

LINKING FRUGIVORES TO THE DYNAMICS OF A FRUIT COLOR POLYMORPHISM¹

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Although fruit color polymorphisms are a widespread phenomenon, the role of frugivores in their maintenance is unknown. Selection would require that frugivores interact differentially with fruit color morphs to alter their relative fitnesses, but such a pattern has yet to be demonstrated. In a 3-yr field study, the interactions of ants and birds with *Acacia ligulata*, an Australian shrub with a red/yellow/orange aril color polymorphism, were examined. Bird species fell into three feeding guilds: seed dispersers, seed predators, and aril thieves; ant species acted either as seed dispersers or aril thieves. While there was no evidence of morph bias in ants, in some years birds fed more frequently on the yellow and orange morphs. Based on patterns of seedling survival and juvenile recruitment in seed deposition sites, bird seed dispersers increased the fitness of yellow and orange morphs (relative to red) in some populations, but decreased their relative fitness in others. Bird seed predators uniformly reduced relative fitness of yellow and orange morphs, while bird aril thieves had unknown effects. Altogether, consumer biases produced spatiotemporal variability in the relative fitness of *A. ligulata* color morphs, a pattern qualitatively consistent with maintenance of the polymorphism.

Key words: ant–plant interactions; Australia; avian frugivore preference; Fabaceae; fruit thievery; seed dispersal; seed predation; seedling recruitment.

Fruit–frugivore interactions are widespread and are fundamental to the structure of terrestrial communities (Wang and Smith, 2002). However, evidence that frugivores exert selection on fruit traits has been scarce (Herrera, 1988, 1992; Jordano, 1989, 1995). Research linking fruit traits to plant fitness has been hampered by the difficulty of tracking dispersed seeds. In vertebrate-dispersed species, for example, we know next to nothing about the ultimate consequences of fruit traits for recruitment of seedlings and adults (Herrera, 2002).

One particular fruit trait, color, has interested biologists since the time of Darwin. Plant species that are polymorphic for fruit color are common, occurring in at least 19 plant families (Forde, 1986; Willson, 1986; Willson et al., 1989). Because fruit color varies substantially (but discretely) among members of a population, species that are polymorphic for fruit color provide perhaps our best opportunity to understand selective pressures on fruit traits. However, despite a long-standing suspicion that frugivores are the most likely agents of selection on fruit color (Willson and Whelan, 1990), we have only limited evidence implicating frugivores in the dynamics of fruit color polymorphisms.

Natural selection imposed by frugivores could contribute to the maintenance of fruit color polymorphisms by acting in a

frequency-dependent or variable manner (Gillespie, 1998). Given abundant spatial and temporal variation in climatic conditions, species densities, and other factors, variable selection is a leading contender for the maintenance of polymorphism (Gillespie, 1991). Under variable selection, frugivores would not uniformly favor a particular morph (which would lead to monomorphism), but instead would act such that each morph has the highest relative fitness in some places or at some times. Significantly, under this scenario, contrasting effects of frugivores are expected; frugivores should increase the fitness of a particular morph in some environments, but decrease its fitness (or have no effect) in others. In contrast, a consistent lack of selection by frugivores cannot by itself actively maintain a polymorphism, as genetic drift ultimately removes neutral variation from populations.

In order to exert selection pressure on a fruit color polymorphism, frugivores must interact differentially with morphs. Such differential interactions, here called biases, may arise through frugivore preferences for particular morphs, through differences in encounter rates (e.g., if morphs differ in conspicuousness), or through frugivore behaviors or physiologies that change the relative fitness of morphs even when feeding itself is unbiased (e.g., if gut passage differentially affects seed viability of morphs). 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), 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; but see Gervais et al., 1999). Importantly, even when feeding biases of frugivores have been found in field settings, the consequences for the relative fitness of morphs have not been investigated. Similarly, while ingestion by frugivores can produce differences among morphs in germination behavior (Willson and O’Dowd, 1989; Gervais et al., 1998), the fitness consequences of these differences are unknown. Without explicit consideration of the effects of frugi-

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vore bias on the relative fitness of morphs, we remain ignorant of the impacts of frugivores (positive, negative, or neutral) on the maintenance of fruit color polymorphisms.

The Australian arid-zone shrub *Acacia ligulata* A. Cunn. ex Benth. (Fabaceae) has three color morphs, producing either red, yellow, or orange arillate diaspores. I investigated the interactions of bird and ant consumers with *A. ligulata* in a 3-yr field study. I asked (1) Are canopy-foraging birds biased toward particular morphs? (2) Are ground-foraging ants biased toward particular morphs? and (3) Do biases of these consumers influence the relative fitnesses of morphs, via dispersal-mediated effects on seedling survival and juvenile recruitment?

MATERIALS AND METHODS

Study species and study area—*Acacia ligulata* is a widespread dune shrub of arid Australia (Maslin and Hopper, 1982) reaching 5 m in height. Both adult plants and seed banks are long-lived (T.D. Auld, New South Wales National Parks and Wildlife Service, personal communication; Auld, 1995a). Initial seed dormancy is high (88–99%; Auld, 1995a; Letnic et al., 2000), and germination is episodic following rains. Seedlings are an especially sensitive demographic stage, as survival can be severely reduced by vertebrate herbivores and dry conditions (Auld, 1995b). Flowering can occur within 3 years of germination (Auld, 1995b).

Diaspores of *A. ligulata* are bicolored: a black seed (ca. 5 mm in length) contrasts with an expanded, colored funicle (the aril or elaiosome, ca. 2.5 mm). Aril color is polymorphic, with a given plant producing arils of single color, either red, yellow, or orange (for an image of the polymorphism, see the Appendix in Supplemental Data accompanying the online version of this article). The polymorphism appears to have a simple genetic basis, with the allele producing the yellow phenotype dominant to that producing red. However, whether the rare orange phenotype is produced by a third allele at the same locus, by a second locus, or by other means is unclear (Whitney, in press). In comparisons of the color morphs, no differences were found in mass or fatty acid composition of arils or seeds. However, arils of red morphs have higher concentrations of carotenoids than those of yellow or orange morphs; additionally, arils of orange morphs are distinguished by elevated levels of P and Mg (Whitney and Lister, 2004).

Mature diaspores are dispersed by a variety of ants and birds attracted to the lipid-rich arils (Forde, 1986; Letnic et al., 2000; Whitney, 2002). A previous suggestion that some populations of *A. ligulata* are specialized for bird dispersal while others are ant-dispersed (Davidson and Morton, 1984) was based on misidentified material (Chapman and Maslin, 1992). Birds generally feed in the canopy, where the diaspores are displayed on the open valves of dehiscent fruits. In contrast, ants remove diaspores that have fallen to the ground. Both taxa contribute substantively to removal: in Kinchega National Park, ants were responsible for an estimated 18–37% of diaspores removed, while birds removed 63–82%, depending on the population (K. D. Whitney, unpublished data). Ant dispersal distances are typically 0.25–94 m (K. D. Whitney, unpublished data) but can reach 180 m (Whitney, 2002).

This study examines three discrete *A. ligulata* populations (separated by 11–28 km) in Kinchega National Park, New South Wales (32°26' S, 142°11' E): Menindee, Big Dune, and Cawndilla. Distribution of color morphs was similar in the three populations (means 77% red, 22% yellow, and 1% orange); for further site details, see Whitney and Lister (2004). In Kinchega, *A. ligulata* flowers in September, and fruits dehisce and seeds are dispersed from mid-December through February.

Morph bias in canopy-foraging birds—To investigate biases of birds for *A. ligulata* color morphs, I compared the actual frequencies of feeding visits with expected values, given a null hypothesis of no bias. A feeding visit was defined as a visit in which the bird was observed to consume diaspores (or parts thereof), or exhibited characteristic feeding behaviors (e.g., jabbing at fruits, making short hops between clusters of fruits). Both the frequency and

duration of visits may influence fruit consumption rates, but duration could not be measured in the current study. Because many of the bird species feeding on *A. ligulata* are nomadic (Forde, 1986) and are not expected to differ locally in morph biases, I focused effort on a single *A. ligulata* population (Big Dune). Feeding visits were recorded from transects arranged to access all shrubs in the ≈10 ha population. Observers walked transects during the peak of bird activity (0630–1100 hours) for each of the 1999–2001 fruiting seasons. Total observer hours in the three seasons were 55, 63, and 94 h, respectively. To increase the independence of observations, when a feeding visit was recorded, observers ignored further activity by that bird species on that plant for a minimum of 30 min. Birds comprised three foraging guilds: (1) seed dispersers ingested entire diaspores and later defecated or regurgitated intact seeds; (2) aril thieves consumed arils while discarding seeds beneath the parent plant; and (3) seed predators breached the seed coat and consumed internal parts of both mature and immature seeds.

Morph biases in each guild were then examined. 2×3 Fisher's exact goodness-of-fit tests compared the observed and expected numbers of visits to the three morphs under the null hypothesis of no bias. Expected proportions of visits to each morph were determined by multiplying the proportion of adult plants of each morph in the population by the average whole-plant diaspore production for that morph, and scaling the expectations to sum to one. Production of undamaged, unparasitized diaspores was estimated for 25 plants/morph (10 for the rare orange morph) using the canopy subsampling methods detailed in Whitney and Stanton (2004).

Seed dispersers were sufficiently abundant to allow the comparison of biases in each year (Breslow-Day test for the homogeneity of odds ratios, Stokes et al., 2000). Seed predators and aril thieves were much less common, so data for these groups were each pooled across years. Results were Bonferroni-adjusted for $k = 5$ tests. After finding significant bias within a guild, biases for or against each morph were assessed via 2×2 tests (e.g., yellow vs. red + orange).

Morph bias in ground-foraging ants—Once diaspores fall to the ground beneath the parent plant, they are quickly removed by ants and ground-foraging birds (K. D. Whitney, personal observation). To determine the relative contributions of ants and vertebrates to removal beneath parent plants and to determine if these animals are biased toward particular aril colors, I conducted depot experiments. The design intentionally deviates from a traditional choice test (in which multiple aril colors would be available at a given location) in order to present diaspores as they are normally available (i.e., in patches of a single color). Depots consisted of 15×15 cm squares of cardboard with shallow grooves to reduce the movement of diaspores by wind. A station consisted of a pair of depots (one with, and one without, a vertebrate exclusion cage) placed underneath a randomly chosen fruiting *A. ligulata* plant. Cages were $20 \times 20 \times 13$ cm (L \times W \times H) and were formed from 13 mm wire mesh. In each population, diaspores were collected from ≥ 4 trees per morph and were pooled by aril color. Each station received diaspores of a single aril color, and station color was random with respect to the aril color of the plant above it. Ten diaspores were placed on each depot and were censused at 1, 3, 6, 12, 18, 24, and 48 h. Experiments were conducted at Menindee (4–6 February 2000), Big Dune (8–15 February 2001), and Cawndilla (2–5 February 2001) using 15 stations/morph/population. At Big Dune and Cawndilla, replicate experiments (seeds placed at 0600 and 1800 hours) tested the effects of diurnal vs. nocturnal consumers. At Menindee, only red and yellow morphs were tested because the rare orange morphs did not provide sufficient material.

For each population, I examined the effects of aril color, time of day, and their interaction (all fixed factors) on the rate of diaspore removal from stations using repeated-measures ANOVA (von Ende, 1993; Proc GLM, SAS Institute, 2000). As the caged and uncaged depots were located next to each other and represent repeated sampling of removal rates at a particular station, cage was designated a repeated factor. For depots that were fully depleted, the removal rate was calculated as 10 divided by the number of hours required for removal; if diaspores remained on the last census, the rate was the number of diaspores removed divided by 48 h. Because residuals were non-normal and did not respond to transformation, the final analysis was nonparametric and was based on ranked data (Conover and Iman, 1981).

TABLE 1. Bird species feeding on diaspores of *Acacia ligulata*, Big Dune, 1999–2001 seasons.

Guild	Species	Common name	No. visits	
Seed disperser	<i>Acanthagenys rufogularis</i>	Spiny-cheeked Honeyeater	61	
	<i>Lichenostomus virescens</i>	Singing Honeyeater	189	
	<i>Plectorhycha lanceolata</i>	Striped Honeyeater	8	
	<i>Lichenostomus pencillatus</i>	White-plumed Honeyeater	1	
	<i>Manorina flavigula</i>	Yellow-throated Miner	6	
	<i>Pomatostomus ruficeps</i>	Chestnut-crowned Babbler	6	
	<i>Oreoica gutturalis</i>	Crested Bellbird	2	
	<i>Gymnorhina tibicen</i>	Australian Magpie	4	
	<i>Cracticus torquatus</i>	Grey Butcherbird	3	
	<i>Cracticus nigrogularis</i>	Pied Butcherbird	4	
	<i>Corvus coronoides</i> , <i>C. benneti</i>	<i>Corvus</i> spp. (Australian Raven, Little Crow)	11	
	Aril thief	<i>Eolophus roseicapillus</i>	Galah	2
		<i>Northiella haematogaster</i>	Blue Bonnet	74
		<i>Malurus lamberti</i>	Variiegated Fairy-wren	2
<i>Acanthiza uropygialis</i>		Chestnut-rumped Thornbill	14	
<i>Aphelocephala leucopsis</i>		Southern Whiteface	28	
<i>Acanthiza chrysorrhoa</i>		Yellow-rumped Thornbill	3	
<i>Struthidea cinerea</i>		Apostlebird	5	
Seed predator	<i>Cacatua sanguinea</i>	Little Corella	2	
	<i>Cacatua leadbeateri</i>	Pink Cockatoo	25	
	<i>Barnardius zonarius</i>	Australian Ringneck	20	
	<i>Psephotus haematonotus</i>	Mulga Parrot	1	

Because morph bias in individual ant species could be masked in the analysis of overall removal rates, ant behavior was also examined directly. During the first 12 h following diaspore placement, the identities of ant species removing diaspores were recorded during 5-min visits (approx. 3 visits/station). For the most active species (those observed removing >25 diaspores), I used χ^2 goodness-of-fit tests to compare the number of diaspores removed from depots of each color to the expected values based on a null hypothesis of no bias. I present pooled results for each ant species because patterns did not differ among *A. ligulata* populations (K. D. Whitney, unpublished data).

Consequences of seed disperser behaviors for seedling survival and juvenile recruitment—Because early life history stages of *A. ligulata* are vulnerable (Auld, 1995b), I looked for potential consequences of disperser biases on seedling and juvenile recruitment. I focus on postemergence survival as intrinsic rates of seed germination and survival through emergence are similar across morphs, as indicated in a field trial (Whitney and Lister, 2004). The investigation was aided by the observation that ants and birds typically deposit seeds in different microhabitats. In general, birds tend to defecate or regurgitate seeds underneath trees (McClanahan and Wolfe, 1993). In particular, the two most important avian seed dispersers of *A. ligulata* (singing and spiny-cheeked honeyeaters) release more than 90% of their defecations while perched (Tester et al., 1987). In *A. ligulata* populations, individuals of other woody species are infrequent (K. D. Whitney, unpublished data); thus bird-dispersed *A. ligulata* seeds tend to fall under conspecifics. In contrast, seed-dispersing ants such as *Rhytidoponera* spp. and *Iridomyrmex* spp. deposit seeds near their nests in open, sandy areas. Nests are rarely underneath live shrubs in Kinchega (4 of 29 *R. mayrii* and 0 of 6 *I. viridiaeneus* nests), consistent with previous observations on *Rhytidoponera* nesting behavior (Davidson and Morton, 1984). Thus I contrasted seedling survival and juvenile recruitment in bird microhabitat (underneath live *A. ligulata* plants) and ant microhabitat (open ground >2 m from the nearest shrub, including refuse piles of the ant *R. mayrii*).

For *A. ligulata* seedlings, I established permanent quadrats, marked annual cohorts of naturally occurring seedlings as they emerged, and monitored their survival at 30-d intervals (14 d in 1999). In each of three populations, I established 40–48 2.0-m² quadrats per microhabitat, and monitored them from October through February 1999–2001. During this period, a single major episode of seedling emergence was observed in each population (Menindee: October 2000; Big Dune: October 1999; Cawndilla: October 2001). Kaplan-Meier survival curves were constructed using Proc LIFETEST (SAS Institute, 2000). The effect of microhabitat type, population, and their interaction on

seedling survival was analyzed using survival analysis (Proc PHREG; SAS Institute, 2000). Following the finding of a significant microhabitat \times population interaction, tests of microhabitat effects on seedling survival were performed for each population.

For *A. ligulata* juveniles, I asked whether densities differed between ant and bird microhabitats, taking into account the expected densities based on concurrent seedling emergence. Juveniles and microhabitat areas were surveyed on 10 randomly placed belt transects in each population. Juveniles were defined as plants between 5 and 100 cm in height, with at least one true phyllode (adult leaf analogue), and with no evidence of flowering. Transect dimensions depended on juvenile density and were either 30 \times 4 m or 100 \times 10 m. Fisher's exact tests for goodness-of-fit were used to compare observed numbers of juveniles in each microhabitat to expected numbers, and populations were compared using a Breslow-Day test (Stokes et al., 2000). The expected proportion of juveniles was determined for each microhabitat by multiplying the relative area of the microhabitat by its density of emerging seedlings and scaling the two expectations to sum to one. Thus, the null hypothesis is that the probability of transitioning from an emerging seedling to a juvenile is independent of microhabitat type. A major assumption of this approach is that the unobserved (historical) seedlings that gave rise to the sampled juveniles had the same microhabitat distribution as the observed (contemporary) seedlings within a population. This assumption is perhaps not unrealistic. While seed distribution may vary annually as bird and ant populations fluctuate, extended seed dormancy (Auld, 1995a) should link seedling distribution to longer-term averages of seed input.

RESULTS

Morph bias in canopy-foraging birds—The only animal species observed removing diaspores from *A. ligulata* canopies were birds. Levels of feeding activity varied over years; 0.75, 1.5, and 3.6 feeding visits per observer-hour were recorded in the 1999, 2000, and 2001 seasons, respectively. Twenty-three species were observed interacting with *A. ligulata* diaspores as either seed dispersers, aril thieves, or seed predators (making 63, 27, and 10% of visits, respectively; Table 1). Singing honeyeaters, the most frequent visitors (40% of 471 visits), acted as both dispersers and aril thieves; usually they ingested entire diaspores, and more rarely they ingested only the aril after knocking the seed off against a branch. In

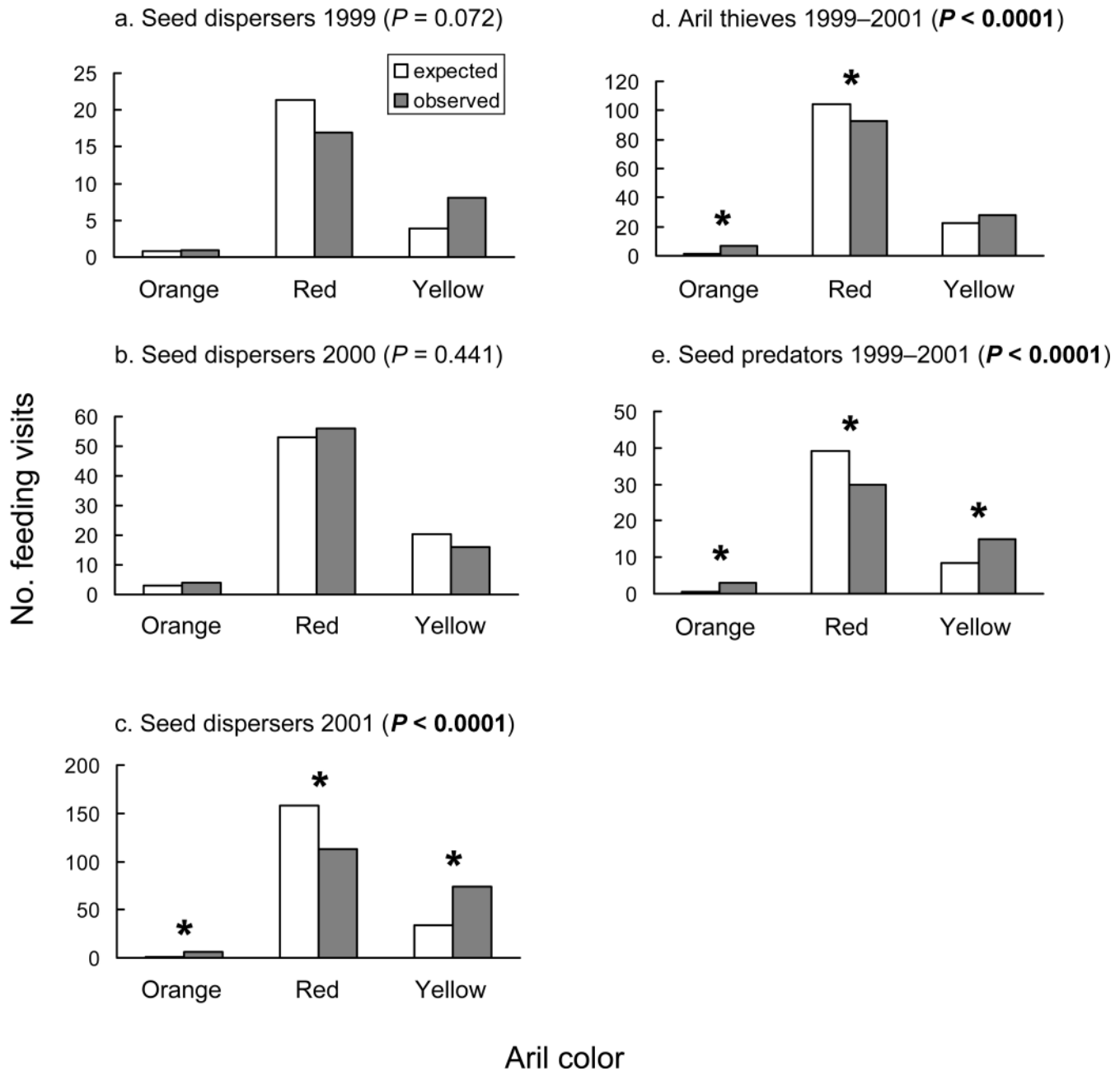


Fig. 1. Distribution of bird-feeding visits to canopies of *Acacia ligulata* aril color morphs at Big Dune. Expected values are based on both relative abundance and relative seed production of morphs. P values above each panel are for the overall hypothesis of no feeding bias; tests significant after Bonferroni adjustment for five tests are in boldface. Asterisks indicate significant differences ($P < 0.05$) for individual color morphs. (a–c) Seed dispersers in 1999, 2000, and 2001, respectively. (d) Aril thieves (data pooled across years). (e) Seed predators (data pooled across years).

the comparison of feeding guilds (presented next), singing honeyeaters were classified with seed dispersers.

All three avian guilds had feeding biases among morphs. Seed disperser visitation patterns varied across years (Breslow-Day test, $\chi^2 = 20.8$, $P < 0.0001$): feeding bias was not apparent in 1999 or 2000 but did occur in 2001 (Fig. 1a–c). In 2001, seed dispersers overvisited yellow and orange morphs ($P < 0.0001$ and $P = 0.005$, respectively) and undervisited red morphs ($P < 0.0001$; Fig. 1c). Aril thieves overvisited orange morphs ($P < 0.0001$) and undervisited red morphs ($P = 0.016$), but visited yellow morphs according to expectations

($P = 0.240$; Fig. 1d). Seed predators overvisited yellow and orange morphs ($P = 0.021$ and $P = 0.009$, respectively) and undervisited red morphs ($P = 0.002$; Fig. 1e).

Morph bias in ground-foraging ants—Animals observed removing diaspores from beneath *A. ligulata* plants included ants, birds (e.g., corvids), and a lizard (a single individual of *Tiliqua rugosa*). However, in all three populations, diaspores were removed equally quickly from caged and uncaged depots (Table 2), implicating ants as the major ground-foraging dispersers. Larger ant species (*Rhytidoponera mayrii*, *R. maniae*,

TABLE 2. Results of repeated-measures ANOVAs testing the effects of aril color, time of day (AM vs. PM), and cage treatment on removal rates of diaspores by ground-foraging animals, primarily ants. Sample sizes were 15 stations per aril color per population.

Population	Effect	df	Pillai's Trace	F	P
Menindee	Aril color	1		0.39	0.5389
	Cage	1	0.028	0.80	0.3787
	Cage × Aril color	1	0.001	0.04	0.8494
	Error	28			
Big Dune	Aril color	2		1.07	0.3481
	Time of day	1		1.16	0.2851
	Aril color × Time of day	2		0.34	0.7161
	Cage	1	0.001	0.12	0.7311
	Cage × Aril color	2	0.015	0.62	0.5379
	Cage × Time of day	1	<0.001	0.07	0.7918
	Cage × Aril color × Time of day	2	0.014	0.60	0.5520
	Error	84			
Cawndilla	Aril color	2		0.01	0.9918
	Time of day	1		27.12	<0.0001
	Aril color × Time of day	2		0.01	0.9915
	Cage	1	0.007	0.60	0.4423
	Cage × Aril color	2	0.002	0.07	0.9345
	Cage × Time of day	1	<0.001	0.01	0.9151
	Cage × Aril color × Time of day	2	0.002	0.07	0.9358
	Error	84			

R. metallica, *Iridomyrmex viridiaeneus*) removed diaspores to their nests, where arils were consumed and intact seeds were discarded. Smaller ant species (*Tetramorium impressum*, *Pheidole* spp., *Myrmicinae* spp., *Camponotus* sp.—*novae-hollandiae* group, *Melophorus* sp.) often consumed arils in situ, but occasionally removed diaspores to their nests. I found no evidence of seed predation by ants.

The ant assemblage showed no discernable morph biases. Removal rates did not differ among aril colors (Table 2), although diaspores at Cawndilla were removed significantly faster at night than during the day (Table 2). Removal rates (diaspores h⁻¹ ± SE, pooled across time of day and caging treatments) for orange, red, and yellow morphs were 3.83 ± 0.65, 3.76 ± 0.54, 4.19 ± 0.41 (Big Dune), and 5.35 ± 0.47, 5.42 ± 0.39, 5.43 ± 0.37 (Cawndilla). At Menindee, where orange morphs were rare and were not used in tests, removal rates for red and yellow morphs were 1.32 ± 0.32 and 1.43 ± 0.49, respectively. Furthermore, the number of diaspores removed by each of the three most active ant species was independent of depot aril color ($\chi^2 = 1.48, 2.65, \text{ and } 1.61; P = 0.48, 0.27, \text{ and } 0.45; N = 137, 149, \text{ and } 27$ for *R. mayrii*, *R. metallica*, and *I. viridiaeneus*, respectively), suggesting a lack of morph bias at the individual species level.

Consequences of seed disperser behaviors for seedling survival and juvenile recruitment—Seed dispersers affected the fitness of maternal plants via the location of seed deposition. The effect of a given microhabitat on survival of emerging seedlings varied among cohorts (microhabitat $\chi^2 = 1.16, P = 0.28$; cohort $\chi^2 = 0.10, P = 0.95$; microhabitat × cohort $\chi^2 = 13.47, P = 0.001$). At Menindee in 2000, seedling survival was greater in ant microhabitat than in bird microhabitat (Fig. 2a; $\chi^2 = 5.51, P = 0.019$). At Big Dune in 1999, survival was significantly greater in bird microhabitat (Fig. 2b; $\chi^2 = 4.03, P = 0.045$). At Cawndilla in 2001, microhabitat had no detectable effect on seedling survival (Fig. 2c; $\chi^2 = 1.64, P = 0.201$), although few seedlings emerged in bird microhabitats, limiting the power of this test.

The effect of a given microhabitat on the abundance of *A. ligulata* juveniles (conditioned on seedling emergence) also

varied with population (Breslow-Day test, $\chi^2 = 43.3, P < 0.0001$). At Menindee, more juveniles were found in ant microhabitat than expected from concurrent seedling emergence ($P < 0.0001$; Fig. 3a). At Big Dune, patterns of juvenile abundance were similar to expectations ($P = 0.35$), with a nonsignificant trend for more juveniles in bird microhabitat than expected (Fig. 3b). At Cawndilla, more juveniles were found in bird microhabitat than expected ($P = 0.004$; Fig. 3c).

DISCUSSION

Consequences of consumer biases for *A. ligulata* morphs—Patterns of selection in the *A. ligulata* system are the first to support the hypothesis that frugivores can have impacts on the dynamics of fruit color polymorphisms. Birds (but not ants) exhibited feeding biases among color morphs, ultimately altering their relative fitness. The effects of avian bias depend on the specific behaviors of each guild (summarized in Table 3):

1. Avian seed predators have an unambiguously negative impact on plant reproduction. Therefore, bias in this guild for yellow and orange morphs will decrease their relative fitness, all else being equal.
2. Avian aril thieves might have a positive, neutral or negative impact on maternal fitness. While aril thieves do not harm seeds, they deposit seeds beneath the parent plant. Subcanopy microhabitat is a beneficial environment for seedling survival in some sites (Figs. 2, 3); on the other hand, seedlings from undispersed seeds must compete with siblings. Thus, the fitness consequences of bias in aril thieves for the orange morph are hard to predict. Like nectar robbing in pollination systems (Irwin et al., 2001), fruit thievery in seed dispersal systems likely has complex effects on plant fitness, and deserves more study.
3. Avian dispersers, via their bias for yellow and orange morphs, appear to decrease relative fitness of those morphs in some populations (e.g., Menindee) and to increase their relative fitness in others (e.g., Big Dune and Cawndilla). This variability depends on two elements: competition between bird and ant consumers for diaspores

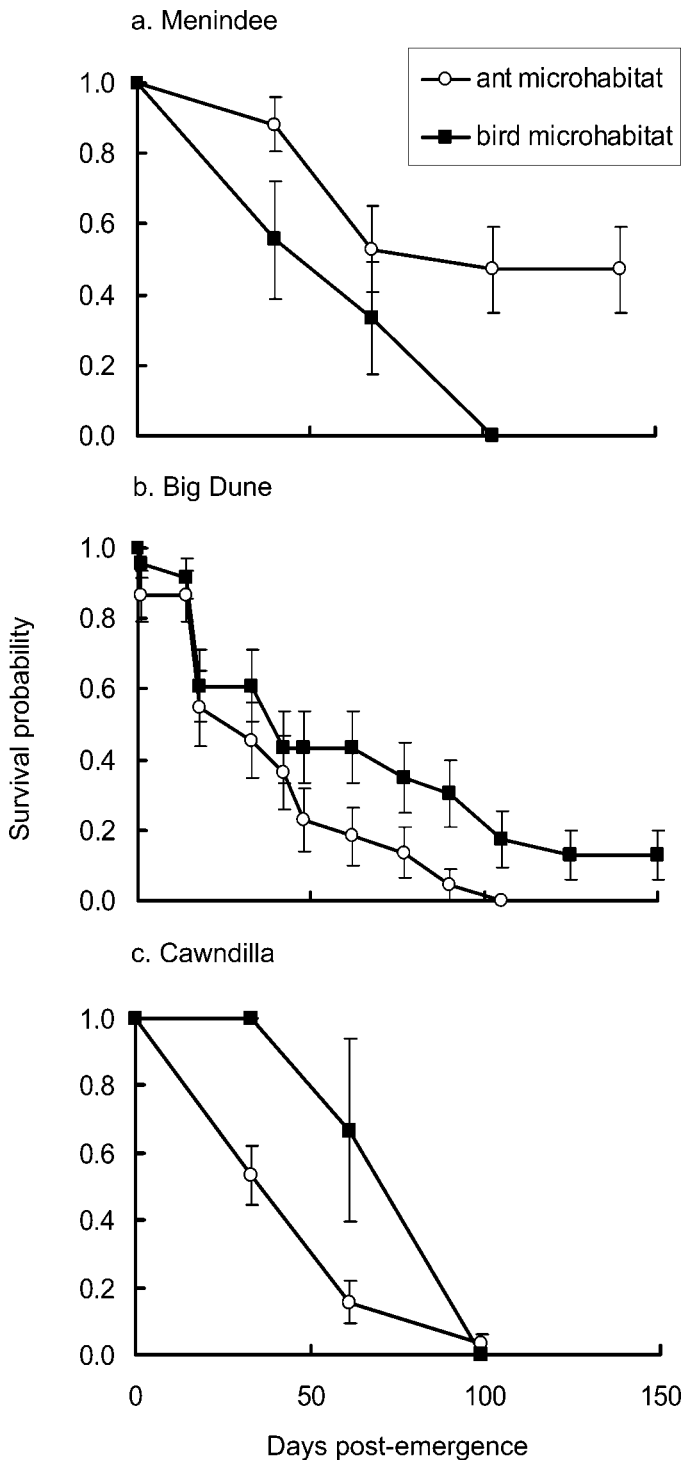


Fig. 2. Kaplan-Meier survival curves (\pm SE) for *Acacia ligulata* seedlings emerging in ant vs. bird (open vs. subcanopy) seed deposition microhabitats. Three populations are shown: (a) Menindee, 2000. $N = 17$ and 9 seedlings in ant and bird microhabitats, respectively. (b) Big Dune, 1999. $N = 22$ and 23. (c) Cawndilla, 2001. $N = 32$ and 3.

and differing fitness effects of seed deposition sites. First, because canopy-foraging birds have access to diaspores before the ground-foraging ants, and because ants generally disperse all diaspores that fall to the ground (K. D. Whitney, personal observation), avian bias increases avian

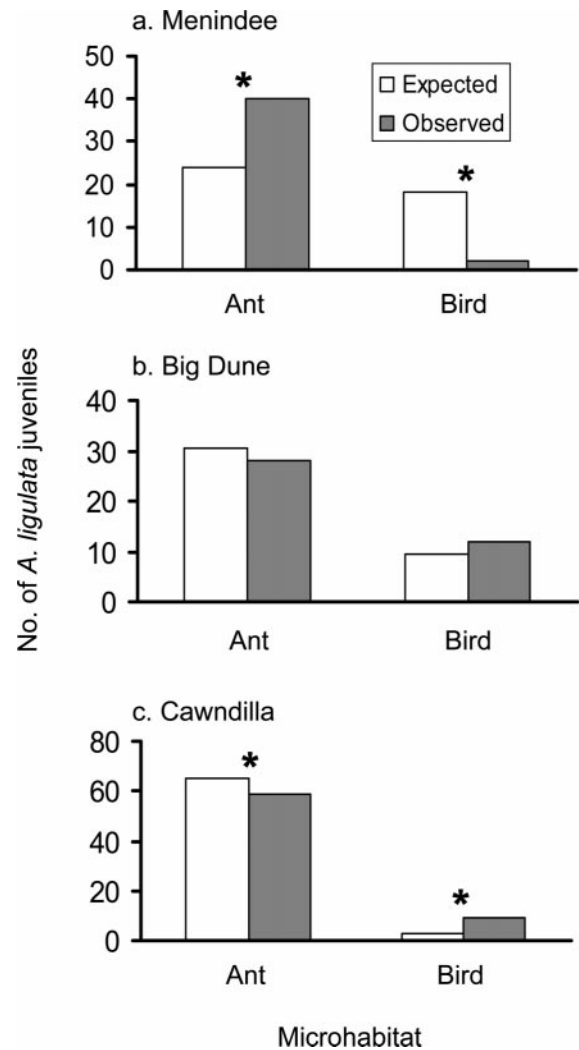


Fig. 3. Abundance of juvenile *Acacia ligulata* plants in ant vs. bird (open vs. subcanopy) seed deposition microhabitats, relative to expectations based on concurrent seedling emergence. Asterisks indicate significant differences ($P < 0.01$) obtained from Fisher's exact test for goodness-of-fit. Three populations are shown: (a) Menindee, (b) Big Dune, (c) Cawndilla.

dispersal (and decreases ant dispersal) of favored morphs. Morphs favored by birds thus have a higher proportion of their seeds arriving in bird deposition sites. Second, the "best" microhabitat (from the plant's perspective) varied spatially. In one population (Menindee), seedlings survived longer and juvenile abundance (conditioned on seedling emergence) was greater in open microhabitats where ants tend to deposit seeds. In the remaining two populations, seedlings survived longer or juvenile abundance (conditioned on seedling emergence) was greater in subcanopy microhabitats where birds tend to deposit seeds (Big Dune and Cawndilla, respectively). Further work is needed to establish whether these patterns reflect nutrient enrichment of ant nests (Holldobler and Wilson, 1990), nurse plant effects (Callaway, 1995), or other processes, and to determine why patterns differ among sites.

Conceivably, the described fitness effects of avian seed dispersers could be negated at other stages of the *A. ligulata* life cycle not examined here. For example, morphs could have

TABLE 3. Summary of spatiotemporal variation in factors affecting relative fitness of *Acacia ligulata* color morphs. Up and down arrows indicate that factors produce increases and decreases, respectively, in average fitness of yellow (Y) or orange (O) morphs relative to the numerically dominant red morph; “–” = no detectable fitness effect. Because the avian species examined were highly mobile (see Materials and Methods, Morph bias in canopy-foraging birds), avian feeding biases found at Big Dune were extrapolated to the nearby Menindee and Cawndilla populations.

Population	Year	Factors				
		Viable seed production ^a	Ant seed dispersers	Avian seed predators	Avian aril thieves ^b	Avian seed dispersers
Menindee	1999	Y↓	–	Y↓ O↓	?	–
	2000	Y↓	–	Y↓ O↓	?	–
	2001	Y↓	–	Y↓ O↓	?	Y↓ O↓
Big Dune	1999	–	–	Y↓ O↓	?	–
	2000	–	–	Y↓ O↓	?	–
	2001	–	–	Y↓ O↓	?	Y↑ O↑
Cawndilla	1999	Y↑	–	Y↓ O↓	?	–
	2000	Y↑	–	Y↓ O↓	?	–
	2001	Y↑	–	Y↓ O↓	?	Y↑ O↑

^a Combined effect of differential fruit production and differential dispersal seed predation by insects (Whitney and Stanton, 2004).

^b Fitness consequences of bias in aril thieves for orange and yellow morphs are unknown.

differential germination responses to gut processing by the dispersers (Willson and O’Dowd, 1989; Gervais et al., 1998). Such responses should be investigated in future trials. However, I note that a highly specific pattern would be required in order for dispersers to be neutral with respect to the polymorphism: relative to the yellow and orange morphs, bird disperser processing would have to reduce germination of red morphs at Menindee but increase their germination at Big Dune and Cawndilla. More likely, morph-specific disperser processing effects would add an additional layer of fitness variability to the system. Another alternative is that morphs may perform differently in ant vs. bird seed deposition microhabitats. However, this situation is unlikely given a field experiment in which seeds from red, yellow, and orange morphs planted into ant (open) microhabitat did not differ in germination success or in survival to 14 mo (Whitney and Lister, 2004).

Lack of morph bias in ants—No evidence was found for ant bias among *A. ligulata* color morphs, either in the collective ant assemblage or in individual species. A lack of bias in ants is consistent with observations on both aril lipid chemistry and the scale of ant foraging. While oleic acid and its derivatives elicit diaspore collecting behavior in several genera of ants including *Rhytidoponera* (O’Dowd and Gill, 1986; Hughes et al., 1994), *A. ligulata* morphs do not differ significantly in aril concentrations of oleic acid or any of 24 other fatty acids (Whitney and Lister, 2004). Furthermore, colony foraging areas for most ant species feeding on *A. ligulata* (all except for *R. mayrii* and *I. viridiaeneus*) are small and typically include few *A. ligulata* individuals. Even if ants perceive a difference in quality among morphs, limited access to plants may mean that a colony’s best strategy is to collect diaspores rapidly, regardless of color.

Mechanisms behind morph bias in birds—Birds did show feeding biases among *A. ligulata* morphs, although for the seed disperser guild bias was apparent in only 1 of 3 years. I

hypothesize that changes in the abundance and species composition of the bird assemblage, as well as in the nature and quality of alternative food resources, may drive temporal variability in the rates of feeding on color morphs. This variability is both expected and important to the evolution of fruit color (Willson and Whelan, 1990).

Feeding of avian seed dispersers (in 2001) and seed predators was biased towards yellow and orange morphs, and feeding of aril thieves was biased toward orange morphs. These patterns are perhaps surprising because much has been made of the link between red fruits and avian frugivores (Willson and Whelan, 1990). Avian visual systems are sensitive to red (Church et al., 2001), and many bird-dispersed plant species have red fruits (e.g., Wheelwright and Janson, 1985), leading to the expectation that birds may have innate preferences for red fruits (and flowers). However, it is clear that preference for red is not fixed within species; there is frequently substantial variability among individuals (Willson and Comet, 1993; Willson, 1994; Traveset and Willson, 1998). More importantly, birds are quick learners and have been trained to associate particular hues with nutritional rewards (Willson and Comet, 1993; Giles and Lill, 1999). Together, these observations suggest that innate preferences for a particular fruit color would not be maintained if other colors were associated with superior rewards.

Color biases could also result if particular fruit colors were especially conspicuous, thereby increasing bird detection and consumption (Willson and Whelan, 1990). There is evidence that red fruits in some floras are more conspicuous than fruits of other colors (Lee et al., 1994) and that red-and-black fruit displays are particularly attractive to birds (Burns and Dalen, 2002). Thus conspicuousness is unlikely to explain the avian bias for yellow and orange *A. ligulata* diaspores. However, conclusive tests would have to consider ultraviolet (UV) reflectance of arils because birds are sensitive to both human-perceived and UV wavelengths (reviewed in Honkavaara et al., 2002).

Bias in the interaction of avian seed dispersers and aril thieves with *A. ligulata* color morphs most likely results from variation in aril nutrients and carotenoids. Slight differences in nutrient composition can have major effects on fruit preferences and assimilation efficiencies in frugivorous birds, especially if micronutrients are scarce (Levey and Martinez del Rio, 2001). Orange morphs have 40–200% higher concentrations of P and Mg than the other *A. ligulata* morphs (Whitney and Lister, 2004). Because both P and Mg are essential nutrients for birds (Murphy, 1996), these differences might explain the bias of aril consumers for the orange morph. Bias could also be a response to quantitative and qualitative differences in carotenoids among morphs (Whitney and Lister, 2004). Because of their inability to synthesize carotenoids de novo, animals must typically obtain carotenoids from their diet (Britton et al., 1995). Carotenoids serve a variety of roles in birds, e.g., as provitamins, antioxidants, and (when deposited in feathers or skin) as sexual signals (Gray, 1996; Hill, 2002). Bias in the avian frugivores against the carotenoid-rich red morph suggests that they are not foraging to maximize carotenoid intake. Birds might be avoiding high concentrations of carotenoids, which are potentially toxic (Olson and Owens, 1998). Alternatively, they could be attracted to particular types of carotenoids specific to yellow and orange morphs; it is suggestive that many of the bird species feeding on *A. ligulata* are brightly colored in hues of yellow, orange, and/or red.

Morph bias among avian seed predators (cockatoos and parrots) was unexpected. These species discard the aril before consuming the seed, and therefore would be unlikely to respond to the observed differences in aril nutrients or carotenoids. Seed predators could be responding to a physical or chemical trait present in seeds and correlated with aril color. However, in analyses of nutrients, flavonoids, carotenoids, and fatty acids in seed tissue, as well as seed mass, no differences have yet been found among color morphs (Whitney and Lister, 2004).

Conclusions—Here, I have demonstrated that feeding biases expressed by avian consumers can alter the relative fitness of *A. ligulata* color morphs. Complementary work has shown that that red and yellow morphs each have the highest seed production in alternate sites, resulting from differences in both fruit production and predispersal seed predation by insects (Whitney and Stanton, 2004). These factors can be integrated to predict that, in the short term, the yellow morph should decrease in frequency in the Menindee population, while trajectories in the Big Dune and Cawndilla populations will depend on the relative strengths of competing factors (Table 3).

Over longer time scales, spatial and temporal variability in relative fitness of *A. ligulata* morphs suggests a mechanism by which frugivores and granivores could contribute to polymorphism maintenance in this species. Variable selection models have been used to demonstrate that, when each morph has the highest fitness in some places (or at some times), and when spatial and/or temporal variability in the relative fitnesses of morphs is sufficiently large relative to the mean advantage one morph has over another, maintenance of polymorphism can result (Gillespie, 1991). While conclusions about the long-term maintenance of the *A. ligulata* polymorphism require modeling of the variation in fitness effects (e.g., Templeton and Levin, 1979; Turelli et al., 2001), this system demonstrates that frugivores are indeed relevant to the ecology and evolution of fruit color.

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