

INSECT SEED PREDATORS AS NOVEL AGENTS OF SELECTION ON FRUIT COLOR

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Abstract. The ecological and evolutionary dynamics of fruit color polymorphisms remain poorly known because patterns and agents of selection have rarely been identified. Here, we examine *Acacia ligulata*, a shrub of the Australian arid zone characterized by a red/yellow/orange aril color polymorphism. Seed production patterns over four populations and three years suggested that spatially variable selection may be acting to maintain the polymorphism: red and yellow aril color morphs each had the highest seed production in alternate sites. Seed production differences between morphs were a function of both intrinsic plant characters (fruit production) and predispersal seed predation, which affects the number of viable seeds matured per ovule. Fruit production differences are hypothesized to result from a genotype-by-environment interaction, perhaps related to plant vigor. In contrast, morph differences in the numbers of viable seeds per ovule are produced via differential seed predation by heteropteran insects, as demonstrated by exclusion experiments. Because these predators feed when aril color is not visible, differential predation is evidently a response to pleiotropic effects of fruit color alleles. We suggest that such pleiotropic effects may be a common feature of fruit color polymorphisms, and that the most obvious selective agents (that is, seed dispersers) may not always be the most important.

Key words: *acacia*; *Acacia ligulata*; *Australian arid zone*; *Coleotichus*; *fruit color polymorphism*; *insect seed predators*; *Melanterius*; *pleiotropic effects*; *pre-dispersal seed predation*; *seed production patterns*; *spatially variable selection*; *Trichilogaster*.

INTRODUCTION

The dynamics of genetic polymorphisms in natural populations have long been a central focus of evolutionary ecology (e.g., Epling and Dobzhansky 1942, Sheppard 1951). Because selectively neutral polymorphisms will eventually disappear under the influence of drift (Wright 1931), balanced polymorphisms are of interest because they imply the action of natural selection. Polymorphisms may be maintained by several selective mechanisms, including overdominance, frequency-dependent selection, and variable (also known as fluctuating) selection (Gillespie 1998). Given abundant variability in the environment, it has been suggested that much of the observed polymorphism in nature could be maintained by variable selection (Gillespie 1991). Empirical evidence consistent with variable selection has been found (for reviews, see Hedrick 1986, Mitton 1997), although demonstration that variable selection maintains a particular polymorphism can be a substantial undertaking (e.g., Turelli et al. 2001). A first step is to evaluate the spatial and/or temporal scales on which selection may be acting, and to verify the necessary (but not sufficient) condition

that each morph have the highest relative fitness in some places or at some times.

Fruit color polymorphisms are widespread, occurring in at least 19 plant families (Forde 1986, Willson 1986, Willson et al. 1989). Quite logically, frugivores historically have been viewed as the most likely agents of selection on fruit color (Willson and Whelan 1990). However, evidence for important roles of frugivores in the dynamics of fruit color polymorphisms has been inconclusive. Although frugivore preferences among color morphs are commonly found in laboratory choice tests (Willson and Comet 1993, Willson 1994, Puckey et al. 1996, Traveset and Willson 1998, Giles and Lill 1999), color biases in frugivore visitation or fruit removal are infrequently found in field studies of natural plant populations (e.g., Willson 1983, Willson and O'Dowd 1989, Traveset and Willson 1998, Traveset et al. 2001). Where biases have been found (e.g., Gervais et al. 1999), it is not known whether they alter the relative fitnesses of the morphs.

Given the limited evidence for selection via frugivore preferences, it makes sense to consider other ways in which selection could act on fruit color polymorphisms. Data on species polymorphic for flower color suggest that pleiotropic effects can be important (Levin and Brack 1995 and references therein, Simms and Bucher 1996, Schemske and Bierzychudek 2001, Irwin et al. 2003). There are also intriguing data from species polymorphic for fruit color. For example, the *hp* allele

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TABLE 1. Repeated-measures ANOVAs for total per-plant seed production and its four subcomponents in four *Acacia ligulata* populations, 1999–2001.

Effect	df	Seed production		Canopy size (m ²)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Aril color	1, 140	0.00	0.989	0.01	0.915
Population	3, 140	4.23	0.007	1.60	0.193
Aril color × Population	3, 140	5.51	0.001	3.14	0.027
Year	2, 139	48.89	<0.001	10.88	<0.001
Year × Aril color	2, 139	0.35	0.704	0.08	0.923
Year × Population	6, 280	11.19	<0.001	4.59	<0.001
Year × Aril color × Population	6, 280	1.49	0.183	0.17	0.984

in cultivated tomato both intensifies fruit color and reduces seedling growth and survival (Jarret et al. 1984). In two wild species (*Rhagodia parabolica* and *Rubus spectabilis*), potentially pleiotropic effects of fruit color alleles on seed germination behavior have been found (Willson and O'Dowd 1989, Gervais et al. 1998, Traveset and Willson 1998).

Pleiotropic effects of fruit color alleles on herbivory and seed predation have received limited attention and have not yet been documented in wild species (Willson 1983, Traveset and Willson 1998). Such effects might be common, given the potential overlap between the biosynthetic pathways of pigments and defensive compounds (Willson and Whelan 1990). Furthermore, there is evidence that flower color morphs can be differentially resistant to herbivores (Simms and Bucher 1996, Irwin et al. 2003). Pleiotropic effects on seed predation could be extremely important in the dynamics of a polymorphism, given that seed predators have large impacts on plant fitness in many species (reviewed in Hulme 1998, Maron and Gardner 2000) and are known to discriminate among individual plants (e.g., Thompson 1985).

To look for evidence of both variable selection and pleiotropic effects in a fruit color polymorphism, we examined patterns of seed production and seed predation in a polymorphic acacia from arid Australia. Diaspores of *Acacia ligulata* A. Cunn. ex Benth. comprise a seed (~5 mm in length) and an expanded, colored funicle (the aril or elaiosome). *Acacia ligulata* populations are composed of two or three color morphs, producing red, yellow, or (more rarely) orange arillate diaspores (O'Dowd and Gill 1986). Preliminary data suggested that *A. ligulata* morphs differ in average seed production, in part as a result of differential attack on seeds by insects. Because these insects attack while fruits are immature and aril colors are not visible, we interpret these differences in seed predation as responses to pleiotropic effects of color alleles, although the effects of linked genes cannot be excluded. We examined patterns of seed production across four populations and three years, focusing on the red and yellow morphs because the rarity of the orange morph precluded sufficient sample sizes. We asked: (1) Do plants producing red vs. yellow arils differ in seed produc-

tion? If so, what subcomponents (e.g., plant size, fruit density, etc.) contribute to that difference? (2) Are seed production differences between morphs variable in space or time? (3) Do insect seed predators contribute to morph differences in seed production? (4) What consequences might these patterns have for the maintenance of the color polymorphism?

METHODS

Study system and study area

Acacia ligulata is a widespread dune shrub of arid and semiarid Australia (Maslin and Hopper 1982), reaching 5 m in height. Both adults and seed banks are long-lived (Auld 1995a; T. D. Auld, *personal communication*). Reproduction is exclusively through seeds (Auld 1995a), and flowering can occur within three years of germination (Auld 1995b). Examination of phenotypes of maternal half-siblings grown in a common environment suggests that aril color in *A. ligulata* is under biparental genetic control, although the numbers of loci and alleles controlling the trait are currently unknown (Whitney and Lister 2004). Within New South Wales populations, red is the most frequent morph (~71% of adults), followed by yellow (~27%) and orange (~1%) (Whitney and Lister 2004). Mature diaspores are dispersed by a variety of ants and birds attracted to the lipid-rich arils (Davidson and Morton 1984, Forde 1986; K. D. Whitney, *unpublished manuscript*).

This study examines seed production and insect seed predation in four discrete *A. ligulata* populations in Kincheha National Park, New South Wales (32°26' S, 142°11' E). These populations are separated by 6–28 km, and occur on dunes (Cawndilla and Big Dune), a lunette (a low, crescent dune; Menindee), and a floodplain (Channel); further details may be found in Whitney and Lister (2004). In Kincheha, *A. ligulata* flowers in September, fruits develop over a two-month period, and fruit dehiscence and seed dispersal occur from mid-December through February. Immature fruits are attacked by a range of insect seed predators, including *Coleotichus costatus* (Scutelleridae: Heteroptera), broad-headed bugs (Alydidae: Heteroptera), the wasp *Trichilogaster* sp. (Chalcidae: Hymenoptera), and wee-

TABLE 1. Extended.

Fruits/m ²		Ovules/fruit		Seeds/ovule	
<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
0.01	0.923	3.09	0.081	0.71	0.402
4.03	0.009	7.72	< 0.001	6.61	< 0.001
5.75	0.001	0.92	0.433	2.70	0.049
7.17	0.001	235.42	< 0.001	122.99	< 0.001
1.67	0.192	0.33	0.723	3.23	0.042
15.97	< 0.001	15.93	< 0.001	5.74	< 0.001
1.13	0.345	0.90	0.497	1.43	0.207

vils of the genus *Melanterius* (Curculionidae: Coleoptera) consisting of *M. vinosus* and an undescribed species (K. Whitney, unpublished data). As in other Australian acacias (New 1983, Gill 1985, Auld 1986), heteropterans kill ovules by piercing the fruit wall and sucking material from the fruit; weevils and wasps oviposit through the fruit wall, and ovules are destroyed by the developing larvae.

Natural patterns of seed production by morphs

Seed production patterns were assessed for each of four *A. ligulata* populations in three years (1999–2001). In each site in 1999, ~21 adult plants of each of the two common color morphs (red and yellow) were chosen at random. The same plants were monitored in subsequent years. Because plants can produce >20 000 seeds, seed production was estimated using canopy subsampling methods. Total seed production was calculated as the product of four components: canopy surface area, fruit density per unit area, number of ovules per fruit, and number of viable seeds per ovule. Canopy surface area (in square meters) was calculated by modeling plants as hemispheres, with a radius equal to the average of three measurements (corresponding to plant height and two horizontal measurements from canopy edge to trunk). Fruit density was estimated by the product of branch density and the number of fruits per branch, where a “branch” is defined as a unit of the canopy consisting of a primary stem (circumference 25 mm) and the secondary stems arising from it. Branch density was measured using three random placements of a 0.25-m² hoop onto the canopy. The number of fruits per branch was an average of counts on six randomly chosen branches. The number of ovules per fruit was estimated from ≥60 fruits per plant.

The final component of seed production, the number of viable seeds per ovule, is sensitive to processes that kill ovules (e.g., plant abortion, insect attack) between ovule initiation and seed maturity. In early October, following fruit initiation, three branches per plant were randomly chosen from among those bearing >20 fruits and were marked with flagging. In early December, just prior to the beginning of the fruit dehiscence period, each marked branch was bagged with a polyester plant sleeve (Fibe-Air 19 × 48 × 58 cm; Kleen Test Products,

Brown Deer, Wisconsin, USA) to prevent seed removal and loss until all fruits matured. After maturation, all fruits and seeds from each branch were collected and pooled, the number of initiated ovules was estimated from the number of chambers in the woody fruits, and the number of viable seeds was counted. Values from the three branches were then averaged to estimate viable seeds per ovule for a given plant.

We first examined the effects of aril color, population, year, and their interactions on total per plant seed production, using repeated-measures ANOVA (SAS Institute 2000) with year as the repeated factor. Because seed production is calculated as a product, we note that propagation of measurement error could be substantial, resulting in large confidence intervals around individual observations and, ultimately, a conservative test for differences between aril colors. Following a finding of significant seed production differences between morphs in some populations, we performed ANOVAs on each of the four subcomponents of seed production. By analogy to a significant overall MANOVA followed by protected ANOVAs (Scheiner 2001), we deemed correction for multiple comparisons overly conservative and report uncorrected *P* values. Response variables were transformed to meet assumptions of normality and homoscedasticity. Transformations used were Box-Cox (seed production), square-root (canopy size, number of fruits per square meter), natural log (number of ovules per fruit), and angular (number of viable seeds per ovule). Orthogonal contrasts within the analysis were used to compare morphs within each population.

Effects of insect seed predators: exclusion experiment

We performed exclusion experiments in 1999 and 2000 to examine whether insect seed predators could cause variation between morphs with respect to the number of seeds matured per ovule. Because resources were limited, experiments were performed in three of the four populations examined for natural seed production. Just after fruit initiation in each year, 20 plants per morph per site were chosen at random from among those with sufficient fruit. In early October 1999, nine branches per plant were randomly chosen from among

those branches bearing >20 fruits. Treatments were assigned at random within a plant (three branches per treatment) and included an exclusion treatment (branch fitted with a polyester plant sleeve that allowed air to circulate but reduced access by seed predators); an exclusion control treatment (branch fitted with a polyester sleeve with six 6-cm holes to allow insect access); and an open treatment (branch tagged and left exposed for the season). In late December, fruits were harvested at maturity and the number of viable seeds per ovule was determined for each branch. In addition, the numbers of heteropteran-killed, weevil-killed, wasp-killed, and aborted seeds per ovule were determined; each of the seed predator taxa leaves characteristic signs of damage (e.g., frass, exit holes, pupal cases). For each treatment on a given plant, values from the three branches were averaged prior to analysis.

In 1999, a preliminary analysis conducted using ANOVA (SAS Institute 2000) showed that bags have no discernible effects on the number of viable seeds per ovule apart from insect exclusion. Viable seeds per ovule (mean \pm 1 SE) for the three treatments (exclusion, exclusion control, and open) were 0.76 ± 0.015 , 0.46 ± 0.012 , and 0.47 ± 0.019 , respectively. Tukey tests indicated that the exclusion control and open treatments did not differ ($P = 0.908$), whereas the exclusion treatment differed strongly from the other treatments ($P < 0.0001$ in both cases). Thus, we concluded that bagging effects were due to insect exclusion, and in 2000 only exclusion and open treatments were applied to plants.

We examined the effects of aril color, population, year, plant (nested within aril color, population, and year), and insect treatment (exclusion vs. open) on the proportion of seeds in different seed fate categories using MANOVA (SAS Institute 2000). Because values of the five seed fate categories sum to one, not all can be included in a single MANOVA. As heteropterans are by far the most damaging of the seed predators (see *Results*), we focused on the viable and heteropteran-killed categories. Response variables were angular-transformed to meet assumptions of normality and homoscedasticity. Aril color, insect treatment, and year were considered fixed factors, whereas plant and population were considered random. Because of the nested design, the variation among plants was used as the error term for testing the effects of aril color, population, year, and their interactions. Following a significant overall MANOVA, ANOVAs and post hoc Tukey tests were carried out on individual responses.

RESULTS

Natural patterns of seed production by morphs

Average per plant seed production varied across populations, years, and (within certain populations) between aril color morphs (Table 1). Because aril color did not interact with year, the data presented are pooled across years (Fig. 1a). In the Channel and Big Dune

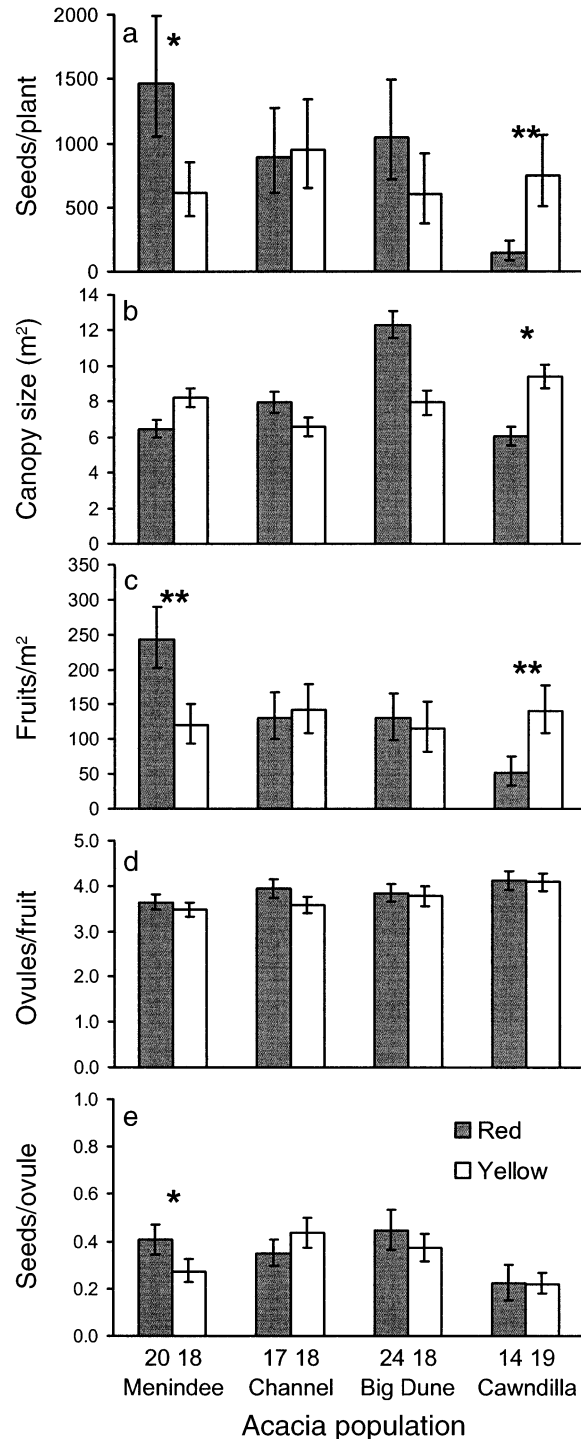


FIG. 1. Comparison of annual seed production (a) and its four subcomponents (b–e) for *Acacia ligulata* color morphs in four populations. Data are pooled across years (1999–2001). Bars represent back-transformed least-square means (and 95% confidence intervals); note that back-transformed means are often substantially smaller than raw means. Contrast P values are indicated by asterisks. Sample sizes are given above each population name.

* $P < 0.05$; ** $P < 0.01$.

TABLE 2. MANOVA and ANOVAs for viable and heteropteran-killed seeds per ovule, insect exclusion experiment, 1999 and 2000.

Effect	MANOVA				Viable seeds		Heteropteran-killed seeds		
	df	Pillai's trace	F	P	df	F	P	F	P
Aril color	2, 235	0.005	0.57	0.565	1, 267	0.46	0.497	0.15	0.702
Population	4, 472	0.070	4.27	0.002	2, 264	1.79	0.170	3.55	0.030
Aril color × Population	4, 472	0.022	1.33	0.257	2, 264	2.14	0.120	0.77	0.463
Year	2, 235	0.449	95.84	<0.001	1, 267	157.17	<0.001	0.63	0.428
Year × Aril color	2, 235	0.004	0.44	0.643	1, 267	0.19	0.667	0.92	0.338
Year × Population	4, 472	0.025	1.48	0.207	2, 264	0.30	0.743	1.67	0.190
Year × Aril color × Population	4, 472	0.007	0.41	0.801	2, 264	0.41	0.661	0.74	0.479
Treatment	2, 215	0.765	349.05	<0.001	1, 216	567.60	<0.001	479.00	<0.001
Treatment × Aril color	2, 215	0.039	4.41	0.013	1, 216	8.53	0.004	3.83	0.052
Treatment × Population	4, 432	0.052	2.89	0.022	2, 216	5.32	0.006	3.10	0.047
Treatment × Aril color × Population	4, 432	0.019	1.01	0.402	2, 216	0.14	0.867	1.43	0.241
Treatment × Year	2, 215	0.031	3.49	0.032	1, 216	6.53	0.011	0.44	0.506
Treatment × Year × Aril color	2, 215	0.038	4.27	0.015	1, 216	2.69	0.102	8.54	0.004
Treatment × Year × Population	4, 432	0.042	2.33	0.056	2, 216	3.54	0.031	3.55	0.030
Treatment × Year × Aril color × Population	4, 432	0.014	0.78	0.540	2, 216	1.18	0.310	0.85	0.430
Plant(Aril color × Population × Year)	472, 432	1.309	1.73	<0.001	236, 216	1.83	<0.001	1.69	<0.001

Note: "Treatment" refers to the insect-exclusion treatment.

populations, morphs did not differ (contrasts within the ANOVA; $F_{1,140} = 0.02, 1.32; P = 0.897, 0.253$, respectively). At Menindee, red morphs produced more seeds than did yellow morphs ($F_{1,140} = 4.93; P = 0.028$). In contrast, at Cawndilla, yellow morphs produced more seeds than did red morphs ($F_{1,465} = 10.25; P = 0.002$).

Differences between morphs in seed production reflected differences in three of four components: canopy size, fruit density, and viable seeds per ovule (Fig. 1b,c,e, Table 1). At Menindee, red morphs had significantly higher fruit densities ($F_{1,140} = 9.43; P = 0.003$) and matured more seeds per ovule than did yellow morphs ($F_{1,140} = 5.16; P = 0.025$); however, canopy size did not differ between morphs ($F_{1,140} = 1.37; P = 0.244$). At Cawndilla, yellow morphs were both larger ($F_{1,140} = 4.08; P = 0.045$) and had higher fruit densities than red morphs ($F_{1,140} = 7.80; P = 0.006$), but morphs did not differ in viable seeds per ovule ($F_{1,140} = 0.02; P = 0.886$). The number of ovules per fruit did not differ among morphs in any population (Fig. 1d, Table 1).

Effects of insect seed predators: exclusion experiment

The fate of ovules varied across years, populations, insect treatments, and (within the open treatment) between aril color morphs (MANOVA; Table 2). Because aril color did not interact with population ($P = 0.12$; Table 2) and because the exclusion treatment was effective in reducing damage in all three populations (Tukey tests, $P < 0.0001$ in all cases), the data presented

are pooled across populations (Fig. 2). A significant Treatment × Year × Aril color interaction (MANOVA, $P = 0.015$; Table 2) suggests that the patterns were predominantly driven by differences in 1999 (Fig. 2). In the exclusion treatment, morphs did not differ in numbers of viable seeds per ovule (Fig. 2a). In contrast, in the open (insect access) treatment, red morphs matured more viable seeds per ovule than did yellow (Table 2; Trt × Aril color $P = 0.004$; Fig. 2a).

Patterns in heteropteran damage identified a mechanism for morph differences in viable seed production. Morphs did not differ in numbers of heteropteran-killed seeds per ovule in the exclusion treatment (Fig. 2b). In contrast, in the open treatment, heteropterans killed fewer seeds per ovule in red morphs than yellow morphs in 1999 but not 2000 (Trt × Year × Aril color, $P = 0.004$; Fig. 2b).

Damage by other insect seed predators was independent of morph color. The insect exclusion treatment strongly reduced the numbers of both weevil-killed (from 0.04 to 0.001 seeds/ovule; $F_{1,236} = 121.22, P < 0.001$) and wasp-killed seeds (from 0.01 to 0.006 seeds/ovule; $F_{1,236} = 10.04, P = 0.002$). However, morphs did not differ in the numbers of weevil- or wasp-killed seeds per ovule in either treatment (main effect of aril color and all interactions nonsignificant at $P > 0.2$; results are not shown).

DISCUSSION

In summary, *Acacia ligulata* color morphs differed in seed production, and differences varied among populations. Red morphs produced more seeds than did

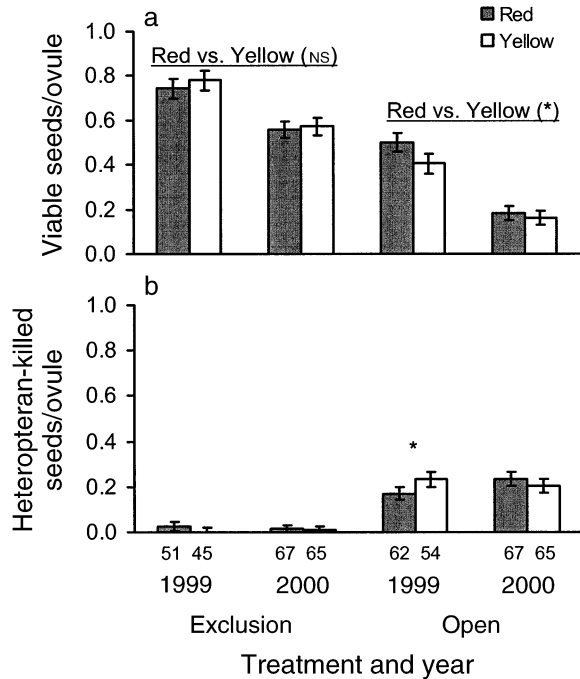


FIG. 2. Effects of exclusion of insect seed predators on ovule fate in *A. ligulata*, 1999 and 2000. Data are pooled across three populations. Bars represent back-transformed least-square means (and 95% confidence intervals). Sample sizes are given beneath each bar. As determined by Tukey tests, differences significant at $P < 0.05$ are marked with an asterisk. (a) Viable seeds/ovule; Treatment \times Aril color, $P = 0.004$. (b) Heteropteran-killed seeds per ovule; Treatment \times Year \times Aril color, $P = 0.004$.

yellow morphs in one population (Menindee); the opposite pattern was seen in another population (Cawndilla); and in two populations, morphs did not differ over the three years of the study. Seed production differences were a function of both the number of fruits produced and the number of viable seeds matured per ovule.

Morph differences in fruit production

Why did color morphs differ in fruit production? Proximal causes varied among populations: red plants had higher fruit densities than did yellow plants at Menindee, and yellow plants were both larger and had higher fruit densities than red morphs at Cawndilla. One hypothesis is that a genotype-by-environment interaction exists, in which adults of a particular morph are most vigorous in particular environments (which may differ in soil nutrients, water availability, etc.). This hypothesis could be tested by planting similarly aged individuals in different sites and evaluating fruit production variables over time. Unfortunately, high seedling mortality rates (Whitney and Lister 2004) and an extended juvenile period (minimum of three years; Auld 1995b) in *A. ligulata* would dictate a long-term experiment tracking thousands of plants.

Effects of insect seed predators

The experimental data suggest that heteropteran seed predators imposed more damage on the yellow morph in 1999 but not in 2000 (temporal variation), and the observational data suggest that populations varied in the effect of aril color on seed predation (spatial variation). Spatiotemporal variation in herbivore preference among plant genotypes has been documented in other systems (e.g., Cronin et al. 2001). Such patterns suggest that preferences of seed predators, when expressed, might not uniformly increase the relative fitness of the red morph in *A. ligulata*, but may occasionally favor the yellow morph as well.

Basis of differential predation

Because heteropteran feeding occurs when aril colors are not visible, we suggest that differential seed predation results from pleiotropic effects of color alleles on plant chemistry or morphology, although linkage cannot be ruled out at present. Although potentially pleiotropic effects of fruit color alleles have been found in wild species (e.g., on seed germination timing; Willson and O'Dowd 1989, Gervais et al. 1998, Traveset and Willson 1998), this is the first time that consequences for fitness components have been demonstrated.

Characteristics of *A. ligulata* that result in differential seed predation are currently unknown. One possibility is that fruit density is important: if seed predators recruit to plants independently of fruit density, a morph with relatively low fruit density (e.g., the yellow morph at Menindee) will sustain relatively high levels of damage per fruit. However, within morphs, fruit density and seed predation rates were uncorrelated (Spearman rank correlation: $0.07 < P < 0.88$ in each of 24 morph/population/year data sets; K. Whitney, unpublished data), suggesting that this is not the mechanism by which differential seed predation is effected. Alternately, differential seed predation could result from active discrimination by seed predators. Levels of nutrients, particularly nitrogen, can influence diet choices in seed-feeding insects (Mattson 1980, Slansky and Panizzi 1987). However, seeds of *A. ligulata* morphs do not differ in concentrations of nitrogen, phosphorus, potassium, or any of 25 fatty acids (Whitney and Lister 2004).

Active discrimination among morphs by seed predators could also result from differences in aril carotenoid concentrations. Because of their inability to synthesize carotenoids de novo, insects must obtain carotenoids from their diet (Kayser 1985). Carotenoids play a variety of roles in insects, as aposematic and sexual signals, provitamins, antioxidants, and defensive compounds (Feltwell 1978, Kayser 1985, Carroll et al. 1997). Although *A. ligulata* seeds are low in carotenoids, arils have high (and morph-specific) concentrations (Whitney and Lister 2004); these com-

pounds are present in the developing aril tissue long before fruit maturity (K. Whitney, *personal observation*). Because seed-sucking heteropterans inject saliva into fruits and feed on the liquefied contents (Slansky and Panizzi 1987), predators of *A. ligulata* could potentially ingest material from arils as well as seeds and thus uptake substantial quantities of carotenoids. This hypothesis is particularly interesting given that the dominant seed predator, *Coleotichus costatus*, becomes sexually dimorphic during the fruiting season of *A. ligulata*. Males retain dull yellow tibiae while female tibiae become bright red (K. Whitney, *unpublished data*), suggesting that the sexes might specialize on different *A. ligulata* morphs. If *C. costatus* sexes differ in their abundance or in their per capita damage to plants, differential seed predation may result. Future studies will examine the link between insect foraging and carotenoid content of *A. ligulata*.

Dynamics of the fruit color polymorphism in Acacia ligulata

This study has documented spatial variation in components of fitness in *A. ligulata*, such that red and yellow aril color morphs each have the highest seed production in some environments. Thus the system is qualitatively consistent with the variable selection model of polymorphism maintenance (Gillespie 1991) and represents the first evidence that fruit color polymorphisms might be maintained by selection. Additional variation in relative fitness is imposed by frugivorous birds, which differentially disperse the morphs (K. D. Whitney, *unpublished manuscript*). Conclusions about the dynamics of the *A. ligulata* polymorphism await more knowledge about the genetics of inheritance of this trait, and either analytical or simulation modeling of the variation in fitness effects (e.g., Templeton and Levin 1979, Turelli et al. 2001). Nevertheless, this study suggests that seed predators can be important in the dynamics of fruit color polymorphisms. Given the evidence for selection by herbivores on a flower color polymorphism (Irwin et al. 2003), we suggest that pleiotropic effects might be commonly associated with color alleles in plants; the most obvious selective agents (that is, seed dispersers and pollinators) may not always be the most important.

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