Male rank, female breeding synchrony, and patterns of paternity in the boat-tailed grackle

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Species in which males directly defend groups of breeding females often have extreme skew in observed male mating success. In only a few species, however, has a corresponding skew in fertilization success been confirmed. Furthermore, the ecological and social factors contributing to variation in fertilization success need investigation. This study examined competition for mates and paternity in the boat-tailed grackle (*Quiscalus major*). Observations at colonies of nesting females revealed that the top-ranking or alpha males performed more than 70% of the copulations. DNA fingerprinting indicated that alpha males sired less than 40% of nestlings. Nevertheless, analysis of band-sharing scores among nestlings from different nests suggested that alpha males sired more than three times as many offspring as any other individual male. Because few nestlings were sired by the nonalpha males that associated with colonies, females must have mated with other males while on trips away from colonies. Analysis of paternity within broods revealed that at least half of all females had their brood fertilized by more than one male. Alpha males' success at fertilizing eggs did not vary with the number of simultaneously receptive females within a colony. Our results suggest that male and female behavior in female-defense polygyny results from complex coevolution of the sexes. *Key words:* boat-tailed grackle, DNA fingerprinting, female-defense polygyny, female synchrony, *Quiscalus major*. [*Behav Ecol 10: 444–451 (1999)*]

Species in which males defend females directly, rather than the resources females require, are characterized by intense competition among males for access to females and extreme sexual dimorphism in size and in the timing of maturation (Robinson, 1986; Webster, 1992). Typically in these species a small percentage of males achieve most matings, and many males fail to copulate during a breeding season. Highly skewed mating success among males creates a large opportunity for selection on males and has presumably favored males that delay breeding until they have achieved large size or high social rank (Clutton-Brock et al., 1982; Le Boeuf, 1974; Post, 1992; Poston, 1997a).

Among species with female-defense polygyny, three aspects of females' breeding biology permit males to defend groups of females during a season: females aggregate during the breeding season, they frequently copulate within these aggregations, and they have a prolonged breeding season (Robinson, 1986; Webster, 1994a). In short, fertile females are spatially clumped and temporally dispersed. Emlen and Oring (1977) proposed that increased synchrony or decreased aggregation among females would limit males' ability to defend and to mate with more than one female, and comparisons among species have confirmed their predictions (Clutton-Brock, 1989; Robinson, 1986; Webster, 1994b). However, few studies have either confirmed that males defending female aggregations actually sire most of the young (see Pemberton et al., 1992; Webster, 1995) or examined the effects of synchrony or aggregation on variation in male mating success within a population.

Several studies of species with a variety of mating patterns

indicate that a female's choice of a mate is not necessarily limited by male behavior. In many species that form pair bonds, females engage in extrapair copulations (EPCs), and EPCs result in extrapair fertilizations (EPFs) in a wide range of species (reviewed by Birkhead and Møller, 1992; Westneat and Sherman, 1997). Because EPCs are often difficult to observe, fertilization success of males can differ significantly from observed mating success. For species in which males defend females directly, male fertilization success is usually inferred from observations of copulations. The high frequency of EPFs in other species suggests that any study of mating success should combine observation of the behavior of males and females with determination of parentage of young by molecular techniques (Westneat and Webster, 1994). In addition, in many female-defense polygynous species, the number of sexually receptive females varies during the course of the prolonged breeding season. Thus these species offer opportunities to examine the effect of synchrony among females on variance in male reproductive success.

In this study we examined mating and fertilization success of male boat-tailed grackles (*Quiscalus major*). Boat-tailed grackles nest in colonies that range in size from 2 to more than 90 nests. Colonies are usually in islands of emergent vegetation in marshes or in isolated trees, sites that presumably offer protection from terrestrial predators. Female grackles build nests and rear offspring unaided by males. Females nest asynchronously, so the number of receptive females per day in a colony ranges widely (Post, 1992; Poston, 1997b). Females make frequent trips away from colonies to forage and to gather nest material. Males pursue alternative strategies for access to females: some males compete for access to females in and near colonies ("colony males"), and other males ("noncolony males") display to females at sites away from colonies (Post, 1992). Colony males form age-dependent dominance hierarchies that represent queues for access to colonies (Post, 1992; Poston, 1997a). The top-ranked male is the alpha male, the second-ranked male is the beta male, and so forth. The alpha male has unrestricted access to the colony; he spends more

time in the colony than does any other male, and he interrupts other males' attempts to copulate within the colony (Poston, 1997a,b). As a result, alpha males perform the majority of copulations in a colony (Post, 1992; this study). Non-alpha colony males display to females within 150 m of the colony, and they venture into the colony when the alpha male is absent. Position in the queue is thus correlated with access to breeding females. This study was designed to determine the mating success of colony males, the conditions under which colony males escort females on trips away from colonies, and the fertilization success of males.

METHODS

General

We observed boat-tailed grackles at Magnolia Gardens near Charleston, South Carolina, during January–June, 1991–1993. The study site adjoined the area used for previous studies of this species by Post (1992, 1994). The grackles nested on islands of emergent vegetation in a 30-ha marsh (see Post and Seals, 1991, and Poston, 1997a, for more details of this site). The study focused on colonies of grackles at seven islands on the northeastern corner of the marsh. Two groups of colony males competed for these seven colonies. Ten males competed for the 4 easternmost colonies, and 12 males competed for the 3 westernmost colonies. Males frequently interacted with members of their group but rarely interacted with males from the other group. Ad libitum observations of agonistic interactions between males revealed linear dominance hierarchies among colony males in each group. The western group was further divided: two high-ranking males (alpha and beta) defended one of the three islands, and three high-ranking males (alpha, beta, and gamma) defended the other two islands. Lower-ranking males in the western group moved between the three islands (see also Poston, 1997a).

By, 1992, 86% of the adult males and 83% of the adult females had been marked with unique combinations of colored aluminum bands. The grackles were observed in their colonies from blinds on wooden platforms, from a canoe, and from foot on the dike that surrounded the marsh. Each season, observations rotated among three to four colonies. Midday attendance at colonies was low, so observations were made for 3–4 h in the morning and 2–3 h in the evening. We visited each colony at least twice per week. Frequencies of courtship displays, copulations, and escorting behavior were based on ad libitum records (Altman, 1974) of events during observation sessions at colonies. A subset of observations based on focal samples of males and colonies (Poston et al., unpublished data) revealed similar patterns of mating success and consorts among males, so we used the larger set of data based on ad libitum observations. In addition to the results presented here, Poston investigated spatial relationships and queuing among males (1997a) and mate choice among females (1997b).

Male mating success and escorts of females

To measure mating success of males at colonies, whenever a male performed a courtship display to a female we recorded the location, identity, and behavior of the male and the female. We observed 12 courtship displays that resulted in copulation (the male mounted the female and made cloacal contact). We assumed that an additional 110 displays resulted in copulation because the pair was hidden from view for at least 10 s, and the male produced the high-pitched vocalization (Post et al., 1996; Selander and Giller, 1961) characteristic of all observed copulations but not heard in other contexts (see

also Post, 1992). To measure the incidence of escorting behavior by males, each time we observed a male depart a colony within 5 s of a female and follow her away from a colony, we recorded the participants, date, time and location.

Synchrony of female receptivity

Previously, Post (1992) found that the females in this population were receptive for 3 days, beginning 4 days before the first egg appeared in the nest. Therefore, we could determine when each female was receptive by back-dating from the day she laid her first egg. Female grackles lay one egg per day, and the modal clutch is three eggs (76% of 1400 clutches; Post et al., 1996). By checking each nest in each colony every 3–4 days, we determined the number of receptive females per day for each colony.

DNA fingerprinting

The techniques for DNA fingerprinting followed those of Westneat (1990, 1993). Blood was sampled from the brachial vein of adults and nestlings and mixed with an equal volume of TNE buffer (0.01 M Tris, 0.001 M NaCl, 0.002 M EDTA) and frozen at $-20°$ to $-70°C$ for up to 3 years. DNA was extracted from blood with a modified phenol-chloroform procedure (Quinn and White, 1987; Westneat, 1993). Approximately 10–15 μg of DNA was incubated with an excess of the restriction enzyme $AluI$. The amount of digested DNA was measured in a spectrophotometer and about 6 μg was subjected to electrophoresis in a 0.8% agarose gel at 33 volts for 48 h. After it was denatured and neutralized (Westneat et al., 1988), DNA was transferred to a nylon membrane with a vacuum blotter. Each membrane was hybridized with a radioactively labeled probe and exposed to film for 1 week. Membranes were stripped of the probe and then reprobed twice for a total of three probings (probes: M13, M2.5 per, Jeffreys 33.15; Jeffreys et al., 1985a,b).

We organized gels with the alpha male in the center lane, nestlings in lanes on either side of the alpha, and other males that attended the colony in the outer lanes. All nestlings were within eight lanes of alpha males, and the majority (69%) were within four lanes. For each of 10 nestlings we also had a sample from the female that attended its nest. Each of these nestlings was placed in a lane between the female and the alpha male. Density of nests in the thick vegetation of colonies made association of other marked females with particular nests uncertain.

Scoring autoradiographs

With an acetate overlay, we marked bands and measured the distance each band had migrated to the nearest 0.5 mm. Bands that had migrated within 0.5 mm of one another were scored as shared. In lanes that hybridized weakly, indicating less DNA, we scored all visible bands; in lanes hybridizing strongly, indicating much more DNA, we only scored distinct bands (see also Westneat, 1993).

We summed the results from all three probes to produce one coefficient of band sharing for each pair of birds on each gel. The proportion of bands shared between a pair of individuals is $2N/(A+B)$, where N is the number of bands in common and A and B are the number of bands for each individual (Wetton et al., 1987).

RESULTS

Male mating success and response to female synchrony

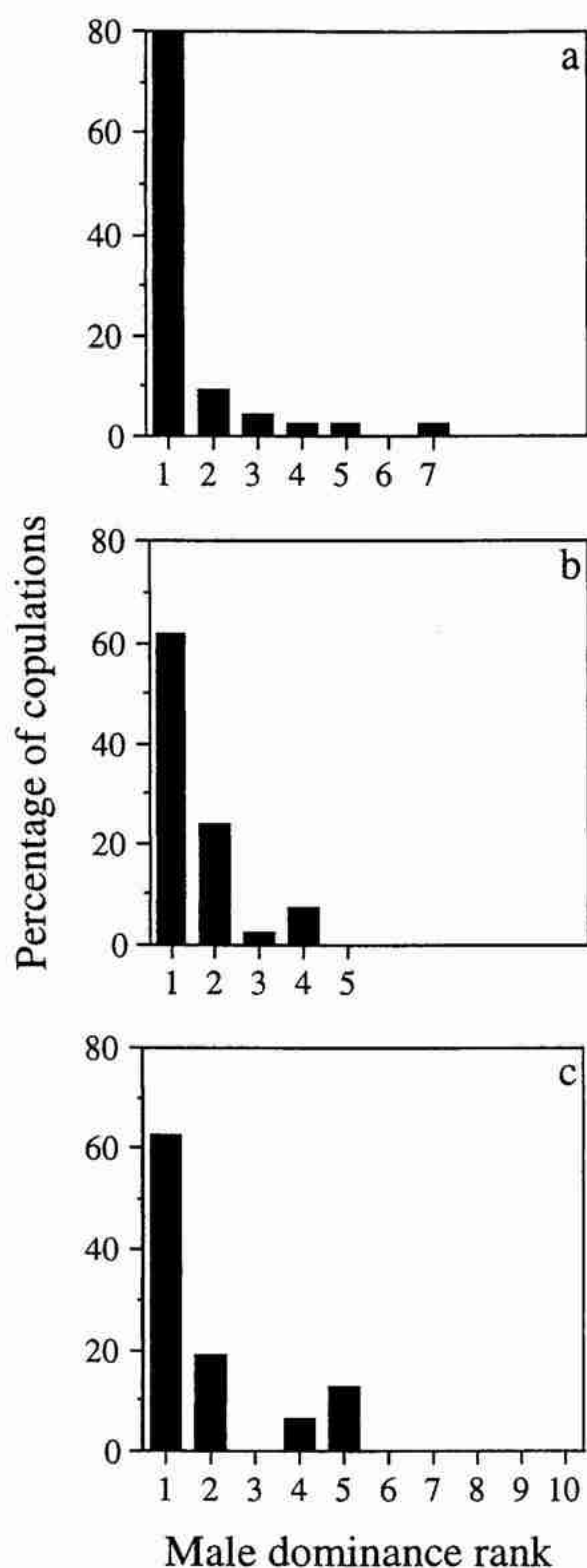The majority of copulations (83 of 122; 74%) was performed by the three alpha males (Figure 1). These three males rep-

Figure 1
Percentage of observed copulations by males at three colonies in 1992. Males are ordered by dominance rank (highest ranking = 1). The three colonies include one for each of the three alpha males observed, the colony where the largest number of total copulations was observed. The alpha male at each colony performed 62–80% of the copulations. (a) Colony attended by seven males. (b) Colony attended by five males. Three of them were also low-ranking males at the colony in a. (c) Colony attended by 10 males. Three other colony males did not attend any of these three colonies.
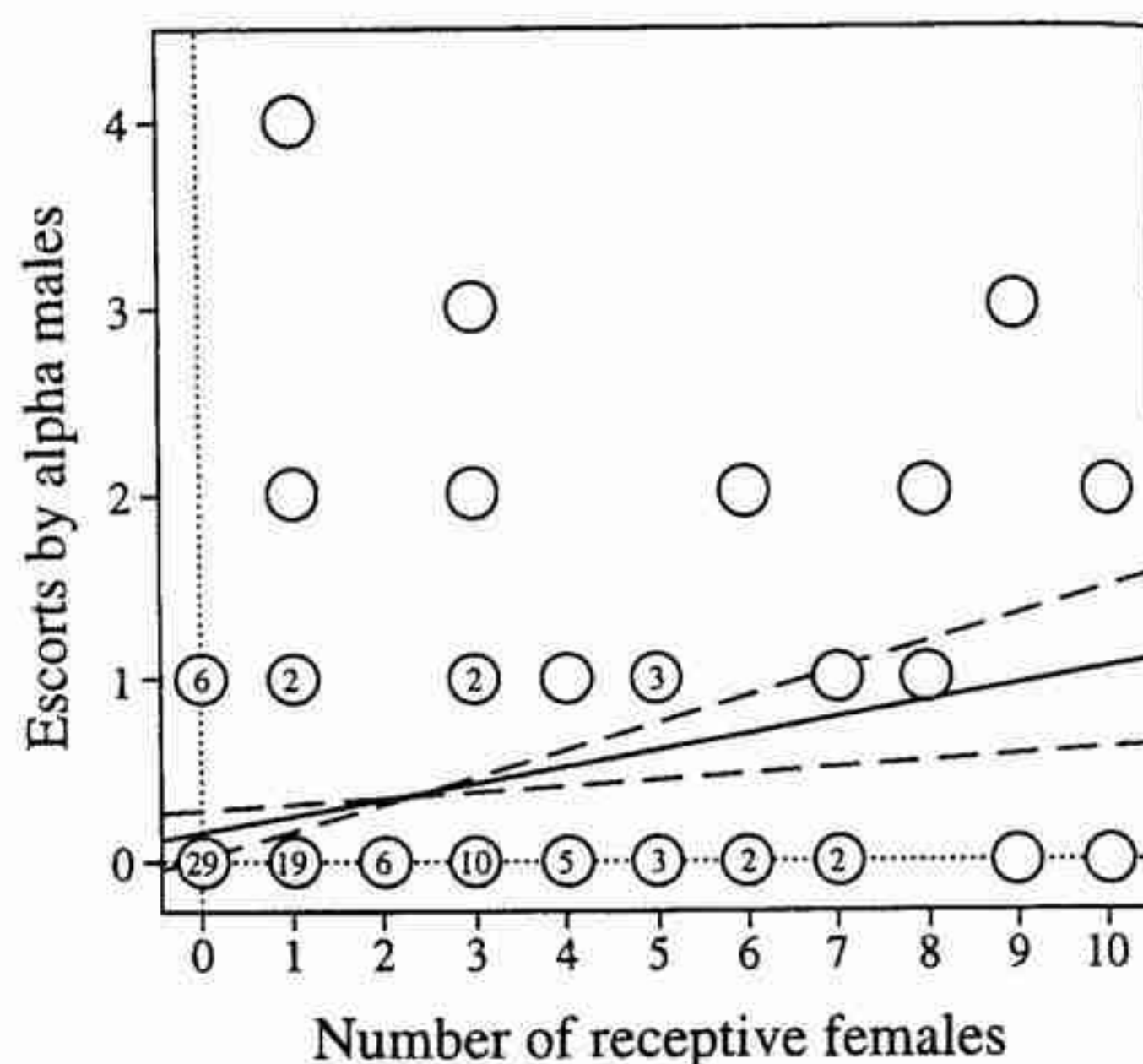

Figure 2
The number of escorts per day by alpha males increased with the number of receptive females (Spearman's $r = .24$, $n = 102$, $p < .05$). Numbers inside circles indicate the number of coincident points. Dashed lines indicate the plus and minus 95% confidence intervals for the slope.

resented 14% of the 22 colony males. Beta males performed 14% of the observed copulations. The lowest-ranking male observed to copulate was ranked seventh in his hierarchy. Four additional copulations involved males that we did not see well enough to identify, and no copulations involved unbanded males.

Although each alpha male spent the majority of his time at the colony (see Post, 1992; Poston, 1997a), each also escorted females on trips away from the colony. There was a significant positive correlation between the number of receptive females per day and the likelihood that we observed the alpha male perform at least one escort that day (logistic regression; $\chi^2 = 6.99$, df = 1, $p < .01$). In addition, the number of trips per day on which an alpha male was observed escorting a female was correlated with the number of receptive females (Figure 2). However, the slope of the relationship ($\pm$ 95% confidence intervals; dotted lines in Figure 2) was much less than one. Consequently, as the number of simultaneously receptive females increased, each female was less likely to be escorted by the alpha male.

The number of different males observed performing a courtship display in a colony per day was positively correlated with the number of receptive females per day (Spearman's $r = .253$, $n = 77$, $p < .05$). However, the correlation between the number of males observed to copulate in a colony and the number of receptive females was not significant (Spearman's $r = .094$, $n = 49$, $p > .50$), perhaps because alpha males frequently interrupted the displays of other males (see Poston, 1997b).

General fingerprinting results

We had scorable fingerprints from 184 individuals on 11 gels. The mean ($\pm$SD) bands scored per individual, by probe, was: M13, 16.5 ± 3.8; M2.5 *per*, 13.6 ± 4.1; 33.15, 17.9 ± 4.8; sum of three probes, 44.0 ± 14.1. To estimate the background level of band sharing for unrelated birds, we determined the propor-
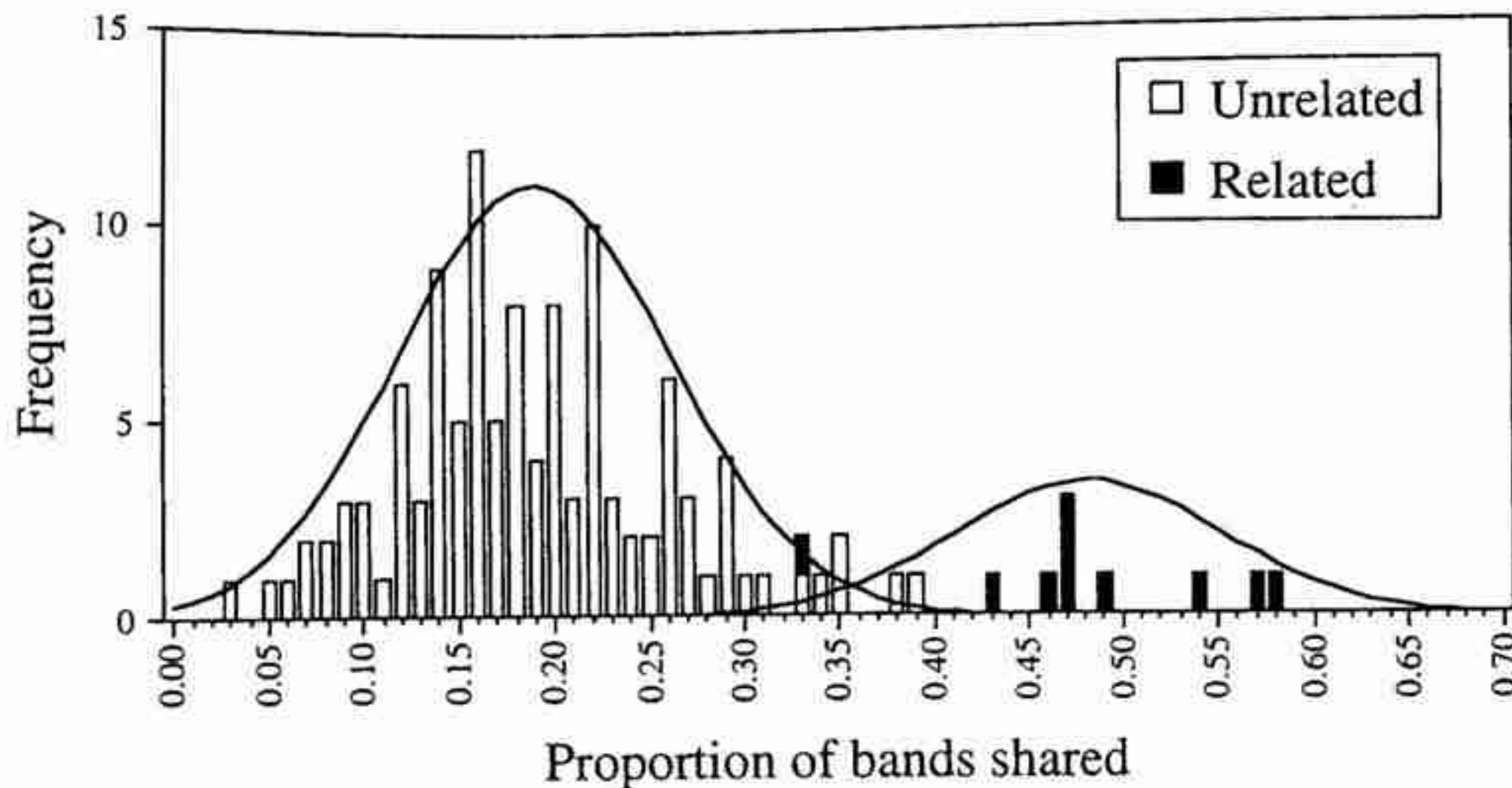
Figure 3
Frequency distributions of the proportion of bands shared between related individuals (adult females and nestlings from their nests) and unrelated individuals (adult females and nestlings from other nests). The distributions are approximated by the normal distributions indicated with lines. Based on these distributions the criterion for assigning parentage was set at 0.334 (see text).

tion of bands shared between an adult female and nestlings from nests other than that female's ($n = 116$, mean $= 0.19\pm0.07$). We expected that band sharing among all adults could be biased because we tested samples from many more males than females, and males did not disperse (Post and Poston, unpublished data); thus some males were possibly related to one another (although low band sharing between males, 0.20 ± 0.06, does not support this view). Band-sharing scores among females and nondescendent nestlings was slightly less than that among all adults (mean $= 0.20\pm0.06$, $n = 154$). The results outlined below do not differ if we use scores from adults as our estimate of background band sharing instead of scores from females and nondescendant nestlings.

Distributions of band sharing between related birds (an adult female and her nestlings) and between unrelated birds overlapped (Figure 3). Coefficients of band sharing between unrelated birds averaged 0.19, and those between females and nestlings averaged 0.48 (Table 1).

Paternity results

We had scorable samples from 109 nestlings from 74 broods (44 broods with 1 nestling sampled, 28 broods with 2 nestlings sampled, and 2 broods with 3 nestlings sampled). Three nestlings could not be assigned to a nest because they were captured within colonies after they had fledged but before they could fly well enough to leave the colony. These 109 nestling samples came from four of the seven colonies for which we had observed behavior. These colonies were controlled by two alpha males. Samples were collected during two seasons.

We had samples from both putative parents for 10 offspring. For these 10, we assigned parentage based on the presence of novel bands and the proportion of bands shared (e.g., Westneat, 1993). Of the 10, 2 had few novel bands (1 and 3) and also had high band-sharing scores with both putative parents

(all > 0.40). The other 8 nestlings had several novel bands (8–21). Each had high band-sharing scores with the female (0.38–0.58) and low band-sharing scores with the alpha males (0.11–0.30). Thus for this small subset of nestlings, the alpha males sired 20% of nestlings.

The remainder of the nestlings had to be assigned a sire based on band-sharing proportions alone. We had to decide on a threshold for assigning parentage because the distribution of band-sharing values for mother–offspring dyads overlapped the distribution for unrelated dyads (Figure 3). We calculated that the value that balanced the chance of a false alarm (unrelated individuals thought to be related) and a missed detection (related individuals thought to be unrelated), based on the mean and SD of both distributions, was 0.334. Less than 2% of true parent–offspring dyads should have band-sharing scores that were below that value, and less than 2% of unrelated dyads should have scores that exceeded that value. With this criterion, the two alpha males sired 33 of the 99 nestlings assigned by band-sharing proportions alone.

Alpha males thus sired 32.1% of the total sample of nestlings, and they sired all the nestlings from 24.3% of the broods (Table 2). These percentages are much lower than the observed percentage of copulations by alpha males (see Figure 1).

Fertilization success of nonalpha males
Of the 109 nestlings sampled, 74 were not sired by alpha males. Our data indicated that few of these nestlings were sired by other colony males. Even though we had DNA samples from many of the other males observed to copulate within the colonies (Table 2), only four nestlings were sired by another male that attended that colony. In one colony at which 46 nestlings were sampled, the beta male and 3 other males were not sampled, so our results could underestimate

Table 1

Mean band-sharing proportions for various types of comparisons

Type of comparison	Mean ± SD	Minimum	Maximum	n
Related (females×their nestlings)	0.481 ± 0.071	0.33	0.58	10
Unrelated (females×other's nestlings)	0.190 ± 0.070	0.03	0.39	116
Nestlings×non-nestmates[a]	0.210 ± 0.072	0.03	0.46	219

[a] Excluding progeny of alpha males.

Table 2

Paternity for boat-tailed grackles at four colonies over two years measured by DNA fingerprinting

Alpha male	Colony[a]	Nestlings sampled	Nestlings sired by alpha male (%)	Other colony males sampled/ observed (%)	Nestlings sired by other colony males	Broods sampled	Broods sired exclusively by alpha male (%)
A-RYY	A5	8	2 (25.0)	6/6 (100.0)	0	5	1 (20.0)
A-RYY	C2	28	11 (39.3)	6/7 (85.7)	2	20	6 (30.0)
A-RYY	W7	27	8 (29.6)	4/5 (80.0)	1	20	4 (20.0)
YBA-B	F2	46	14 (30.4)	3/7 (42.9)	1	29	7 (24.1)
Totals		109	35 (32.1)		4	74	18 (24.3)

[a] W7 sampled in 1991; A5, C2, and F2 sampled in 1992.

the success of colony males. However, only 1 of 63 nestlings from colonies at which the beta males were sampled was sired by them. The low success of nonalpha colony males suggests that many if not nearly all offspring that were not sired by the alpha male were sired by males not present in the colony.

After omitting nestlings sired by the alpha male, the mean proportion of bands shared between nestlings from different nests (0. 21) was slightly greater than the mean proportion of bands shared between unrelated birds (0.19; Table 1). To evaluate whether this slight difference was significant, we compared these means with a randomization test (Manly, 1991) because dyads represent nonindependent data points (Danforth et al., 1996). We pooled the observed values and drew two random samples (without replacement) from the pool ($N_1 = 116$; $N_2 = 219$). We measured the mean for each sample and the difference between the means. This procedure was repeated 10,000 times. The observed difference between unrelated birds and nestlings from different nests was greater than the difference we obtained in 9939 out of 10,000 simulations ($p = .0061$). Thus, the proportion of bands shared between nestlings that were in different nests was slightly but significantly higher than the proportion shared between unrelated birds.

The difference between band sharing of unrelated dyads and that between nestlings at different nests could be affected by three situations: (1) relatedness among females, (2) relatedness among different sires, or (3) some individual (nonalpha) males siring nestlings in more than one nest. Options 1 and 2 seem unlikely, given that band sharing between females was 0.199 (SD = 0.072, $n = 13$) and that between males was 0.202 (SD = 0.064, $n = 74$).

Half-sibs should have an average band-sharing score of 0.39 (see below). The observed value of 0.21 is clearly much below 0.39, so one nonalpha male was not the sire of all unassigned offspring. To estimate the bounds on success of noncolony males, we calculated the proportion of dyads of half sibs that would be necessary to raise the proportion of bands shared between non-nestmates from 0.19 to 0.21. We make the simplifying assumption that the distribution of band-sharing scores for nestlings from different nests is a composite of dyads of unrelated birds and dyads of between-nest half-sibs. This assumption will provide an upper limit estimate of the success of nonalpha males. The mean proportion of bands shared between nestlings from different nests (x_t) is the sum of the mean for half sibs (x_h) and the mean for unrelated pairs (x_u), each multiplied by the proportion of dyads of each type [n_h/n_t and ($n_t - n_h$)/n_t, respectively]:

$$x_t = (n_h/n_t)x_h + [(n_t - n_h)/n_t]x_u. \quad (1)$$

Solving equation 1 for n_h yields

$$n_h = (n_t x_t - n_t x_u)/(x_h - x_u). \quad (2)$$

From above, $n_t = 219$, $x_t = 0.21$, and $x_u = 0.19$. To estimate x_h we applied a rearranged form of equation 8 from Reeve et al. (1992), which provides an estimate of relatedness within groups. If w is the mean band-sharing proportion within groups and b is the mean band-sharing proportion between groups, then $w = r(1 - b) + b$. In the present case, $r = 0.25$ (half sibs) and $b = 0.19$. The expected proportion of bands shared between half-sibs is thus w (or x_h) = 0.39. Entering these values into equation 2 gives $n_h = 21.9$ (95% confidence intervals = 0–41.7) dyads. This means that out of 219 cross-brood dyads, about 22 dyads were half sibs. The number of nestlings that these 22 dyads represent depends on the number of sires involved. If we assume that each dyad of half-sibs was sired by a different male, then the 22 dyads would represent 44 of the 74 nestlings not sired by an alpha male. Each male would have sired at most 2 offspring (1.9% of all nestlings), and 44 (95% CI = 0–74) of the nestlings sired by other males would be cross-brood half sibs. If at the other extreme we assume that all half-sib dyads were sired by a single male (an unlikely assumption, but one which provides an upper bound on the success of individual noncolony males), then the 22 dyads of cross-brood half-sibs would represent at most 8 (95% CI = 0–10) nestlings. This one male would have sired 7.3% (95% CI = 0–9.2) of all nestlings. Thus, the maximum estimate of fertilization success of an unsampled colony or a noncolony male (9.2%) is less than a third of the measured fertilization success of alpha males (32.1%). Note that this analysis included nests from four different colonies. Although additional nearby colonies that were not sampled could contain young sired by the same male(s) siring offspring in our sample, it is unlikely that one nonalpha male gained as much success as most alpha males.

Mixed paternity within broods

To estimate the proportion of females that mated with more than one male, we determined the proportion of clutches with mixed paternity. For this analysis we included nests with more than one nestling for which the sire of at least one nestling had been identified. Sixteen nests fit these criteria, and from each of these nests we had sampled two nestlings. In 8 of the 16 nests the nestlings did not have the same sire. Thus, at least 50% of these 16 females had mated with more than one male.

Factors influencing paternity by alpha males

The number of receptive females per day within these colonies ranged from 0 to 16 over the course of a breeding season (see also Poston, 1997b). There was no significant correlation between the number of receptive females and the likelihood that a nestling or an entire brood was sired by the alpha male (Table 3). Similarly, there was no significant effect of date in the season (Table 3).

Table 3

Logistic regression of the number of receptive females and the date on likelihood of paternity by alpha males

Factor	Broods			Nestlings		
	df	t	p	df	t	p
Females	71	−0.644	0.53	103	−0.39	0.70
Date	71	1.19	0.24	103	1.44	0.15

Females refers to the number of receptive females at the focal colony on the day of the focal female's peak of receptivity (3 days before clutch initiation). Broods sired partially by the alpha male were combined with broods sired entirely by nonalpha males.

The preceding analysis could be confounded by several factors, such as differences between the individual males competing for a colony, physical aspects of the colony and its surroundings, and environmental factors that change from one season to the next. The proportion of young sired by each of the two alpha males did not differ (nestlings: 33.3% and 30.4%, Fisher's Exact test, $p = .84$; broods: 24.4% and 24.1%, $p = 1.0$). Similarly, the percentage of young sired by the alpha male did not vary among colonies (nestlings: G test, $G = 0.97$, df $= 3$, $p = .81$; broods: $G = 0.61$, df $= 3$, $p = .90$). Finally, the percentage of young sired by the alpha male did not vary with the year in which the samples were collected (nestlings: 29.6% and 32.9%, Fisher's Exact test, $p = .82$; broods: 20.0% and 25.9%, $p = .76$). Although based on small samples, these results suggest that fertilization success was the same for these two alpha males and that effects of colony site or year did not influence paternity within this study.

DISCUSSION

Boat-tailed grackles differ from most birds in having a social mating system of female-defense polygyny. The most conspicuous feature of this system is the competition between males over groups of nesting females, in which the top-ranking males perform 74% of the copulations (see also Post, 1992). Just as in many socially monogamous birds (e.g., Westneat and Sherman, 1997), we have found that the actual pattern of fertilizations deviated from the observed mating relationships. Despite the high proportion of matings by alpha males in colonies, alphas sired only 32% of the nestlings. Only two other studies have measured paternity with DNA fingerprinting in species with similar mating systems. Webster (1995) found a similar pattern of mating and fertilization success in Montezuma's oropendola (*Psarocolius montezuma*): alpha males performed at least 90% of the copulations within nesting colonies, but they sired only 7 of 21 nestlings (33%). In a study of red deer (*Cervus elaphus*) by Pemberton et al. (1992), alpha (or harem-holding) males sired all or nearly all offspring. In oropendolas and grackles, observations of mating success overestimate variance in male fertilization success, whereas in red deer algorithms for assigning paternity based on gestation length and harem membership of females underestimate variance in male mating success.

One or more of three possibilities might explain the surprisingly low success of alpha male grackles. First, alpha males could have transferred fewer sperm per copulation than males that copulated away from colonies. Passerines produce sperm during a short period each night (citations in Birkhead et al., 1994), and Birkhead et al. (1994) calculated that male house sparrows (*Passer domesticus*) use nearly all their available sperm each day. Males in highly polygynous species could be particularly prone to sperm limitation. For example, in a cap-

tive group of the harem-polygynous hamadryas baboons (*Papio hamadryas*), females that came into estrus synchronously were less likely to conceive than females that came into estrus asynchronously (Zinner et al., 1994). We did not find an effect of synchrony on paternity in this study. However, alpha males sometimes refuse to mount females that give solicitation displays (Poston, unpublished data). Male refusals to copulate might indicate low sperm reserves (Hatchwell and Davies, 1992; Hunter et al., 1993). Our data do not allow us to test whether alpha male grackles refuse copulations more than other males or whether rates of refusal are linked to synchrony.

Second, paternity by alpha males could be limited by their ability to guard females away from colonies. Alpha males occasionally follow females off the colony, and they interrupt other males' courtship displays on such trips. We would expect synchrony among females to affect alpha males' success in guarding them, and indeed we found that when several females were receptive simultaneously each female was less likely to be escorted by the alpha male than when only one female was receptive. However, the lack of a correlation between synchrony and paternity suggests that alpha males have relatively low success in preventing other males from copulating even during periods of asynchrony. We hypothesize (but as yet cannot test) that male mate-guarding is limited by the combination of females' pursuit of matings with other males and conflicting demands on alpha males. An alpha male must balance guarding females away from his colony with defending his colony from other males in the queue. Thus, although alpha males probably have the most access to females and consequently sire the most offspring, they cannot monopolize matings.

Third, females could make it difficult for males to guard them. Females often leave colonies, and some trips might be attempts to mate with other males. At least 8 of 16 females we tested in this study had mated with more than one male. We have limited information on female behavior or potential benefits of multiple mating, and we cannot reject the possibility that females are forced into mating with other males, although all copulations we observed involved the cooperation of the female.

Our results raise some interesting questions about male and female reproductive tactics. Because we have more data on male grackles, we will focus on males. Post (1992) observed that male grackles adopt alternative strategies of competing for colonies or displaying to females away from colonies. Individual males do not switch between strategies (Post, 1992; Poston, 1997a). In the present study, we documented that many nestlings were sired by males away from colonies, but that no one male sired more young than an alpha male. One alpha male in our study maintained his status at least 4 years and defended at least two colonies per year. At the colonies we observed, there were an average of 37 nests. Assuming that 60% of nests fledge one young (Post et al., 1996) and alpha males sire 32% of the nestlings, then an alpha male would sire more than 50 fledglings during a 4-year tenure.

Such success appears to come only after a long wait. A striking result of our study was the rarity of paternity by beta and lower-ranking colony males in the queue. Young males apparently face a decision between joining a queue for a colony and not reproducing until they reach alpha status at 6 or more years of age (see Poston, 1997a) or displaying to females away from colonies and perhaps reproducing at an earlier age but at a lower rate. These alternatives are similar to those faced by individuals in species with other social systems that form queues for access to reproductive opportunities (Apollonio et al., 1992; Ens et al., 1995; Wiley, 1981; Wiley and Rabenold, 1984). Theory predicts that the proportion of in-

dividuals adopting each strategy should produce equal expected payoffs for the two alternatives (Fretwell, 1972). In the case of grackles, we do not know what proportion of individuals choose to queue or to display away from colonies, so we cannot test Fretwell's prediction. The high reproductive success of alpha males indicates that many males do not reproduce at all during their lives, either because they unsuccessfully attempt to mate with females away from colonies or because they die in the queue for a colony before they reach alpha status (see Post, 1992; Poston, 1997a).

We know little about the behavior of noncolony males. The genetic results reveal that this gap in our knowledge is much more important than we would have thought, and filling that gap could reveal new patterns of male competition and fertilization success. For example, males off the colony could be displaying to females in a mating congregation similar to the leks razorbills (*Alca torda*) form away from their breeding sites (Wagner, 1991). However, the behavior of females and the patterns of paternity we uncovered suggest this behavior is unlikely. Females leave a colony in a variety of directions (Poston, unpublished data). In addition, we found no evidence that any single noncolony male had sired large numbers of young. Neither of these patterns fit the expectation that males are congregating to display to females in a traditional site with no resources and with considerable skew in male success. Further research on noncolony males is needed to estimate mating skew among noncolony males and to establish the patterns of male competition for access to mates. Our results best fit the possibility that males away from colonies engage in scramble competition for access to fertilizable females foraging or collecting nesting material at a variety of sites.

This study demonstrates that even when males compete intensely for matings, females have opportunities to mate with several males. Indeed, whether females actively seek copulations from different males or simply set the conditions under which they copulate, their behavior has important consequences for the success of male competition for mates (Poston, 1997b; Wiley and Poston, 1996). Previous studies have often overlooked opportunities for females to influence paternity in species in which males compete for access to mates (Ahnesjö et al., 1993; Wiley and Poston, 1996). Because of the mix of female and male behavior in boat-tailed grackles, their mating system is much more complex than the easily observed female-defense polygyny. The present study also emphasizes the growing need for sophistication in mating system theory. These grackles confirm the predictions of Emlen and Oring (1977) that clustered females and low male parental care favor female defense. Yet female mating behavior clearly limits males' ability to monopolize females. Recent theory (e.g., Davies, 1991; Reynolds, 1996; Wiley and Poston, 1996) has adopted a more balanced view of the ways in which each sex influences selection on the other, and thus of the coevolution of female and male behavior.

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