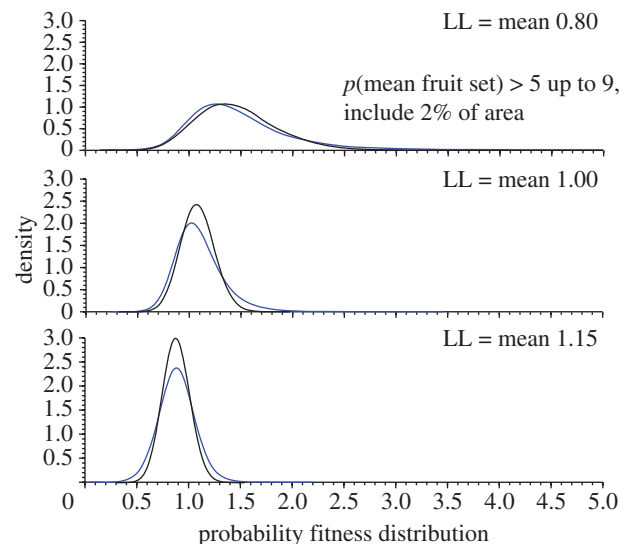


Figure 6. Probability distribution of fitness within individuals with mean lip length of *T. variegata* flowers at 0.8, 1.00 and 1.15 cm for plants grown in the sun. The sum of the density below each curve equals 1. Black lines show the probability distribution of fitness within individuals that are invariant and blue lines consider variation in size across reproductive bouts. LL, lip length.

fruits includes over 2 per cent of all possible events. This range of distribution is absent when variation across reproductive bouts is excluded and the inclusion of the annual variation could result in large differences in fitness among an individual with the same mean phenotype (figure 6).

4. DISCUSSION

Darwin (1859) emphasized the presence of variation as it formed a fundamental condition for his theory of natural selection. Since then, numerous sources of

variation have been identified and here we have shown that annual individual variation in reproductive traits can also be important in the process of natural selection.

Individual variation generated by *C. valida* among reproductive bouts does alter the fitness landscape and this is not uniformly applicable across morphological space. The probability of reproductive success in plants of small or large flowers is not only quite variable but may also be higher than that of intermediate sized flowers. Should these plants consistently produce flowers of specific size over time, they should attain mean fitness and reveal the general pattern of selection only after many reproductive bouts. If plants are relatively short lived, then it is unlikely that they would follow the mean trend in fitness over morphological space. Size can be age dependent or resource limited, and their status at one point in the morphological space may be temporary. Under these conditions, phenotypic selection on size would be much more predictable with age or under more optimal resource conditions.

Morphological variation among reproductive bouts in lip length of *T. variegata* alters the probability distribution of fitness, increasing the variance in outcomes, which may explain in part why previous attempts to detect selection on floral characteristics in *T. variegata* have not been successful (Sabat & Ackerman 1996; Ackerman *et al.* 1997). Variation in morphological characters among reproductive bouts was inconsequential when no effect of size was present on the fitness landscape, as for plants found in shady habitats. However, variation in the fitness landscape was revealed for plants in sunny sites, and variation across reproductive bouts produced a more platykurtic distribution of fitness.

When variants are heritable and differ in fitness, selection occurs with a predictable outcome (Ender 1986). Across the range for a given character, differential reproductive success creates a fitness landscape (Gavrilets 2004). If trait expression of an individual does not vary among reproductive periods and the environment remains constant, then the selection coefficient is likely to be constant or nearly so over time. Alternatively, if character expression varies extensively among reproductive periods (genetic basis of character can be influenced by the environment), the strength and direction of phenotypic selection experienced by individuals may fluctuate over time, slowing evolutionary change, even reducing it to a random process. Moreover, since variation in traits could reduce selection to a random process, it may also have a role in maintaining variation within populations.

The main assumption we have imposed on this model is the limitation in possible character variation among reproductive events to half of the variation observed in the population. Although much data are available on trait variation among individuals, published data on variation in an individual among reproductive bouts in natural populations seem unavailable. Clearly, this component of variation deserves further study. It is a statistical artefact of sample size that one observes more variation within individuals than among individuals. If large variation

within individuals among years is observed, it would logically result in even larger variation among individuals if individuals are equally plastic. Furthermore, we assume that the fitness landscape among reproductive periods is consistent.

Our model diverges from the general approach in the literature dealing with variation. Usually, when variation in the context of selection is discussed it is referred to as the effect of how selection varies as a result of density-dependent processes or that selection *per se* varies among time periods (DeWitt & Yoshimura 1998), such as frequency-dependent processes (Gavrilets 2004 and references therein). Here, we bring forth a concept of variation that is likely to be common in plants and not completely absent in animals, where the effect of the rate of selection is likely to be muddled as a consequence of variation in morphology of individuals across reproductive bouts. We expect that when such variation in a morphological trait is small and genetically determined, then selection could be fast. When morphology varies extensively among reproductive bouts, even if selection for some specific character is strong, evolutionary rates in large populations could be reduced. In small populations, the rate of selection-driven change is likely to be further diminished and perhaps indistinguishable from random processes.

For the species-rich Orchidaceae, Tremblay *et al.* (2005) noted that indirect evidence for selection is substantial yet direct evidence is not often apparent, particularly in small populations. They suggested that genetic drift may be common and punctuated by strong bouts of selection. We have shown here that these evolutionary dynamics are likely to be even more complicated when one considers morphological variation across reproductive bouts for relatively short-lived plants. The frequency and amplitude of such changes will certainly affect the dynamics between selection and genetic drift.

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REFERENCES

- Ackerman, J. D. 1995 An orchid flora of Puerto Rico and the Virgin Islands. *Mem. NY Bot. Gard.* **73**, 1–203.
- Ackerman, J. D. & Galarza-Pérez, M. 1991 Patterns and maintenance of extraordinary variation in the Caribbean orchid, *Tolummia (Oncidium) variegata*. *Syst. Bot.* **16**, 182–194. (doi:10.2307/2418982)
- Ackerman, J. D. & Montero Oliver, J. C. 1985 Reproductive biology of *Oncidium variegatum*: moon phases, pollination and fruit set. *Am. Orchid Soc. Bull.* **54**, 326–329.
- Ackerman, J. D. & Ward, S. 1999 Genetic variation in a widespread, epiphytic orchid: where is the evolutionary potential? *Syst. Bot.* **24**, 282–291. (doi:10.2307/2419553)
- Ackerman, J. D., Meléndez-Ackerman, E. J. & Salguero-Farías, J. 1997 Variation in pollinator abundance and selection on fragrance phenotypes in an epiphytic

- orchid. *Am. J. Bot.* **84**, 1383–1390. (doi:10.2307/2446136)
- Bradshaw, A. D. 1965 Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* **13**, 115–155. (doi:10.1016/S0065-2660(08)60048-6)
- Brooks, S. P. & Gelman, A. 1998 Alternative methods for monitoring convergence of iterative simulations. *J. Comp. Graph. Stat.* **7**, 434–455. (doi:10.2307/1390675)
- Calvo, R. N. 1993 Evolutionary demography of orchids: intensity and frequency of pollination and the cost of fruiting. *Ecology* **74**, 1033–1042. (doi:10.2307/1940473)
- Darwin, C. 1859 *On the origin of species by means of natural selection on the preservation of favoured races on the struggle for life*. London, UK: John Murray.
- Darwin, C. 1862 *The various contrivances by which orchids are fertilised by insects*. London, UK: John Murray.
- Darwin, C. 1877 *Effects of cross and self-fertilisation in the vegetable kingdom*. London, UK: John Murray.
- Darwin, C. 1885 *The various contrivances by which orchids are fertilised by insects*, 2nd edn. London, UK: John Murray.
- DeWitt, T. J. & Scheiner, S. M. 2004 *Phenotypic plasticity: functional and conceptual approaches*. New York, NY: Oxford University Press.
- DeWitt, T. J. & Yoshimura, J. 1998 The fitness threshold model: random environmental change alters adaptive landscapes. *Evol. Ecol.* **12**, 615–626. (doi:10.1023/A:1006564911480)
- Dixon, K. & Tremblay, R. L. 2009 Natural history of *Caladenia*. *Aust. J. Bot.* **57**, 247–258. (doi:10.1071/BT08183)
- Endler, J. A. 1986 *Natural selection in the wild*. Monographs in Population Biology 21. Princeton, NJ: Princeton University Press.
- Fowler, N. L. & Antonovics, J. 1981 Small-scale variability in the demography of transplants of two herbaceous species. *Ecology* **62**, 1450–1457. (doi:10.2307/1941501)
- Gavrilets, S. 2004 *Fitness landscapes and the origin of species*. Monographs in Population Biology 41. Princeton, NJ: Princeton University Press.
- Harder, L. D. & Johnson, S. D. 2009 Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptations. *New Phytol.* **183**, 530–545. (doi:10.1111/j.1469-8137.2009.02914.x)
- Herrera, C. M. 2009 *Multiplicity in unity. Plant subindividual variation and interactions with animals*. Chicago, IL: University of Chicago Press.
- Lande, R. 2007 Expected relative fitness and the adaptive topography of fluctuating selection. *Evolution* **61**, 1835–1846. (doi:10.1111/j.1558-5646.2007.00170.x)
- Lande, R. 2008 Adaptive topography of fluctuating selection in a Mendelian population. *J. Evol. Biol.* **21**, 1096–1105. (doi:10.1111/j.1420-9101.2008.01533.x)
- Lande, R. 2009 Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J. Evol. Biol.* **22**, 1435–1446. (doi:10.1111/j.1420-9101.2009.01754.x)
- Lande, R. & Arnold, S. J. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226. (doi:10.2307/2408842)
- Lunn, D. J., Thomas, A., Best, N. & Spiegelhalter, D. 2000 WinBUGS: a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comp.* **10**, 325–337. (doi:10.1023/A:1008929526011)
- McCarthy, M. A. 2007 *Bayesian methods for ecology*. Cambridge, UK: Cambridge University Press.
- Meléndez, E. J. & Ackerman, J. D. 1993 The effects of a rust infection on fitness components in a natural population of *Tolumnia variegata* (Orchidaceae). *Oecologia* **94**, 361–367. (doi:10.1007/BF00317110)
- Paenke, I., Sendhoff, B. & Kaweski, T. J. 2007 Influence of plasticity on evolution under directional selection. *Am. Nat.* **170**, E47–E58. (doi:10.1086/518952)
- Rice, S. 2008 A stochastic version of the Price equation reveals the interplay of deterministic and stochastic process in evolution. *BMC Evol. Biol.* **8**, 262. (doi:10.1186/1471-2148-8-262)
- Price, T. D., Qvarnström, A. & Irwin, D. E. 2003 The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B* **270**, 1433–1440. (doi:10.1098/rspb.2003.2372)
- Roubik, D. W. 1989 *Ecology and natural history of tropical bees*. Cambridge, UK: Cambridge University Press.
- Sabat, A. M. & Ackerman, J. D. 1996 Fruit set in a deceptive orchid: the effect of flowering phenology, display size, and local floral abundance. *Am. J. Bot.* **83**, 1181–1186. (doi:10.2307/2446202)
- Schlichting, C. D. 1986 The evolution of phenotypic plasticity in plants. *Ann. Rev. Ecol. Syst.* **17**, 667–693. (doi:10.1146/annurev.es.17.110186.003315)
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & Van der Linde, A. 2002 Bayesian measures of model complexity and fit (with discussion). *J. R. Stat. Soc. Ser. B* **64**, 583–616. (doi:10.1111/1467-9868.00353)
- Sultan, S. E. 1987 Evolutionary implications of phenotypic plasticity in plants. *Evol. Biol.* **21**, 127–178.
- Tremblay, R. L. 2005 Larger is better: the effect of floral display on reproductive success in two populations of *Caladenia* (*Stegostyla*) *gracilis* R. Br. *Muelleria* **22**, 77–85.
- Tremblay, R. L. 2006 The effect of flower position on male and female reproductive success in a deceptively pollinated tropical orchid. *Biol. J. Linn. Soc.* **151**, 405–410. (doi:10.1111/j.1095-8339.2006.00504.x)
- Tremblay, R. L., Ackerman, J. D., Zimmerman, J. K. & Calvo, R. 2005 Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biol. J. Linn. Soc.* **84**, 1–54. (doi:10.1111/j.1095-8312.2004.00400.x)
- Tremblay, R. L., Pérez, M.-E., Larcombe, M., Brown, A., Quarmby, J., Bickerton, D., French, G. & Bould, A. 2009a Dormancy in *Caladenia*: a Bayesian approach to evaluating latency. *Aust. J. Bot.* **57**, 340–350. (doi:10.1071/BT08163)
- Tremblay, R. L., Pérez, M.-E., Larcombe, M., Brown, A., Quarmby, J., Bickerton, D., French, G. & Bould, A. 2009b Population dynamics of *Caladenia*: Bayesian estimates of transition probabilities and probability of extinction. *Aust. J. Bot.* **57**, 351–360. (doi:10.1071/BT08167)
- Wilson, W. G. & Harder, L. D. 2003 Reproductive uncertainty and the relative competitiveness of simultaneous hermaphroditism versus dioecy. *Am. Nat.* **162**, 220–241. (doi:10.1086/376584)
- Zhang, X.-S. & Hill, W. G. 2005 Evolution of the environmental component of the phenotypic variance: stabilizing selection in changing environments and the cost of homogeneity. *Evolution* **59**, 1237–1244. (doi:10.1554/05-038)