

Mate choice and competition for mates in the boat-tailed grackle

JOSEPH P. POSTON

Curriculum in Ecology, University of North Carolina at Chapel Hill

(Received 18 March 1996; initial acceptance 20 May 1996;
final acceptance 19 November 1996; MS. number: A7554R)

Abstract. Behavioural studies have implicated both female choice of mates and male competition for access to mates as proximate mechanisms of sexual selection. Few studies have examined the interactions between these mechanisms in a natural setting. In this study, I explored how dominance interactions between male boat-tailed grackles, *Quiscalus major*, determine the mating success of males and how the behaviour of female boat-tailed grackles influences this process. Male grackles defended colonies of females and performed courtship displays to females that were building nests. These conspicuous displays incited dominance interactions between males, with the result that dominant males interrupted subordinate males' attempts to copulate. Female grackles were receptive only to males that performed courtship displays, but their receptivity to males did not vary with male dominance rank or tail length. Females were more likely to be receptive in a colony than away from a colony, and females became receptive asynchronously during the breeding season. The timing and spacing of females' receptivity to males permitted dominance interactions between males to determine male mating success. By establishing the conditions for male competition, females indirectly chose high-ranking males. Recent studies have emphasized discrimination among potential mates as a behavioural mechanism for mate choice. The results reported here, however, demonstrate that other aspects of females' behaviour can produce mate choice, indirectly rather than directly.

© 1997 The Association for the Study of Animal Behaviour

Darwin (1871) suggested that traits that improve an individual's access to mates would evolve by sexual selection. Subsequent treatment of sexual selection (reviewed by Harvey & Bradbury 1991; Andersson 1994; Andersson & Iwasa 1996) has followed Darwin's proposal that there are two proximate mechanisms for sexual selection: mate choice and competition for mates. Although many studies have documented both of these mechanisms (reviewed in Bateson 1983; Andersson 1994), few investigators have examined interactions between them (Bradbury & Davies 1987).

For species in which some males prevent other males from mating, it is difficult to demonstrate that females choose mates. Some investigators have examined mate choice by females by preventing males from interacting, either by tethering males or by placing them in separate cages, and

then allowing females to associate with preferred males (e.g. Long & Houde 1989; Zuk et al. 1990). Nevertheless, aspects of a female's behaviour might permit mate choice within the context of male competition for mates. A growing number of studies have demonstrated that a female's choice of a mate is not limited by male behaviour (Westneat et al. 1990; Birkhead & Møller 1992; Ahnesjö et al. 1993). Therefore, investigation of the proximate mechanisms of sexual selection must include careful investigation of the behaviour of both males and females in natural settings.

In the present study, I examined mate choice and competition for mates in boat-tailed grackles, *Quiscalus major*, large blackbirds (Icterinae) of the coastal southeastern U.S.A. Males have black iridescent plumage and long tails; females are brown and about half the size of males. Females nest in colonies that can contain dozens of nests during a season. These colonies are located in isolated patches of emergent vegetation in marshes or in isolated shrubs or trees protected from predators. Females build nests and rear

Correspondence and present address: J. P. Poston, Center for Ecology, Evolution and Behavior, T. H. Morgan School of Biological Sciences, 101 Morgan Building, University of Kentucky, Lexington, KY 40506-0225, U.S.A. (email: jposton@darwin.ceeb.uky.edu).

offspring without aid from a male. They often fly 1 km or more from a colony while searching for nesting material and while foraging for themselves and their nestlings. Male boat-tailed grackles compete for access to a colony of females. Males associated with a colony form a linear dominance hierarchy, and the top-ranking or alpha male performs 70–80% of the copulations in a colony (Post 1992; J. P. Poston, R. H. Wiley & D. F. Westneat, unpublished data). Older males dominate younger males, and males' relative positions in a hierarchy remain stable within and between years. Therefore, the hierarchy represents a queue for males' mating opportunities (Post 1992; Poston, in press).

To investigate male competition for mates and female choice of mates, I made detailed observations of the courtship displays of free-ranging males, and I recorded the responses of females and other males to a displaying male. I addressed the following three questions. (1) How do interactions between males limit the mating success of low-ranking males? (2) Do females discriminate between males based on a male's dominance rank or tail length? (3) Does the behaviour of females establish the conditions for male competition for mates? The results suggest that competition for mates determines the mating success of males and that females show no direct preferences for individual males. Nevertheless, females copulate in situations that incite dominance interactions between males, and this behaviour by females results in their mating with dominant males.

METHODS

Study Site and General Methods

The study population nested in a 30-ha marsh in an impoundment at Magnolia Gardens, Charleston, South Carolina. The marsh was bounded by an earth dike on three sides that separated it from the tidal Ashley river; the fourth side was an upland garden. Water depth in the marsh averaged 1 m. Approximately 75% of the marsh was open water and 25% was emergent vegetation, primarily cattails (*Typhus* spp.). Female grackles nested in colonies on small islands or peninsulas of cattails. The nests in a colony were often close together, and occasionally were in contact with one another. In a nearby population, the mean area of colonies was 310 m²

(Post et al. 1996). I concentrated my observations on seven colonies of grackles in the northeastern corner of the marsh. At these colonies the number of nests ranged from five to 85 (mean \pm SE = 37.3 ± 9.6). The colonies closest to each other were 30 m apart; those most distant were 500 m apart. Post & Seals (1991) have given other details of the study site.

The study was conducted in January–June of 1991–1993. From late January until late March of each year, I trapped grackles and marked them with unique combinations of coloured aluminum bands. I took several measurements of each grackle captured, including the length of the tail. During the grackles' breeding season, from late March until late June of each year, I divided my time between capturing grackles (2–3 days per week) and observing their behaviour (4–5 days per week) from blinds on wooden platforms near colonies, from a canoe, or from foot on the dike around the perimeter of the marsh. The birds had habituated to people sufficiently to allow me to approach within 20 m without disturbing their behaviour.

Each season I observed grackles at three to four colonies. I visited each colony to collect observations of grackles' behaviour three or four times per week until no females initiated new nests (2–10 weeks per colony). Observations were collected for 3–4 h and either started at sunrise or ended at sunset, because during the heat of midday few grackles attended colonies. In addition to the samples described below, observations included focal samples of individual males, scan samples of the locations of individual males in and near colonies at 5-min intervals, and ad libitum samples of dominance interactions between males (total > 500 h).

I captured and marked 133 males, 144 females and 270 nestlings with unique combinations of coloured bands. By 1992, only 14% of the adult males and 17% of the adult females that attended colonies remained unbanded. The number of males that attended colonies (those observed within 50 m of the colonies in at least 10% of the scan samples) ranged from one male at the smallest colony to seven males at the largest colony. Some males attended more than one colony during and between seasons, but males at the colonies I observed belonged to one of two groups. One group competed for the four easternmost colonies and the other group for the three westernmost

colonies. For three colonies in which I observed interactions between nearly all dyads of males, the males' relationships fit a linear dominance hierarchy, as reported for nearby colonies by Post (1992). For the other four colonies, I assumed that a linear hierarchy existed, although I did not document it completely. For those males whose relationships I did not resolve, I assigned the median rank they would have received had I resolved their relationships ($N=5$ dyads and 1 triad). Spatial relationships between males are analysed in detail elsewhere (Poston, in press).

Courtship Displays

Males performed courtship displays to females both in the colonies and elsewhere. During courtship displays, males pointed their bills downward, periodically vibrated their wings above their backs and sometimes spread their tail feathers, all while producing a conspicuous and distinctive vocalization (Selander & Giller 1961; Post et al. 1996). In many birds, females respond to a male's courtship display by performing a solicitation display before copulating. Studies have relied on females' solicitation displays as a measure of females' preferences for males with particular traits, especially characteristics of males' songs (e.g. West et al. 1981; reviewed by Searcy 1992). The solicitation display of female boat-tailed grackles is similar to that of other passerines; a female boat-tailed grackle crouches, arches her back, droops and vibrates her wings, and elevates her tail and bill (Selander & Giller 1961; Post et al. 1996). Although male boat-tailed grackles often do not attempt to mount a female that has performed a solicitation display, solicitation displays always precede copulation. Therefore, I focused on females' solicitation displays as a measure of females' preferences to mate with particular males. For each male's courtship display that I witnessed, I noted the location and the identity of the male and female, and whether the female responded to the males' courtship display with a solicitation display.

Males performing courtship displays were frequently interrupted by other males. I scored a display as interrupted if another male supplanted the displaying male or if another male approached closely enough to cause the displaying male to chase him away. For each interrupted display, I recorded the identities of the displaying male and

the male that interrupted him. For uninterrupted displays, I recorded the identities of males within 50 m. These displays were audible at distances of over 100 m, so I assumed that males within 50 m could hear the display although they did not interrupt it.

Timing of Female Receptivity

The synchrony of receptivity among females can determine whether a male defends more than one female (Emlen & Oring 1977; Davies 1991). To measure the synchrony between females at each colony, I estimated the number of receptive females per day. Post (1992) reported that female boat-tailed grackles are most receptive to male's courtship displays for 3 days, beginning 4 days before they lay their first egg. I tracked the stages of each nest in each colony to estimate when the female's 3-day receptive period had occurred. Since females laid only one egg per day and the modal clutch was three eggs (68% of 417 nests), it was not necessary for me to check nests daily to determine when the first egg appeared. Consequently, I visited each colony every 3–4 days to record the contents of each nest. I could not be sure when the first egg had been laid in some nests with clutches of one or two eggs, and I failed to find some nests until after the clutch had been completed. For these nests, I estimated when the first egg had been laid by using the date when the eggs hatched or the size of nestlings to estimate when they had hatched, and then back-dating based on a 13-day incubation (Post et al. 1996). These procedures allowed me to determine when the first egg had been laid to within ± 0.5 days for 82% of the nests (Poston 1995).

Male Response to Female Behaviour

Since high-ranking males limit low-ranking males' access to females at colonies (Post 1992; Poston, in press), low-ranking males might not know which females are receptive. I examined this possibility by measuring the responses of low-ranking males to females in two ways. First, during 30-min samples, I observed each female that flew to a colony and noted any items she carried. I also noted whether any males followed the female or performed a courtship display to her. Second, I tested the responses of low-ranking males to females away from a nesting colony. I

placed approximately 500 g of food (white bread) and 500 g of nest-lining material (pine needles) 5 m apart and approximately 100 m from an active colony. For 1 h, I recorded the identity of each female that visited each item and which females' visits elicited courtship displays from males. This procedure was replicated five times from 1 April to 25 May 1993.

Statistical Analysis

Some females received courtship displays on more than one occasion. In these cases, a female's responses on the two occasions were not independent; females that were unreceptive to the first courtship display were unreceptive to the second courtship display more often than expected by chance (G -test: $G_1=4.87$, $P<0.03$). Therefore, for the nine females that received more than one display (mean=4.8 displays, range=2–14), I randomly chose one instance for analysis. Also, some females were observed returning to colonies or visiting food and nesting material away from a colony on multiple occasions. I randomly chose one such visit by each female for analysis. Finally, I had multiple observations of males that performed courtship displays to females in the vicinity of other males. For each dyad of males, I included only one randomly chosen instance for analysis.

Measures of male tail length were normally distributed, so these data were analysed with parametric tests; all other data were analysed with non-parametric tests. All tests were two-tailed.

RESULTS

Females' Responses to Males' Courtship Displays

I identified both the male that performed a courtship display and the female to which it was directed in 95 instances. Fifty-two displays were directed at females that received a courtship display only once in my observations. The others were directed at nine females that were observed to receive courtship displays two or more times. Since each female that received more than one courtship display was included only once, the sample size for assessing females' responses to males was 61 displays.

Females' responses to males varied with the location and behaviour of the males, but not with

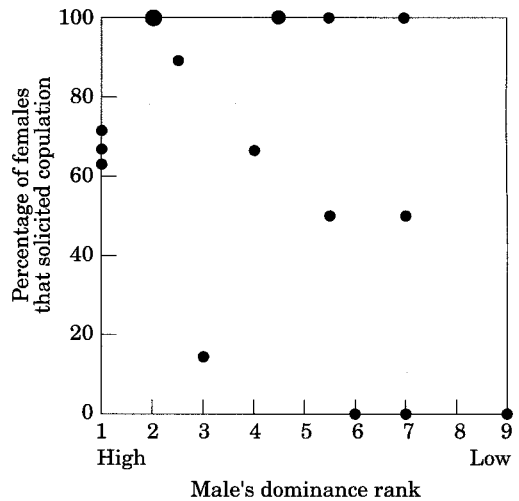


Figure 1. Relationship between a male's position in a dominance hierarchy (dominance rank) and the percentage of females that performed a solicitation display in response to his courtship displays ($r_s = -0.333$, $N=18$, $P>0.10$). For females that received a display from a male more than once, one interaction was randomly selected for this analysis. Larger symbols indicate coincident points from two and three males. Only interactions that occurred within a nesting colony are included.

male dominance rank or tail length. Females were more likely to perform a solicitation display when a male displayed in a colony (27 of 45 displays) than when a male displayed away from a colony (two of 16 displays; Fisher's exact test: $P<0.001$). Females' preferences for displays in a colony might represent a preference for top-ranking (alpha) males, because alpha males spent the most time in the colonies and they performed the most courtship displays there (Post 1992; Poston, in press). Nevertheless, females that received displays in a colony did not discriminate between males based on dominance rank. I found no correlation between males' ranks and the proportion of females that solicited copulation in response to the males' courtship displays (Fig. 1). Similarly, females' responses did not vary with the length of males' tails (Fig. 2). Females' responses did, however, vary with the behaviour of the male. Although males directed bill-up, cock-posture and courtship displays towards females (described in Post et al. 1996), females performed solicitation displays to a male only after that male had just performed a courtship display.

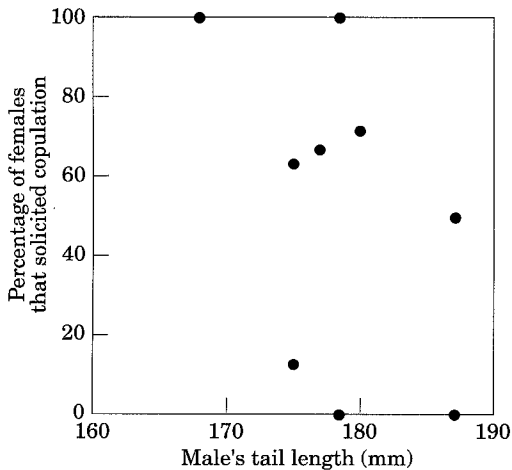


Figure 2. Relationship between a male's tail length and the percentage of females that responded to his courtship displays by performing a solicitation display ($r = -0.458$, $N=9$, $P>0.20$; interactions were selected as in Fig. 1). Only interactions that occurred within a nesting colony within 2 months of measuring the male's tail are included.

Synchrony of Females

During this study, the number of receptive females per day at a colony ranged from 0 to 16 (mean \pm SE = 1.9 ± 0.2). There were two seasonal peaks in the number of receptive females per day, one in late March and early April, and the other in mid-May. For five of seven colonies, the number of receptive females per day throughout the season did not differ significantly from a Poisson distribution (Fig. 3a). This result suggests that females nested at random with respect to other females, despite weak clustering into two seasonal peaks (Fig. 4a). For the other two colonies, the number of receptive females per day differed significantly from a Poisson distribution (Fig. 3b) because of unusually strong peaks of receptive females (Fig. 4b). Each of these peaks occurred after the eggs and nestlings from a nearby colony had been depredated by a snake, and the peaks included re-nesting females from the depredated colonies. Since the snakes eliminated the colonies within 4–5 days, all of the females that moved to the focal colony and began another nesting attempt were synchronized. Thus, although events could bring females into synchrony, there was no evidence that they otherwise nested synchronously.

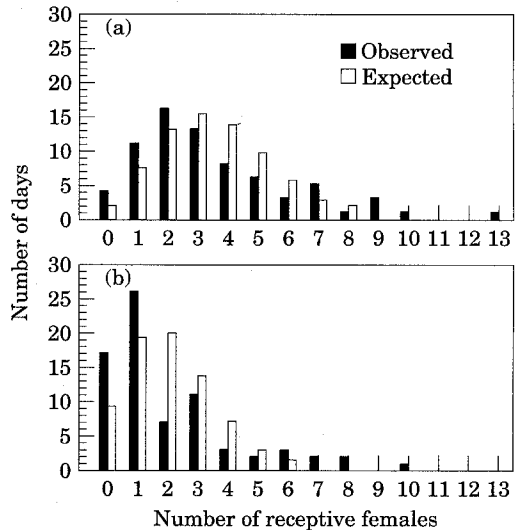


Figure 3. Distribution of receptive females for two representative colonies. Expected values were calculated from a Poisson distribution. (a) These distributions do not differ significantly (Kolmogorov–Smirnov test: $P>0.20$). (b) These distributions differ significantly (Kolmogorov–Smirnov test: $P<0.05$).

Interactions Between Males

A male interrupted another male's courtship display in 41 of 129 instances in which I could determine the relative ranks of the displaying male and a nearby male (within 50 m of the displaying male). After I eliminated multiple observations, my sample included 56 pairs of males observed within 50 m of each other while one performed a courtship display. When the nearby male had higher rank than the displaying male, it was more likely to interrupt the display (20 of 24 displays) than when the nearby male had lower rank (one of 32 displays; Fisher's exact test: $P<0.001$). The response of higher-ranked males was remarkably fast, and lower-ranked males were interrupted before they had a chance to mount the female.

Even though alpha males defended colonies from lower-ranked males (Post 1992; Poston, in press) and interrupted lower-ranked males' attempts to copulate, they did not prevent lower-ranked males from assessing the reproductive status of the females in a colony. At one colony where I could unambiguously determine the nests at which males displayed, both alpha and other males directed more displays to females during the

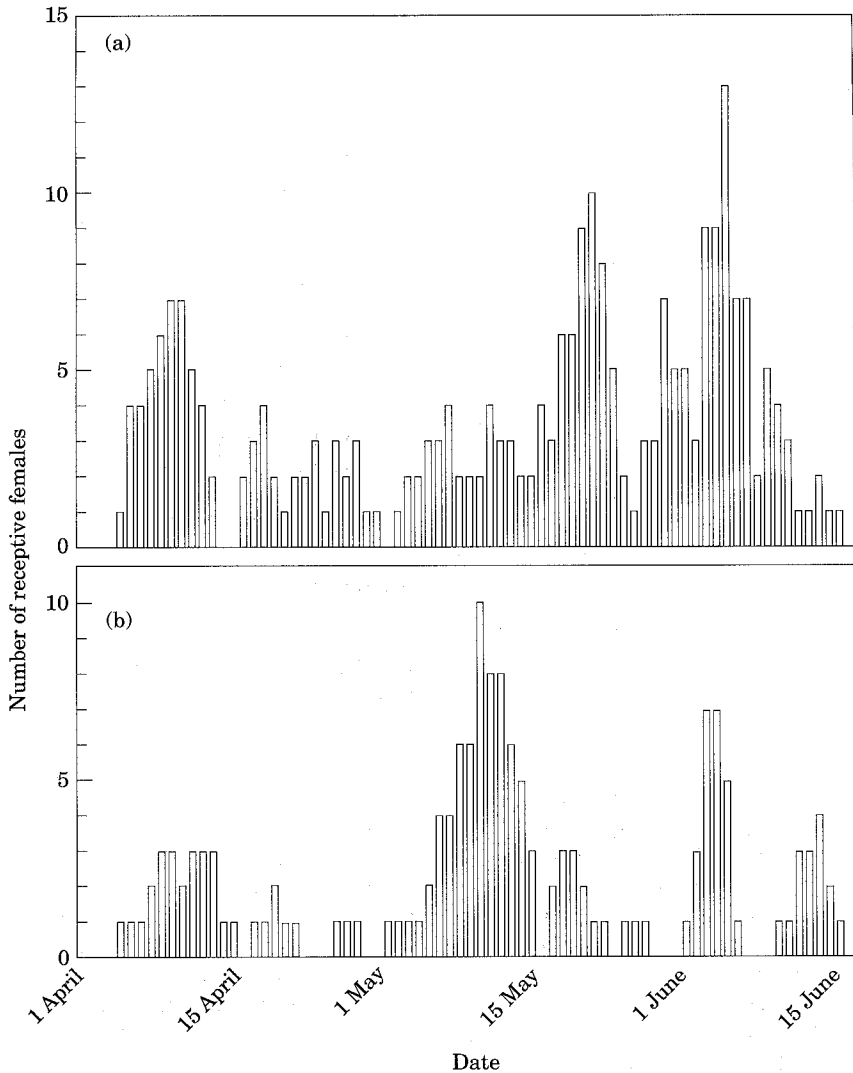


Figure 4. Number of receptive females per day for the same two colonies (a, b) illustrated in Fig. 3, respectively. For both colonies, females were receptive throughout the season. (b) The peak near 15 May represents several females that moved from a nearby colony that had been eliminated by predators.

female's peak of receptivity than to females at other stages of their nesting cycle (Fig. 5).

Males could determine which females were most likely to copulate by observing their nest-building behaviour. Nest construction progressed through well-defined stages (Post et al. 1996). During the time that females lined their nests with mud and grass, they were at their peak of receptivity. Nest-lining carried by a female thus pro-

vided a visual cue for her receptivity. Males were significantly more likely to respond to females returning to a colony with nesting material than to females returning with food or nothing (Fig. 6). Away from a colony, low-ranking males were also significantly more likely to display to females collecting material to line their nests (11 of 15 females) than to females gathering food (two of 102 females; Fisher's exact test: $P < 0.001$).

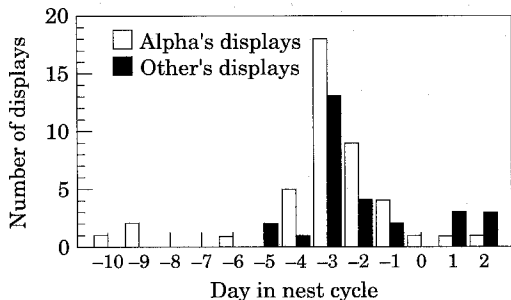


Figure 5. Frequencies of courtship displays performed by alpha males and by other males at nests in various stages. Day 0 is the day the first egg is laid. Females are receptive from day -4 to day -2 (Post 1992). These distributions do not differ significantly (Kolmogorov-Smirnov test: $P=0.58$).

DISCUSSION

Male Competition and Female Choice in Boat-tailed Grackles

The results provide additional evidence for Post's (1992) conclusion that male competition for access to mates contributes to the mating success of alpha male boat-tailed grackles. Males of all dominance ranks interrupted lower-ranked males' attempts to copulate, but males rarely interrupted higher-ranked males. Thus, dominance interactions at the time of copulation limited the mating success of low-ranked males. Despite the frequent interruptions, low-ranked males displayed preferentially to females that were at their peak of receptivity. Males could have determined a female's receptivity by observing her nest-building behaviour.

Females were more likely to solicit when a male displayed to them in a colony, but they were not more likely to solicit high-ranking than low-ranking males, and they were not more likely to solicit long-tailed than short-tailed males. Because of the dense vegetation in colonies, interactions between males and females in the colonies were more difficult for me to observe than those away from the colonies. This difference in visibility probably did not affect my conclusions about females' preferences to mate in a colony, because I analysed only observations in which I saw the female well enough to identify her colour bands. Furthermore, the difference in visibility does not affect my conclusions about females' lack of discrimination between males based on dominance

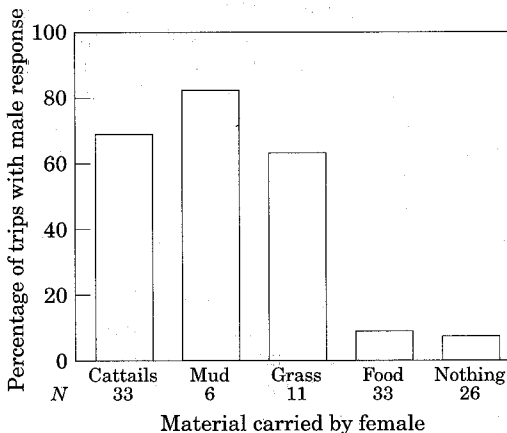


Figure 6. Males' responses to females that arrived at a colony varied with the kind of material carried by the female. Male responses included following the female or displaying to the female after she landed. Females carrying nesting material (cattails, mud and grass) were significantly more likely to receive responses than females carrying food or nothing (G -test: $G_3=48.0$, $P<0.001$).

rank or tail length, because I included only observations in which males displayed in a colony.

DNA fingerprinting of this population has revealed that females also copulated with males that did not attend their colony. Although alpha males sired considerably less than half the offspring at their colonies, they nevertheless sired more young than any other individual males (Poston 1995; J. P. Poston, R. H. Wiley & D. F. Westneat, unpublished data). It seems unlikely that many copulations with other males occurred within 200 m of a colony because boat-tailed grackles were easily observed within this distance. Evidently copulations occurred when females made trips of greater distances. Females sometimes flew 1 km or more from the colony to gather nest material or to forage. Nothing is known about possibilities for female mate choice in locations distant from colonies.

In a study of a nearby population, Post (1992) also found that females are more likely to be receptive in a colony than away from a colony and that females become receptive asynchronously. In contrast to the present study, Post (1992) found that females are more likely to be receptive to an alpha male's display than to other males' displays. Two differences in procedure could account for the different conclusions. First, Post observed

only one colony and I observed seven, although my colonies were defended by only two queues of males (Poston, in press). Second, since some of the females Post observed were unbanded, Post may have included some females more than once in his analysis (W. Post, personal communication). I excluded multiple observations of individual females because a female's responses when observed on two occasions were not independent.

Although females' receptivity to individual males does not vary with the male's dominance rank or tail length, three aspects of female behaviour increase their chances of mating with an alpha male. First, females are more likely to be receptive to males in a colony than elsewhere. Since alpha males defend colonies from lower-ranked males (Post 1992; Poston, in press), females that are receptive at colonies are more likely to mate with an alpha male. Second, females solicit copulations only from males that perform courtship displays. Females incite dominance interactions between males by requiring males to perform conspicuous displays. Third, females are not highly synchronized. Within a colony, the average number of receptive females per day is less than two, and females are receptive throughout the breeding season. These three aspects of females' behaviour establish the conditions for male competition for mates and increase a female's chances of mating with an alpha male. Therefore, females appear to show an indirect form of mate choice, mediated by competition between males.

Forms of Mate Choice

Female boat-tailed grackles do not discriminate between males based on dominance rank; nevertheless their behaviour results in their mating disproportionately with alpha males. Does the behaviour of females represent mate choice for alpha males? Boat-tailed grackles demonstrate that individuals need not make direct discriminations between potential mates to choose mates. In the broadest sense, mate choice is any behaviour by an individual that influences (Halliday 1983; Kirkpatrick & Ryan 1991; Andersson 1994), or more specifically restricts membership in (Wiley & Poston 1996), that individual's set of potential mates. In this sense, many aspects of an individual's behaviour can contribute to its choice of a mate (Halliday 1983; Andersson 1994; Wiley &

Poston 1996). An understanding of the range of behaviour that produces mate choice is crucial to understanding the scope of sexual selection.

Wiley & Poston (1996) proposed two categories of mate choice, direct and indirect, to distinguish between mate choice that involves discrimination between the features of potential mates and that which results from setting the conditions for competition between potential mates. Direct mate choice occurs when a female performs a discrimination between males based on individual differences in their features. For example, female widowbirds, *Euplectes progne*, discriminate between males based on the lengths of their tails and prefer to nest in the territories of males with experimentally elongated tails (Andersson 1982). Likewise, female sticklebacks, *Gasterosteus aculeatus*, discriminate between males based on body colour and prefer to mate with more brightly coloured males (Milinski & Baker 1990). Most studies of mate choice have examined the potential for direct mate choice.

Indirect mate choice is any behaviour other than discrimination that restricts membership in a female's set of potential mates. For example, female blue-headed wrasse, *Thalassoma bifasciatum*, prefer to spawn at sites on the downcurrent ends of coral reefs, and they remain faithful to a site regardless of the male that defends it (Warner 1987). Since several females prefer a few sites, competition between males is greatest for those sites. Thus, without discriminating between males, a female's behaviour restricts membership in her set of potential mates to competitive males. Elephant seals, *Mirounga angustirostris*, with a harem-polygynous mating system similar to that of boat-tailed grackles, illustrate another form of indirect mate choice. Vocalizations by copulating females alert dominant males, which then often interrupt subordinate males' attempts to copulate (Cox & Le Boeuf 1977). The result is that top-ranking males perform most of the uninterrupted copulations and are most likely to be the first male to mate with a female when she comes into oestrus (Cox & Le Boeuf 1977). In many other species as well, the behaviour of females incites dominance interactions that influence males' mating success (Trail 1985; Montgomerie & Thornhill 1989; Poole 1989). Synchrony and aggregation of fertile individuals and advertisement of fertility can have similar effects on mate choice (Wiley & Poston 1996). In these cases, female behaviour

sets the conditions for male competition for mates and thus represents indirect mate choice for competitive males.

The evidence from boat-tailed grackles demonstrates that direct and indirect mate choice can occur in the same species. As described above, female grackles solicit copulations only from males that perform courtship displays. Therefore, females discriminate between males that do and that do not perform displays. This discrimination represents a simple case of direct mate choice based on male behaviour. Females' spacing and timing of receptivity also make them more likely to mate with dominant males. These aspects of females' behaviour represent indirect mate choice for dominant males.

Implications of Indirect Mate Choice

Indirect mate choice is compatible with all current mathematical models of sexual selection, which specify that females with a preference are more likely to mate with males that possess a trait. These models do not require females to perform a behavioural discrimination. Any behaviour that serves to restrict potential mates, either direct or indirect mate choice, can fit the assumptions of these models (Wiley & Poston 1996).

In many cases, indirect mate choice could be a more reliable means for females to choose particular males than direct mate choice. For example, indirect mate choice by female boat-tailed grackles results in their mating with males that have competed for females over several years. In boat-tailed grackles, colonies are often in the same sites for several years (Post 1992; Post et al. 1996), and males enter a dominance hierarchy associated with a colony in their first year and retain their relationships with other males in subsequent years. The hierarchy thus represents a queue, and males remain in the queue for 5 or more years before becoming an alpha male (Post 1992; Poston, in press). Female boat-tailed grackles indirectly choose competitive males by copulating under conditions that promote prolonged competition between males.

These results suggest an important procedural issue for studies of mate choice. To document the full range of behaviour that contributes to a female's choice of a mate, it is important to preserve the natural context for courtship behaviour. Context is particularly important for indirect

mate choice mediated by competition between members of the opposite sex. Studies of experimentally isolated males and females would fail to identify important features of mate choice in boat-tailed grackles.

The asynchrony and spatial localization of receptivity among females in a colony permit high-ranked males to obtain many copulations. If females were more clumped in time or less clumped in space, they would be more likely to mate with a low-ranked male. On the other hand, if females were distributed more evenly in time or more clumped in space they would be more likely to mate with a high-ranked male (e.g. Webster 1994). Ecological consequences of clustering are less clear. Although female grackles appear to nest in islands of cattails or clumps of trees that afford their nests protection from predators, Post (1994) reported no detectable ecological advantages of synchrony or spatial clustering of nests within these islands. Furthermore, it seems unlikely that females prefer to mate in colonies to avoid interruptions, since courtship displays in colonies are frequently interrupted. Thus, although the spatio-temporal distribution of females has long been explained by exclusively ecological factors (Emlen & Oring 1977; Davies 1991), it seems possible that temporal dispersion and spatial clustering of nesting female grackles have evolved at least partly in response to sexual selection for indirect mate choice.

Indirect mate choice is likely to be widespread. Many kinds of behaviour by a female can influence which male is likely to fertilize her eggs (Wiley & Poston 1996). Female boat-tailed grackles illustrate some of the range of female behaviour that can influence mate choice, both directly and indirectly.

ACKNOWLEDGMENTS

For their help with many aspects of this research, I am indebted to R. H. Wiley and W. Post. For comments on the manuscript, I thank T. Hass, L. Isaacson, H. Mueller, W. Post, M. Webster, D. Westneat, R. H. Wiley, L. Wollerman and three anonymous referees. This work received financial support from Sigma Xi Grants-in-Aid of Research, the Frank Chapman fund of the American Museum of Natural History, the Charleston Museum, and the Curriculum in

Ecology at the University of North Carolina at Chapel Hill. I thank D. Hastie for allowing me to study grackles at Magnolia Gardens. Finally, I am grateful for the help and support provided by A. Poston and J. Poston.

REFERENCES

- Ahnesjö, I., Vincent, A., Alatalo, R., Halliday, T. & Sutherland, W. J. 1993. The role of females in influencing mating patterns. *Behav. Ecol.*, **4**, 187–189.
- Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature, Lond.*, **299**, 818–820.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andersson, M. & Iwasa, Y. 1996. Sexual selection. *Trends Ecol. Evol.*, **11**, 53–58.
- Bateson, P. 1983. *Mate Choice*. Cambridge: Cambridge University Press.
- Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.
- Bradbury, J. W. & Davies, N. B. 1987. Relative roles of intra- and intersexual selection. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 143–163. Chichester, U.K.: John Wiley.
- Cox, C. R. & Le Boeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.*, **111**, 317–335.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- Davies, N. B. 1991. Mating systems. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 263–294. Oxford: Blackwell Scientific Publications.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Halliday, T. R. 1983. The study of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 3–32. Cambridge: Cambridge University Press.
- Harvey, P. H. & Bradbury, J. W. 1991. Sexual selection. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 203–233. Oxford: Blackwell Scientific Publications.
- Kirkpatrick, M. & Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature, Lond.*, **350**, 33–38.
- Long, K. D. & Houde, A. E. 1989. Orange spots as a visual cue for female mate choice in the guppy (*Poecilia reticulata*). *Ethology*, **82**, 316–324.
- Milinski, M. & Bakker, T. C. M. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature, Lond.*, **344**, 330–333.
- Montgomerie, R. & Thornhill, R. 1989. Fertility advertisement in birds: a means of inciting male–male competition? *Ethology*, **81**, 209–220.
- Poole, J. H. 1989. Mate guarding, reproductive success and female choice in African elephants. *Anim. Behav.*, **37**, 842–849.
- Post, W. 1992. Dominance and mating success in male boat-tailed grackles. *Anim. Behav.*, **44**, 917–929.
- Post, W. 1994. Are female boat-tailed grackle colonies neutral assemblages? *Behav. Ecol. Sociobiol.*, **35**, 401–407.
- Post, W. & Seals, C. A. 1991. Bird density and productivity in an impounded cattail marsh. *J. Field Ornithol.*, **62**, 195–199.
- Post, W., Poston, J. P. & Bancroft, G. T. 1996. Boat-tailed grackle (*Quiscalus major*). In: *The Birds of North America*, No. 207 (Ed. by A. Poole & F. Gill). Philadelphia: The Academy of Natural Sciences. Washington, D.C.: The American Ornithologist's Union.
- Poston, J. P. 1995. Male competition for mates and mechanisms of mate choice by females in the boat-tailed grackle (*Quiscalus major*). Ph.D. dissertation, University of North Carolina at Chapel Hill.
- Polston, J. P. In press. Dominance, access to colonies, and queues for mating opportunities by male boat-tailed grackles. *Behav. Ecol. Sociobiol.*
- Searcy, W. A. 1992. Measuring responses of female birds to male song. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 175–189. New York: Plenum Press.
- Selander, R. K. & Giller, D. R. 1961. Analysis of sympatry of great-tailed and boat-tailed grackles. *Condor*, **63**, 29–86.
- Trail, P. W. 1985. Courtship disruption modifies mate choice in a lek-breeding bird. *Science*, **227**, 778–780.
- Warner, R. R. 1987. Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. *Anim. Behav.*, **35**, 1470–1478.
- Webster, M. S. 1994. The spatial and temporal distribution of breeding female Montezuma oropendolas: effects on male mating strategies. *Condor*, **96**, 722–733.
- West, M. J., King, A. P. & Eastzer, D. H. 1981. Validating the female bioassay of cowbird song: relating differences in song potency to mating success. *Anim. Behav.*, **29**, 490–501.
- Westneat, D. F., Sherman, P. W. & Morton, M. L. 1990. The ecology and evolution of extra-pair copulations in birds. *Curr. Ornithol.*, **7**, 331–369.
- Wiley, R. H. & Poston, J. 1996. Perspective: indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution*, **50**, 1371–1381.
- Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990. Mechanisms of female choice in red jungle fowl. *Evolution*, **44**, 477–485.