The Condor 89:349–356

PAIR FORMATION IN COWBIRDS: EVIDENCE FOUND FOR SCREAMING BUT NOT SHINY COWBIRDS[1]

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Abstract. Sixty Screaming Cowbirds (*Molothrus rufoaxillaris*) and 150 Shiny Cowbirds (*M. bonariensis*) were trapped and banded in Buenos Aires Province, Argentina. Analysis of recaptures provided statistical evidence for pair formation in Screaming but not Shiny cowbirds, a result supported by observations of free-living birds. Pairs of Screaming Cowbirds were stable throughout the breeding season. They are probably monogamous. Shiny Cowbirds showed no pattern of association between the sexes. This is consistent with a promiscuous mating system, although this conclusion is tentative.

I also present ancillary data on sexual size dimorphism, sex ratio, and related aspects of behavior. Both species are dimorphic in size to a similar extent, although the Screaming Cowbird is slightly larger. Neither species departs from an adult (quaternary) sex ratio of unity. Pairs of Screaming Cowbirds are conspicuous near host nests. Female Shiny Cowbirds are not accompanied by males at nests, but may be accompanied by other females. Shiny Cowbird females were surreptitious near nests. Differences in host selection behavior may have profound effects on other aspects of the species breeding biology.

Key words: Screaming Cowbird; Shiny Cowbird; pair formation; mating systems; brood parasitism; Argentina.

INTRODUCTION

The unusual extent of behavioral and morphological variation in Icterinae has served to make this subfamily a compelling example of adaptive radiation in birds (Lack 1968, Selander 1972). Study of these birds has contributed substantially toward the construction of a general theory of sexual selection and mating systems (Selander 1965, 1972; Orians 1969, 1972). I add further detail to this panorama by contrasting the pairing behavior of two brood parasites, the Screaming Cowbird (*Molothrus rufoaxillaris*) and the Shiny Cowbird (*M. bonariensis*) at a site in Buenos Aires Province, Argentina, where the species are sympatric. I also present ancillary data on sexual dimorphism, sex ratio, and other related aspects of behavior.

On the one hand, we might expect the species to resemble each other very closely. First, taxonomic differences are minimal between congeners. Second, habitat differences are minimized in areas of sympatry for species with similar feeding ecologies. Finally, the species are brood parasites.

On the other hand, the species differ greatly with respect to host selection behavior and this single difference might be responsible for contrasts in a variety of other traits. The Screaming Cowbird is a host specialist, thought to use the communally breeding Bay-winged Cowbird (*M. badius*) almost exclusively (Friedmann and Kiff 1985; but see Hudson 1874, 1920; Grant 1911, 1912; Pereyra 1938; Hoy and Ottow 1964; Sick 1985). The Shiny Cowbird lays its eggs in the nests of many species, and the pattern of host selection, at least in the Río de La Plata region (Argentina and Uruguay), seems to vary with the structure of the host community (Mason 1986a). A total of 201 species of birds are known as hosts (Friedmann and Kiff 1985).

Another difference is in the extent of plumage dimorphism. Screaming Cowbirds are monomorphic in plumage (both sexes a dull black), while Shiny Cowbirds are strongly dimorphic (females are drab gray, while males are black with a blue gloss). This difference is associated with a putative difference in mating system: Hudson (1874, 1920) and Friedmann (1929) described Screaming Cowbirds as monogamous since they typically travelled in pairs, but Shiny Cowbirds as promiscuous since they apparently lacked any regular association between the sexes. Both authors drew these conclusions without the aid of individually marked birds.

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[1] Received 19 May 1986. Final acceptance 10 December 1986.

METHODS

The study site was conducted at Estancia El Talar (Site II of Mason 1986a, described in Mason 1985), near Magdalena, Buenos Aires Province, Argentina from 21 September 1978 to 10 February 1979. Birds were trapped on 27 days between 6 October 1978 and 20 January 1979 in a walk-in decoy trap, baited with grain and water, and similar in construction to that described by Carter (1986). The trap was left baited but open on nontrap days, so that birds could habitually enter the trap to eat.

Sixteen of the 27 trap days were in October. The others occurred sporadically in the remaining interval. Poor weather and destruction of the trap by cattle and horses prevented a regular trapping schedule.

To identify possible pairs of birds, I occasionally observed animals near the trap and removed pairs immediately after entry. The trap was usually left unattended. On first capture, birds were weighed to the nearest 0.5 g with a spring scale and given a unique color combination of enamelled aluminum leg bands (≤ 2 each leg). Shiny Cowbirds were sexed by plumage. Screaming Cowbirds were laparotomized (Risser 1971).

Identification of pairs through the analysis of recaptures is sensitive to any difference between the sexes in susceptibility to enter the trap. Two tests were performed to assess trapability. First, distributions describing the frequency of capture were compared using the Heterogeneity G test (Sokal and Rohlf 1981). Second, probability of recapture was calculated for retrapped birds (Darley 1971), and sexes were compared using the Mann-Whitney *U*-test (Siegel 1956). These techniques have two additional benefits. First, if no evidence is found of a sex-specific bias in capture, then the population sex ratio is estimated by the observed sex ratio. Sex-ratio was tested for skewness with the Chi-square test (Siegel 1956). Second, equivalent rates within sexes allow the sexes to be pooled such that species comparisons can be made.

A difference in capture frequency (which could affect the ease with which pairs could be identified) might be due to differences in site fidelity. Site fidelity was calculated by recording how many days separated the first and last date of observation for each bird that was recaptured or resighted. Differences between sexes were tested with the *U* statistic. Species comparisons were performed when no intersexual differences were found.

Pairwise relationships were recognized using a randomization procedure for testing the association between two species (Pielou 1977), but substituting individuals for species. On each trap day, birds were recorded as either present or absent, and then 2 × 2 tables were constructed describing the frequency with which each bird of every possible pair was present or not. The entries in the four cells represent the number of times that: (1) both birds were caught together; (2) and (3) one bird was caught but the other was not; and (4) neither bird was caught. The randomization procedure then calculates a 1-tailed probability that those two particular birds enter the trap independently. In this sense, the procedure is similar to Fisher's exact test (Siegel 1956).

Positive association is indicated by disproportionate scores in cells 1 and 4 of a particular 2 × 2 table. To eliminate the possibility of inflating the absent-absent cell (Cell 4), I made conservative assumptions about survivorship: a bird was not assumed to be in the population until it was trapped, and not assumed to live after it was last trapped. Tests were carried out only for pairs whose period of joint observation was at least six trap days, the minimum sample size needed to show significance ($P = 0.05$ when both birds were caught together three times, and neither caught on three other days).

Other kinds of information are made available if the probability of independent recapture is also calculated for intrasexual pairs. Although comparison of inter- with intrasexual pairs cannot be construed as a control procedure, doubt would be cast on the entire approach if intersexual pairs were identified as frequently as intrasexual pairs and no biological correspondence could be established between them. In some cases, an appropriate explanation might be available. For example, if males are polygynous and hold stable harems, then significant pairwise associations should occur between the harem members as well as between the male and each female.

Data collected through the trapping program were compared with observations on free-living birds (both marked and unmarked). I comment on the behavior of cowbirds at nests where I made repeated "spot checks" of less than 15 min duration (Mason 1986b).

RESULTS

TRAPPING RESULTS

I trapped 60 Screaming Cowbirds (27 females, 33 males) between 9 October 1978 and 20 January 1979, and 150 Shiny Cowbirds (70 females, 80 males) between 6 October 1978 and 29 December 1978. While Shiny Cowbirds were calm in the trap, Screaming Cowbirds (especially males) were restless. They typically struggled, and crashed against the walls. The lores were generally bloodied and recaptured birds often possessed infected lesions, a source of injury that may have increased mortality and made the detection of pairs more difficult. Infections were not observed around laparotomy wounds.

The ratio of male weight to female weight, an index of sexual dimorphism, is approximately equal between the two species, despite differences in body weight: ratio = 1.20 for the Screaming Cowbird (mean male weight = 58.0 g, ±4.0 g SD, n = 33; mean female weight = 48.4 g, ±4.4 g, n = 27); ratio = 1.24 for the Shiny Cowbird (mean male weight = 55.5 g, ±7.6 g, n = 69; mean female weight = 44.9 g, ±4.3 g, n = 78).

Trapability was statistically indistinguishable for the sexes within each species, as judged by both the frequency distribution of captures (Table 1) and by recapture rates (Screaming Cowbirds: U = 114, ns, for 15 females, 16 males; Shiny Cowbirds: U = 21.5, ns, for 6 females, 11 males). Screaming Cowbirds repeated more than Shiny Cowbirds (Table 1). This difference is reflected in the greater site fidelity of Screaming Cowbirds relative to Shiny Cowbirds, although the difference does not quite reach the conventional level of significance (z = 1.95, P = 0.052, 2-tailed, for 31 Screaming Cowbirds, 16 Shiny Cowbirds). Sexes within each species show similar site fidelity (Screaming Cowbirds: U = 117, ns, for 15 females, 17 males; for Shiny Cowbirds, U = 60.5, ns, for 9 females, 17 males). The equivalent susceptibility to trapping between the sexes (in both species) establishes a precondition for the successful identification of intersexual pairs. However, the lower site fidelity of Shiny Cowbirds means that pairs will be more difficult to identify in this species. No Shiny Cowbird was observed in the study area for more than 54 days (a female) while 14 Screaming Cowbirds exceeded this total. No evidence suggests a departure from a sex ratio of unity in either species (Screaming Cowbird: $\chi^2 = 0.60$ for 1 df, ns; Shiny Cowbird: $\chi^2 = 0.67$ for 1 df, ns, $0.5 < P < 0.7$ in both cases).

TABLE 1. Frequency distribution of captures. In both Screaming Cowbirds and Shiny Cowbirds, males and females are equally as likely to be trapped and retrapped (GH = 0.58, df = 3, $P > 0.75$, GH = 3.78, df = 3, $P > 0.25$, respectively). Screaming Cowbirds are trapped more readily than Shiny Cowbirds (GH = 42.18, df = 3, $P \ll 0.001$).

		No. captures			
		1	2	3	>3
Screaming Cowbirds:	Females	12	6	3	6
	Males	17	5	4	7
	Total	29	11	7	13
Shiny Cowbirds:	Females	74	5	0	1
	Males	59	7	1	3
	Total	133	12	1	4

Among Screaming Cowbirds, sufficient data were collected to calculate the probability of independent occurrence of 175 pairs of birds. Three of 90 intrasexual comparisons were significant, while eight of 85 intersexual comparisons were significant. Later, 10 additional intersexual comparisons were performed; one was significant (see below). All significant interactions indicated that birds tended to occur together more likely than chance would predict. No evidence suggested that any birds avoided each other (that is that they co-occurred in the trap less likely than by chance), although the technique would identify such a response. The intersexual comparisons involved 10 males and 12 females; 13 individuals accounted for all eight significant relations (Table 2). These data identified six pairs (F1–M1, F2–M2, F3–M3, F4–M4, F5–M5, F6–M6). Females F1 and F5 were also significantly associated with male M7, although to a lesser extent than to their putative mates. This unusual male (M7) accounted for four significant associations, two with these females and two with other males, one of them (M1) the mate of female F1 (Table 3). The role of male M7 is discussed more precisely below.

On 10 occasions I observed two birds enter the trap together. In each case, one was a male and the other a female. Four of the six pairs identified above accounted for eight of the 10 observations. Pairs F1–M1 and F3–M3 were each observed to enter once each. Pairs F5–M5 and F6–M6 were each observed to enter three times.

TABLE 2. Probability of independent recapture of male and female Screaming Cowbirds. Significant associations underlined. Dashes indicate pairwise interactions lacking a sufficient period of joint observation.

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
F1	<0.001	0.400	0.286	0.441	0.113	0.162	0.002	0.341	0.500	0.400
F2	0.441	0.018	0.359	0.458	0.495	0.533	0.288	0.206	0.467	0.333
F3	0.476	—	0.048	0.833	—	—	0.286	—	—	—
F4	0.222	0.385	0.490	0.038	0.280	0.667	0.189	0.189	0.536	—
F5	0.294	0.450	0.343	0.525	<0.001	0.303	0.021	0.341	0.525	0.533
F6	—	0.200	0.500	0.500	0.303	0.015	0.303	0.212	—	—
F7	0.417	—	0.300	0.700	0.222	—	0.300	0.300	0.175	0.667
F8	0.600	—	0.450	—	0.500	—	0.600	0.450	—	0.200
F9	0.530	0.909	0.485	0.833	0.889	—	0.545	0.545	0.300	—
F10	0.343	0.154	0.343	0.743	—	—	0.267	0.385	—	—
F11	—	—	—	—	0.429	0.514	0.429	0.429	—	—
F12	0.667	—	0.333	0.333	—	—	—	—	—	—

On the only occasion when F6 was trapped and M6 was not, I saw M6 perch on top of the trap and call to F6. She responded by trying to fly up to him. The remaining two cases of seeing birds enter the trap together are discussed below.

Pairs were simultaneously and unequivocally identified in the field and away from the trap on 18 occasions. In each case, one was a male and the other a female. Pairs F2–M2 and F6–M6 were each seen twice, whereas pairs F1–M1, F3–M3, and F5–M5 were identified three times each. The remaining five cases of visually identifying pair members in the field are discussed below.

Four pairs (F2–M2, F4–M4, F5–M5, F6–M6) were apparently stable: three remained intact until the end of the observation period (when all three pairs were trapped), and neither member of a fourth pair was recaptured or resighted after 29 December 1978. The first three pairs were observed over a period extending nearly 4 months. This is a minimal estimate for the duration of the pair bond, since all birds were probably paired before they were captured. In the remaining two pairs, the termination of the period of joint observation (in the trap) was defined by the disappearance of only one bird (male M1 in the first case, female F3 in the second). By analyzing the data after the disappearance of the mate, I detected that F1 remated with M8 ($P = 0.018$), a previously unmated male. Three other males showed nonsignificant patterns of association. Female F1 and male M8 were observed once in the field during this period, whereas she had been identified only with male M1 previously (see above). Male M3 apparently failed to find a mate (after F3 disappeared) among the six females for whom sufficient data were collected to test his association. However, he was observed twice in the field with female F10, and the two of them were observed to enter the trap together on a single occasion.

Three additional pairs were visually but not statistically identified. No individual of these three putative pairs appears in Table 2. In the first case, a pair was observed to enter the trap together. The observation and the trap data are consistent with pair formation, but the sample is too small to find statistical significance. ($P = 0.167$ for four trap days, two with both present and two with both absent.) In the second case, a pair was identified in the field. Each of these birds had been trapped only once (different days). The final case consists of two birds which were trapped together once (but not watched while they entered), but then identified together once in the field. If the field identification is counted as a trap day, and the intervening trap days are scored as entries in the absent-absent cell, this pair would be identified with a probability of 0.038.

Three lines of evidence suggest strongly that male M7 was an interloper or "satellite" rather than a secondary mate of females F1 and F5 (Table 3). First, male M7 was not recorded in any of the encounters when pairs F1–M1 and F5–M5 were seen together. Second, he was never observed with either female. Third, he failed to maintain a significant association with female F1 ($P = 0.286$) when male M1 disappeared and female F1 apparently paired with male M8.

The only other pairwise interaction recognized among Screaming Cowbirds was between females F1 and F11. With the exception of this interaction and those of male M7, all other significant interactions were exclusive and occurred between members of the opposite sex.

Forty-five pairwise interactions, 23 intersexual, were examined between Shiny Cowbirds. None was significant.

ADDITIONAL OBSERVATIONS OF FREE-LIVING BIRDS

The two species behaved differently at host nests. Pair formation in Screaming Cowbirds is more apparent than in many nesting species. Males remain close to females, usually following within 2 m of them in flight. Nest inspections occur throughout the day. Pairs and nest inspections were observed at the beginning of the study period, before the trap was constructed. As females inspect host nests, males typically perch above them, vocalizing and performing "song-spread" displays (Orians and Christman 1968). I saw pairs of Screaming Cowbirds at host nests on 29 of 128 (23%) spot checks at nests. In 30 hr of intensive observations, I recorded 42 visits, or one every 43 min. Nest visits were often performed by several pairs at a time; once five pairs inspected a nest simultaneously. Since several eggs may appear in a nest in a single day, several females will lay in the same nest.

Shiny Cowbirds, on the other hand, displayed no obvious pair formation. Males often perched at tree tops, but also followed females and courted them almost anywhere. Females were also seen alone and in the company of other females. Several female Shiny Cowbirds will lay in the same nest of preferred hosts since several eggs may appear in nests in the same day (Fraga 1985, Mason 1986a). The approach of females to nests and their behavior at nests is quiet and surreptitious, contrasting greatly with that of Screaming Cowbirds. Females will often perch within 5 to 10 m of host nests, apparently watching the activity there. On several occasions, females emitted "chatter" calls from their perches as I examined host nests. I have only a single observation of nest inspection by these cowbirds: two female Shiny Cowbirds examining a nest of the Chalk-browed Mockingbird (*Mimus saturninus*, a species whose data base consists of over 350 spot checks). Two females entered the nest, each giving "bill-up" displays to the other (a common icterine aggressive display, Orians and Christman 1968). The females alternated jumping in and out of the nest and settling on the eggs. They were silent, and no egg was laid during this sequence. I never saw males at nests.

TABLE 3. Association of male Screaming Cowbird, M7, with other birds. Significant associations underlined. Birds listed at ends of columns are mated pairs.

M1	M5	M3
0.020	0.113	0.047
	M7	
0.002	0.021	0.290
F1	F5	F3

DISCUSSION

The Screaming Cowbird forms pairs (Table 2) which are stable throughout the season. Of six statistically identified pairs, three remained intact for nearly four months, and a fourth may have left the study area after about three months. Two pairs broke up, probably because of the death of a mate. At least one bird, a female, remated. Visual identification offered corroborating evidence for five of the six original pairs, and for the female that remated.

The statistical technique demonstrated here to identify pairs appears to be successful. Direct observational data are consistent with the statistical analysis. This is encouraging, since observation of marked birds in the wild is often difficult and time consuming. Despite their value, observational data are often vague in the sense that their explanatory power frequently depends on no criterion stronger than intuition or plausibility. Consider the example of the male and female captured together on two trap days (and seen to enter as a pair once) but both absent on two other trap days. Some observers might wish to label these individuals a pair, whereas others might not. The technique used here indicates that the data are too few to make a statistical judgment.

Several phenomena explain why only one member of a pair-forming species might be recaptured. First, pairs may not remain together all day long. Their tendency to travel independently will naturally be reflected by a greater likelihood of capturing one but not the other. Second, birds may enter the trap sequentially rather than simultaneously. The second member of the pair might have been trapped had the trap been left in operation more time. The observation of male M6 calling to female F6 while the latter was in the trap is germane in this context. Third, some birds managed to escape before I could identify them. The analysis has shown itself robust to these aspects of behavior which tend to weaken the sensitivity of the test.

Monogamy is probably the predominant mating system in Screaming Cowbirds. Hudson (1874, 1920) and Friedmann (1929) described Screaming Cowbirds this way, although their conclusion was drawn without the advantage of marked birds and without seeing copulations. Both authors implied that pairs were stable, since they felt that this species displayed strong site fidelity (relative to Shiny Cowbirds). This study supports that claim as well, at least within a season. More recently, Fraga (1986) banded a single pair in Buenos Aires Province; the birds remained paired for the entire breeding season. Pair association does correspond to the observed pattern of mating in Brown-headed Cowbirds (*M. ater*) in the Owens Valley of California (Yokel 1986, the only study of a monogamous brood parasite which reports extensive data on both pair formation and copulatory behavior).

One male, M7, showed a complex pattern of interaction with other birds (Table 3). During most of the study period, he apparently followed two females mated to other males. It is unlikely that this male was bigamously mated to both females. He was not observed with them away from the trap and when the mate of one of these females disappeared, he was unable to maintain his association with her. Fraga (1986) observed occasional unpaired male Screaming Cowbirds. His only two records of male-male aggression occurred when unpaired males attempted to copulate with mated females.

Two patterns of interaction are puzzling. Male M7 showed a significant association with male M3, but not his mate, F3 (Table 3). Two females also showed a significant interaction with each other. I cannot offer any reasonable biological interpretation of such behavior. Perhaps Type I error (false rejection of the null hypothesis) is the most appropriate explanation, given that 185 tests were run. Lacking more detailed observations of individual behavior, I suspend judgment on the importance of such results.

The trapping data offer no evidence that Shiny Cowbirds form any kind of regular association. This would be consistent with a promiscuous mating system, as claimed by Hudson (1874, 1920) and Friedmann (1929). This conclusion should remain tentative, however, since Shiny Cowbirds are probably more mobile than Screaming Cowbirds.

The behavior of free-living Shiny Cowbirds similarly gives no hint of pair formation. Males may be more sedentary than females, although I failed to find a significant effect with a small sample. Eight males but only two females resided in the study area for more than three weeks. Fraga (1985) reported that none of five banded female Shiny Cowbirds in Buenos Aires was present in his study area for more than three weeks. He felt that this interval was the typical time spent in one area by a female, since unusually marked eggs (attributed to single females) were not found for more time than this. The breeding season of Shiny Cowbirds lasts at least three months (Mason 1986a).

Although the Shiny Cowbird is strongly dimorphic in plumage, both species are dimorphic in size to a similar extent. It is incorrect to assume that a particular level of dimorphism is necessarily associated with a promiscuous or polygynous mating system (Orians 1972:309). Sexual dimorphism in plumage also fails to have much predictive value. By comparison, Brown-headed Cowbirds (also strongly dimorphic in plumage) are monogamous in some areas (Darley 1982; Dufty 1982a, 1982b; Yokel 1986), while at least one other population is promiscuous (Elliott 1980) and another polygynous (three of seven males mated polygynously, Teather and Robertson 1986).

A difference in mating system between the two species cannot be explained by reference to a difference in the sex ratio (Murray 1984), since neither species departed from a sex ratio of unity.

Eventually, contrasts in host selection behavior may help to explain variation in mating system, particularly if populations of brood parasites are host limited. Brood parasites are obligately dependent upon the parental care of host species and Screaming and Shiny cowbirds contrast greatly with respect to their use of the "host niche."

Behavior near the nest is extremely different in the two species. Pairs of Screaming Cowbirds visit host nests throughout the day; often several pairs are simultaneously involved in such nest visits. Male Shiny Cowbirds do not accompany females as they seek host nests, although the latter may be accompanied by other females. Fraga (1985) observed gregarious nest inspections during seven of 42 (17%) visits of female Shiny Cowbirds to Chalk-browed Mockingbird nests. Twice he saw five females simultaneously inspecting the same nest.

The adaptive significance of monogamy in brood parasites is difficult to explain. In two Brown-headed Cowbird populations, mate-guarding by males appears to be the appropriate explanation (Dufty 1982a, 1982b; Teather and Robertson 1986, for the four males that mated monogamously). In another population, the mate guarding explanation fails (Yokel 1986). The limited amount of data presented for the Screaming Cowbird is equivocal. Although M7's significant interaction with M1 (of pair F1–M1) could be interpreted as evidence of mate guarding, no such effect occurred between M7 and M5 (of pair F5–M5). Males may plausibly provide service to females in the form of detection of host nests, distraction of hosts from nests (allowing females to enter host nests more easily), or protection of a territory from parasitism by another female. In the case of the Screaming Cowbird, we can eliminate only the territorial hypothesis since the gregarious nest searching of these birds is inconsistent with territoriality. Such male roles, suggested for some cuckoos (Liversidge 1970, Riddiford 1986), must remain speculative until appropriate tests are designed. Male removal will most likely result in the formation of new pairs, as it did here. Even if this were not to occur, the female's performance without male service would probably be impossible to measure. In addition, males are not uniquely qualified to perform these tasks: females may use other females to find nests (Wyllie 1981) or to distract hosts (Smith 1968), and a female herself can defend a territory against other females (Dufty 1982a). Manipulation of the resource (host) base may be a more feasible research method. In Buenos Aires, a change in host selection in the Shiny Cowbird was attributed to a change in the structure of the host community (Mason 1986a), although this comparison was made between two study sites. Local variation in host selection may be common.

Mating systems should not be conceived as fixed properties of species, even in brood parasites which at first glance seem to share the same mode of reproduction (Ankney and Scott 1982). Rather, they appear to be dynamic adaptations to particular patterns of resource availability (Orians 1969). In the case of brood parasites, differences in the quality and distribution of host nests could create varying opportunities for sexual selection to act.

ACKNOWLEDGMENTS

Field research, partially funded by the Chapman Fund of the American Museum of Natural History, New York, was performed while the author was a graduate student at the University of Texas. Analysis was performed while the author was a postdoctoral fellow at the University of California, Santa Barbara, supported by NSF grant DEB 8214999 to S. I. Rothstein. The manuscript was improved by comments from R. M. Fraga, L. Hunt, S. I. Rothstein, D. Yokel, and two anonymous reviewers.

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