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Dominance, access to colonies, and queues for mating opportunities by male boat-tailed grackles

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Abstract Species characterized by female-defense polygyny have extreme variance in male mating success. Many studies have considered alternative male strategies for access to females, but few have considered age-specific strategies. Male boat-tailed grackles (*Quiscalus major*) compete for access to colonies of females and form linear dominance hierarchies. I observed two groups of males that competed for females at seven colonies. Dominance rank was significantly correlated with mass, but not after controlling for age. In contrast, the correlation between dominance rank and age remained significant after controlling for mass. Older males dominated younger males and dominance relationships were very stable. Thus, dominance hierarchies represent queues for mating opportunities. A male's rank in the hierarchy determined how closely he approached a colony. Furthermore, males of all ranks prevented lower-ranked individuals from approaching the colonies. Dominance rank thus determined access to nesting females. One top-ranking male's loss of mass over the course of the breeding season presumably reflected the energetic cost of defending females, but he maintained his position in the hierarchy despite the small loss of mass. One alpha male held a colony for at least 4 years, and the ages of males from two queues indicated that males wait 6 or more years before becoming an alpha male. Therefore, most males die before acquiring a colony of females. Spatial structure such as that documented here could obscure recognition of queues and explain why they have not been documented in more species.

Key words Alternative mating strategies · Dominance · Female-defense polygyny · Queuing · *Quiscalus major*

Introduction

Female-defense polygyny differs from other polygynous mating systems because males compete for access to females directly, instead of for resources females require or for display sites females visit (Emlen and Oring 1977; Wittenberger 1979; Davies 1991). Female-defense polygyny occurs either when males defend groups, or harems, of females (Le Boeuf 1974; Clutton-Brock et al. 1982; Post 1992; Herrera and Macdonald 1993; Webster 1994) or when males defend individual females in sequence (Robinson 1986a,b). In some species the most successful males defend dozens of females over the course of a single breeding season (Le Boeuf 1974; Post 1992; Webster 1994). If some males defend several females and the adult sex ratio is near unity, then other males are left with no female to defend. Consequently, female-defense polygyny is frequently associated with extreme skew in male mating success (Le Boeuf 1974; Clutton-Brock et al. 1982; Pemberton et al. 1992; Post 1992; Webster 1994).

Males that are unsuccessful in defending females often adopt alternative strategies that increase their chances of encountering sexually receptive females. For species in which males defend harems, some males sneak into the harem to mate, and in some instances they successfully copulate before being chased out by the harem male (Le Boeuf 1974; Post 1992; Poston 1995). Alternatively, males wait at the edges of harems to intercept females arriving or departing the harem (Le Boeuf and Mesnick 1990; Mesnick and Le Boeuf 1991) or to herd females away from the harem (Clutton-Brock et al. 1982). In some species males associate with females at sites away from the harem such as foraging areas (Post 1992). For species in which males defend individual females in sequence, males compete to defend

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females during the time that copulations are most likely to fertilize eggs, and less successful males defend females before or after this time (Robinson 1986a).

Many studies of alternative mating strategies have focused on phenotypic limitations that prevent some individuals from competing successfully. Few of these studies have considered that males could be pursuing optimal age-specific allocation of reproductive effort (but see Howard 1984). One such possibility involves queues for reproductive positions. In a queue, individuals are arranged by their order of arrival. Individuals that arrive first are at the head of the queue and are next to receive a reproductive position (a harem of females, for example), whereas individuals that arrive last are at the tail of the queue and must wait until individuals ahead of them leave the queue before they can gain reproductive opportunities. Individuals typically advance through the queue as those ahead of them die (Wiley and Rabenold 1984). Evidence that individuals queue for breeding positions requires studies that follow animals for a significant portion of their lives or at least follow enough animals to estimate how quickly they move through positions in the queue (Wiley 1981). The long life spans of many queuing species could explain why so few studies have considered queues.

Another difficulty in studying queues is that they are often obscured by the spatial relationships of individuals. Rarely do queues in animal societies resemble a group of humans waiting at a bus stop. Instead, males in a queue for a harem of females could defend areas surrounding the harem in relation to their position in the queue. In this case, individuals that join the queue occupy an area on the periphery and gradually move nearer the harem as individuals ahead of them die (see Wiley 1991 for a review of this pattern in lekking species). Individuals would not interact with all other members of the queue, and the queue would only become apparent after observing the settlement and transition of individuals.

Queues have been documented in a variety of mating systems, including monogamy (Smith 1978; Ens et al. 1995), leks (McDonald 1989, 1993a), cooperative breeding (Wiley and Rabenold 1984), scramble-competition polygyny (Schwagmeyer and Parker 1987), and female-defense polygyny (Post 1992; Herrera and Macdonald 1993). Queues among males seem especially relevant to species characterized by female-defense polygyny because of the extreme skew in male mating success. Several studies describe social structures that are suggestive of queuing (e.g., McCracken and Bradbury 1981; Webster 1994). The most complete evidence of queuing comes from the study of boat-tailed grackles (*Quiscalus major*) by Post (1992). He found that male grackles competed for colonies of females and formed linear dominance hierarchies. The highest-ranking or alpha males spent the most time in the colonies and performed the most copulations there. Post's results suggest that the hierarchy represents a queue for the colony because: (1) older males dominated younger males, (2) mass and dominance rank were not correlated, and (3) when a male disappeared the male below it ascended to its position in the hierarchy.

Boat-tailed grackles are sexually dimorphic and dichromatic blackbirds (*Icterinae*) of the southeastern United States. Females nest in colonies of 2 to more than 90 nests in islands in freshwater marshes or in isolated trees or bushes; these sites appear to afford protection from terrestrial predators. Males, which are nearly twice the size of females, do not help females build nests or rear young. Instead they compete for access to colonies and the highest-ranking male performs 70–80% of the copulations at a colony (Post 1992; Poston 1995).

This study was designed to examine the interactions among male boat-tailed grackles that competed for colonies of females. To examine further whether males form queues, I examined the stability of dominance relationships and the effects of age and mass on dominance rank. In addition, I examined spatial relationships of males competing for colonies, access to colonies by males below the alpha male, and interactions between males that limit low-ranking males' access to colonies. My results provide additional evidence that male boat-tailed grackles queue for colonies.

Methods

Study site

This study was conducted during January–June 1991–1993 at Magnolia Gardens near Charleston, South Carolina, where a population of grackles nested in a 30-ha marsh in an impoundment bordering the Ashley River. Water depth in the marsh averaged approximately 1 m. Cattails (*Typhus* spp.) covered approximately 25% of the marsh; the remaining 75% was open water. Management of the marsh varied over the course of the study; usually the marsh was filled with fresh water, but occasionally tidal water from the Ashley River was allowed into the marsh, and on two occasions the marsh was drained for 2–4 days. Post and Seals (1991) provide a more detailed description of this site. I concentrated my observations on two groups of males that competed for seven nesting colonies of female grackles in the northeastern corner of the marsh (Fig. 1), but I monitored nests, banded nestlings, and trapped grackles over a wider area of the marsh. This area was about 500 m from the colonies studied by Post (1992) on the opposite side of the marsh.

General procedures

During this study, I banded 277 adults and 270 nestlings and recaptured 201 adults, many of which were birds banded previously by Post. By 1992 only 14% of the adult males and 17% of the adult females attending colonies remained unbanded. I netted or trapped birds 2–3 days per week during the breeding season (March–June) and more frequently before and after the season. Adults were marked with unique combinations of colored aluminum bands. Males' ages were classified by characteristics of plumage and eye color (Post et al. 1996) as hatching year, second year, or after second year (see below).

Each season I conducted observations at three or four colonies of grackles, each of which I visited two or three times per week until females no longer initiated new nests (2–10 weeks per colony).

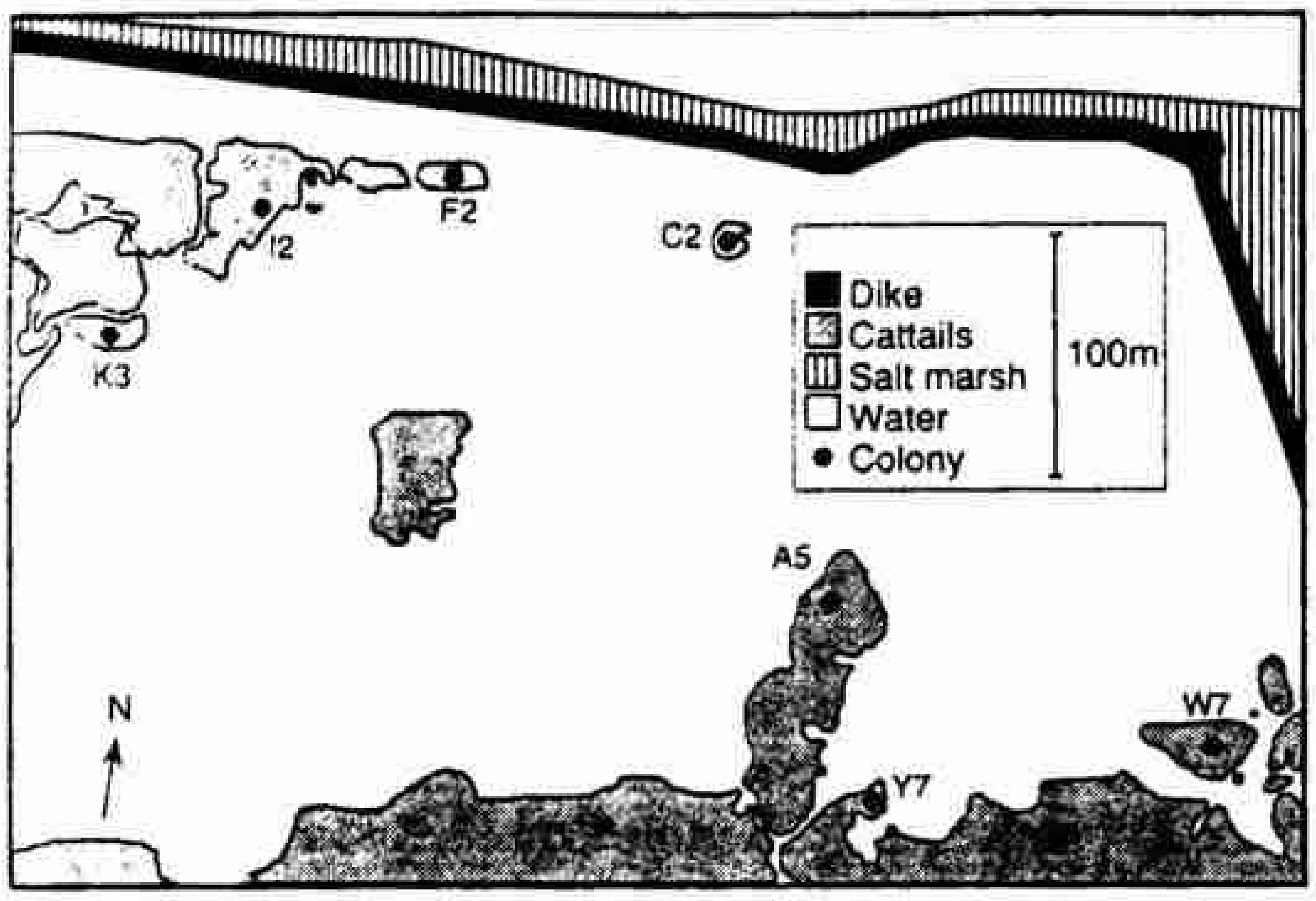

Fig. 1 Map of the study area. *Black dots* indicate the seven colonies of grackles observed in the course of this study. Colonies F2, I2 and K3 were defended by one group of males (the West group), and colonies A5, C2, W7 and Y7 were defended by another group (the East group)

Grackles were observed from blinds on wooden platforms, from a canoe, and from foot on the dike that surrounded the marsh. Attendance of grackles at colonies was low in the middle of the day. Therefore systematic observations were made for 3–4 h after sunrise or before sunset for a total of over 500 h. In addition to the observations described below, I investigated mate choice by females and males' responses to other males' courtship displays (Poston, in press) and the mating success and fertilization success of males in colonies (J.P. Poston, R.H. Wiley and D.F. Westneat unpublished work).

Dominance relationships of males

Males' agonistic interactions (supplants, chases and fights) were recorded ad libitum. Males supplanted other males for access to food or for perches near the colonies. Chases were less common. Fights were rare but sometimes severe. On one occasion two males locked legs in the air and fell to the water. Although the water was too deep for either male to stand, they continued to grapple for about 10 s before both flew away. McGowan and Dunham (1988) also report a case of extreme aggression between male boat-tailed grackles. Dominance interactions were entered in a matrix and tested for linearity (Appleby 1983). Because dominance relationships were very stable (see Results), for each pair of males observed to interact only once ($n = 11$ dyads), I assumed their relationship was indicated by the outcome of that interaction.

Correlates of dominance

Mass

During the 1993 breeding season I attached a perch to an electronic balance to measure the mass of free-ranging males. When a male landed on the perch, I used a telescope to read his mass to the nearest gram. I placed the balance in and near colonies so that I could measure as many males as possible. All measurements were obtained within 3 h of sunrise on calm days.

Age

Males attain definitive plumage in the fall of their second calendar year. Before this, males can be aged as hatching year or second year based on plumage and eye color (Post et al. 1996). I restricted the analyses of age to males captured before attaining definitive plumage. Several males with ages older than this study were banded by Post within their first 2 years. In addition, because several males occurred in the study site during more than one year, I limited my analysis of age and dominance rank to the 1992 season, the year for which I had the most complete information on males' dominance relationships. For partial correlation analyses between age, mass and rank, I used data from 1993 because this was the year I obtained mass measurements of free-ranging males.

Spatial relationships of males

Scan samples

To examine males' spatial relationships in and near colonies, I produced detailed maps of each colony and the surrounding area within 200 m. During scan samples (Altman 1974) at each colony, I plotted the locations and identities of all males at 5-min intervals for 30 min. Scan samples were collected two or three times per week for each colony. Only males that were within 50 m of the colony in 10% of the scans were included in subsequent analyses of spatial relationships.

Repeated observations of the same individuals should be analyzed for autocorrelation (Swihart and Slade 1985; Cresswell and Smith 1992). Such an analysis revealed that a male grackle's successive locations were not statistically independent unless sufficient time had elapsed between observations. To determine the interval necessary to obtain statistically independent locations of males, I collected a separate set of observations from six males in which I recorded a male's location at 10-s intervals. These observations revealed that successive locations of males were independent after 4.3 min. Therefore, I accepted locations 5 min apart as statistically independent. As a conservative precaution against autocorrelated observations, if a male did not change perches during the 5 min between scans, I included this location only once.

Activity space

I refer to the space that a male occupied around a colony as his activity space (Waser and Wiley 1980). This area was not a home range, because males often foraged and roosted far from the colonies. On the other hand, it was not a territory because males' activity spaces overlapped considerably. I produced an activity space from each male's observed locations with the harmonic mean method (Dixon and Chapman 1980; Spencer and Barrett 1984). This method places an arbitrary two-dimensional grid over all observations and then assigns a value to each grid point based on the distance between that grid point and each observation. Grid points with equal values are connected with lines, called isopleths, which are analogous to the contour lines on a contour map. I defined a male's activity space as the isopleth that included 95% of his observed locations. I also calculated the arithmetic center of each male's observed locations to determine its distance from the colony.

Sample sizes for spatial analyses

The asymptotes (Waser and Wiley 1980; Harris et al. 1990) of the area of each male's activity space allowed me to determine if I had sufficient observations to characterize its size and location. Only males whose area changed by less than 5% over the last five observations or males that had been observed at least 50 times were included in analyses of area. Eight males' activity spaces fit this criterion. Because seven were from the West group, I analyzed the size and percentage of nests overlapped by the activity spaces of these seven males. I performed a similar analysis of the location of males' activity spaces. Only males whose arithmetic centers shifted by less than 9 m (equal to 5% of the average diameter of activity spaces) over the last five observations were included in analyses of location. Of the 13 males that fit this criterion, 4 were from the East group and 9 were from the West group.

Female receptivity

To determine whether the number of males that attended a colony varied with the number of receptive females, I estimated the number of receptive females per day for each colony. A female was receptive for 3 days, beginning 4 days before the first egg appeared in her nest (Post 1992). Therefore, I could determine when the female at each nest had been receptive by backdating from the day the first egg appeared in the nest. Females laid one egg per day and the modal clutch was three eggs (68% of 417 clutches; J.P. Poston, unpublished work). I visited each colony every 3–4 days to record the contents of each nest. This interval allowed me to estimate each female's receptive period to within ±0.5 day for 82% of nests (Poston 1995).

Results

Male grackles in the northeastern corner of the Magnolia Gardens marsh belonged to two groups. One group of ten males defended females at the four easternmost colonies in Fig. 1 (East group), and the other group of 12 males defended females at the three westernmost colonies (West group). Males frequently interacted with males within their group, but they rarely interacted with males from the other group. Males within a group moved between the colonies in response to the number of receptive females: the mean number of males that appeared in scan samples within 50 m of a colony was positively correlated with the number of receptive females that day (Table 1).

For subsequent analyses I divided males into either the East or West groups. There was another more subtle division within the West group. Two high-ranking males (alpha and beta) defended the F2 colony and three high-ranking males (alpha, beta and gamma) defended the I2 and K3 colonies (see Fig. 1). The lower-ranking males in this group moved between these colonies. In 1992, after the I2 colony no longer recruited new females, the three high-ranking males from I2 occupied the western one-third of the F2 colony, and the two alpha males frequently displayed to one another along a boundary within the colony. Most of my observations of the West group were at I2. Therefore for analyses of spatial data I present results both for all males from the West group and for males that I observed at I2 (excluding the two high-ranking males from F2). For the East group, only spatial data from the A5 colony were analyzed.

Table 1 Spearman correlation coefficients between the number of receptive females per day and the mean number of males appearing within 50 m of the colony per day for six colonies. Sample sizes are the number of days each colony was sampled

Colony	Year	r_s	n	P
I2 K3	1991	0.660	16	<0.01
W7	1991	0.799	22	<0.001
A5	1992	0.551	9	<0.20
C2	1992	0.646	10	=0.05
F2	1992	0.691	14	<0.01
I2	1992	0.404	24	=0.05

Dominance hierarchies

Post (1992) reported a highly linear hierarchy for males at a nearby colony. Likewise, I documented highly linear hierarchies at three colonies where I observed interactions between nearly all pairs of males (h = 0.71–0.95, $P < 0.03$ for each; see Table 2 for a sample hierarchy). For four additional colonies, measures of linearity were low (h = 0.27–0.60, $P > 0.25$), not because of intransitive relationships, but because I did not witness interactions between enough dyads. Nevertheless, I usually observed enough interactions to rank males on the assumption that they had transitive relationships, like those in hierarchies with more complete documentation. For males with adjacent positions in a hierarchy but unknown relationships (n = 5 dyads and 1 triad), I assigned each the median of the dominance ranks they would have received had I known their relationships. Males' dominance relationships were extremely stable; in the hierarchies I observed, only 10 out of 502 interactions were reversals, and I did not observe any dominance relationships change over time for any pair of males.

Correlates of dominance rank

For males in the East Group, higher-ranked males tended to be heavier than lower-ranked males (Spearman's $r = -0.707$, $n = 8$, $P < 0.10$). When I included the two males from the West group, the relationship became significant (Spearman's $r = -0.685$, $n = 10$, $P < 0.05$; Fig. 2). In addition, of the six males for which I had multiple measurements, five of them lost mass as the season progressed. For one of the six, the alpha male from the East group, the correlation between date and mass was significant (Table 3). This male lost less than 3% of his body mass and maintained his position in the hierarchy.

Post (1992) reported that older male grackles were dominant to younger males. I observed a similar pattern. Among 14 males for which I knew their ages, none was

Table 2 Interaction matrix for males at one colony. The number in each cell is the number of interactions observed. Note that I did not observe males AYB-G and RA-YB interact with one another. Both are assigned a rank of 3.5

Winner	Loser						
	A-RYY	-A	AYB-G	RA-YB	AG-BG	YG-AG	BB-AY
A-RYY	–	34	19	31	35	2	12
-A		–	10		4	4	4
AYB-G			–		1	2	6
RA-YB				–	5	1	18
AG-BG		2			–	2	1
YG-AG		1				–	5
BB-AY		1					–

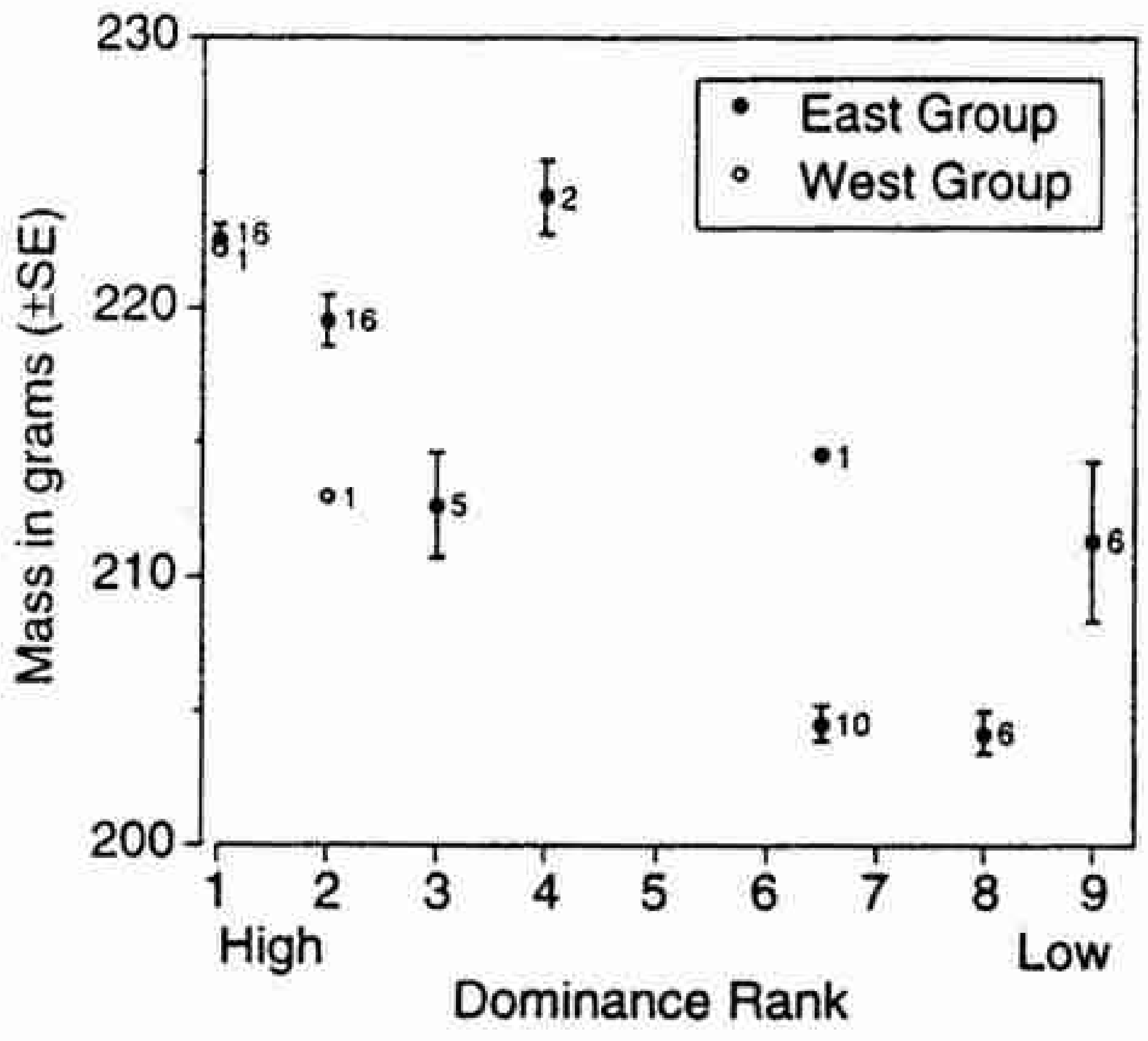

Fig. 2 Mean body mass (g) was related to dominance rank for 10 males. For each male, the measurements from each day were averaged and then these daily averages were averaged to obtain a male's overall average mass. The number beside each data point indicates the number of days each male was sampled. Bars indicate 1 SE. Note that the ordinate does not start at zero

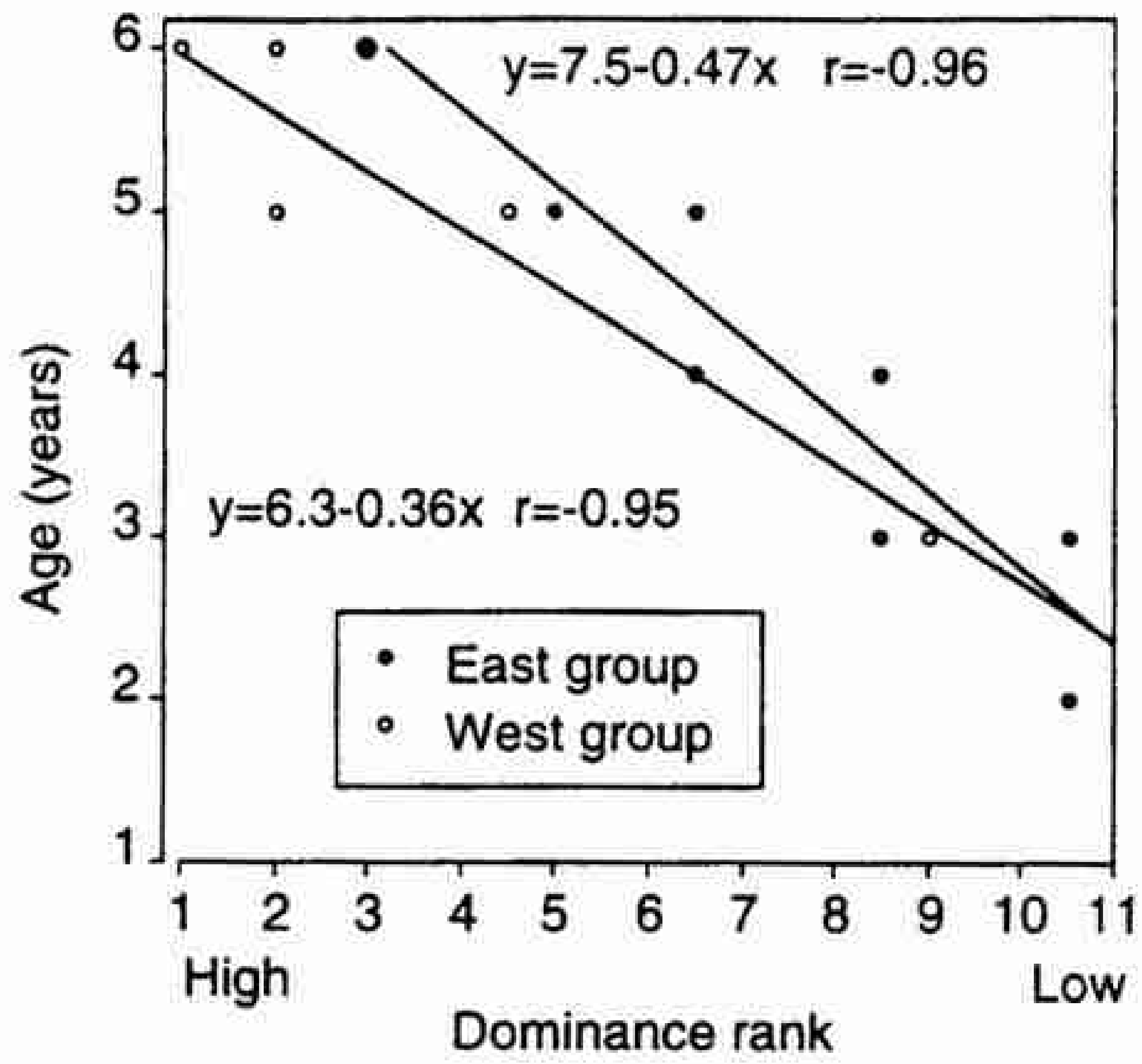

Fig. 3 Correlation between age and dominance rank for males from the East and West groups (East group Spearman's $r = -0.963$, $n = 8$, $P < 0.01$; West group $r = -0.925$, $n = 6$, $P < 0.05$). *Large symbol* indicates coincident points from two males

dominant to an older male. Figure 3 shows the relationship between age and dominance rank for males from the two social groups. I observed a significant correlation between rank and age for both groups. The regression of age on rank provides a crude estimate of the rates of movement through the queues and the time necessary to reach the head of the queues. The slopes of the two regressions did not differ significantly ($t = -1.2$, $df = 10$, $P > 0.20$). The difference between the intercepts was nearly significant ($t = 2.1$, $df = 11$, $P = 0.052$). The values of these regression equations for a dominance rank of one suggest that males in these queues waited 5.9–7.0 years to attain alpha status.

I examined the independent effects of age versus mass on dominance rank with Kendall's partial correlation. The sample of males for which I knew both their mass and age was small (East group $n = 6$; West group $n = 2$). For the East group, the correlation between rank and age with mass held constant was significant ($T = -0.958$, $P < 0.01$) but the correlation between rank and mass with age held constant was not ($T = 0.171$, $P > 0.50$). The significance of these relationships did not change if the two males from the West group were included in the analysis.

Table 3 Correlation coefficients between date and mass for six males measured on at least 3 days. Sample size is the number of days during the season the male was weighed. Only the alpha male experienced a statistically significant decline in mass with date

Male	Rank	r	n	P
A-RYY	1	−0.616	16	<0.02
RA-YB	2	−0.118	16	>0.50
AG-BG	3	−0.195	6	>0.50
ABB-B	6.5	−0.286	12	<0.50
A-RRR	8	0.055	6	>0.50
GAR-Y	9	−0.800	6	<0.10

Activity spaces

Because many copulations occur within colonies (Post 1992; Poston 1995), access to colonies is an important component of male mating success. My observations reveal that male dominance rank predicted access to colonies. Compare, for example, the locations of nests at one colony (Fig. 4a) with activity spaces for three males from that colony (Fig. 4b–d). The alpha male's activity space overlapped the nests completely, and males of decreasing rank occupied activity spaces of increasing distance from the nesting colony.

This relationship between rank and access to colonies was supported by three measures of males' activity spaces. First, there was a significant negative correlation between a male's dominance rank and the percentage of scans I observed the male in the colony (Fig. 5; East group Spearman's $r = -0.739$, $n = 10$, $P < 0.05$; West group $r = -0.698$, $n = 12$, $P < 0.05$; I2 colony $r = -0.518$, $n = 10$, $P < 0.20$). The correlation coefficients for the two groups did not differ significantly ($Z = -0.325$, $P > 0.50$; for both groups combined $r = -0.732$, $n = 22$, $P < 0.001$). Second, the distance from the center of a male's activity space to the center of the colony was correlated with his rank in the dominance hierarchy (Fig. 6; East group Spearman's $r = 1.0$, $n = 4$, $P = 0.10$; West group $r = 0.734$, $n = 9$, $P < 0.05$; I2 colony $r = 0.436$, $n = 7$, $P < 0.50$). Sample size from the East group was too small to test whether correlation coefficients differed between groups (for both groups combined $r = 0.742$, $n = 13$,

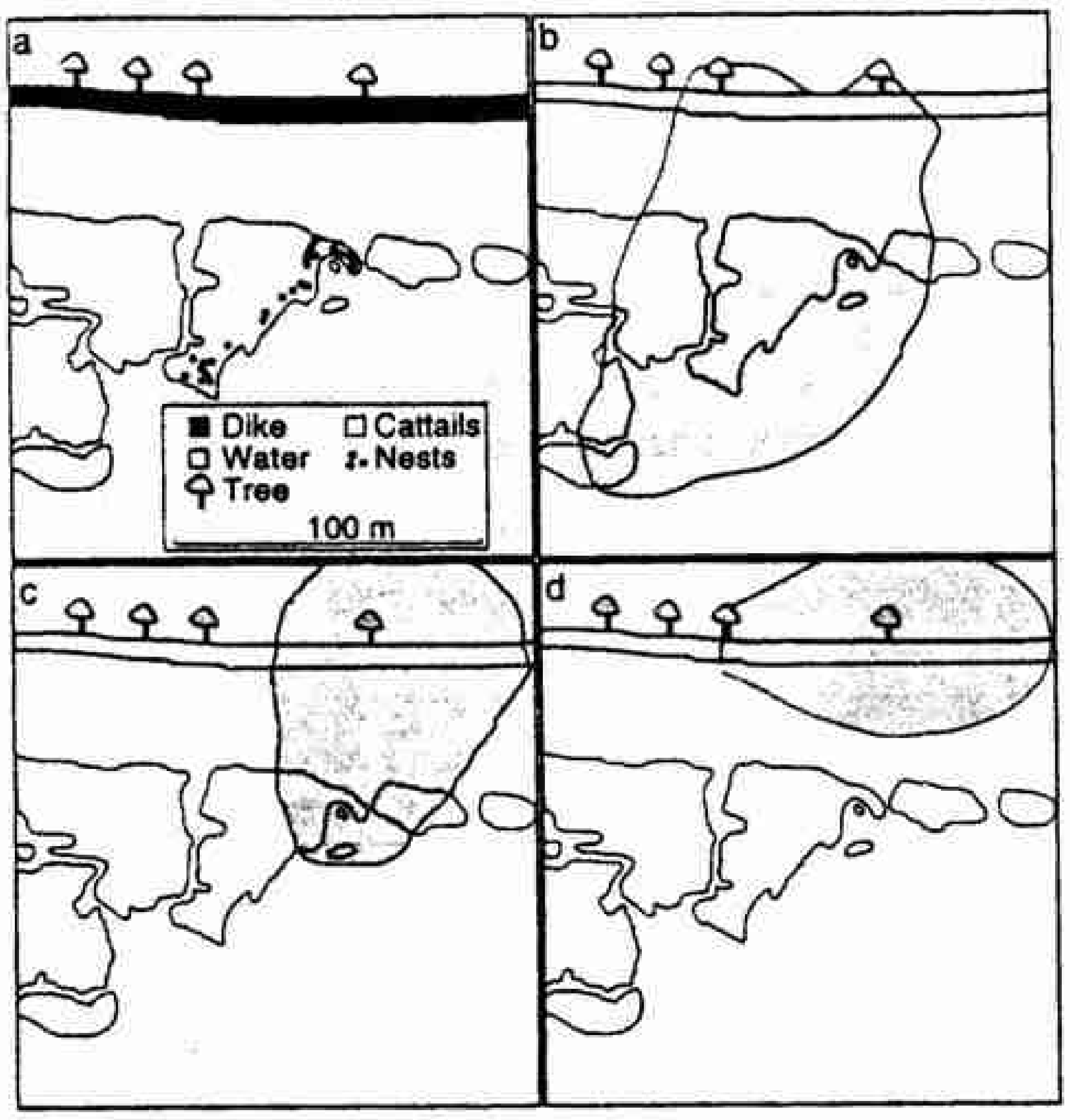

Fig. 4a–d Maps of the I2 colony showing locations of nests and sample activity spaces of three males. **a** Nests were spread along the bottom right edge of the central island of cattails. **b** Activity space of the top-ranked (alpha) male included all nests. **c** Activity space of a male ranked 2.5 included about half of the nests. **d** Activity space of the male ranked 9 included none of the nests

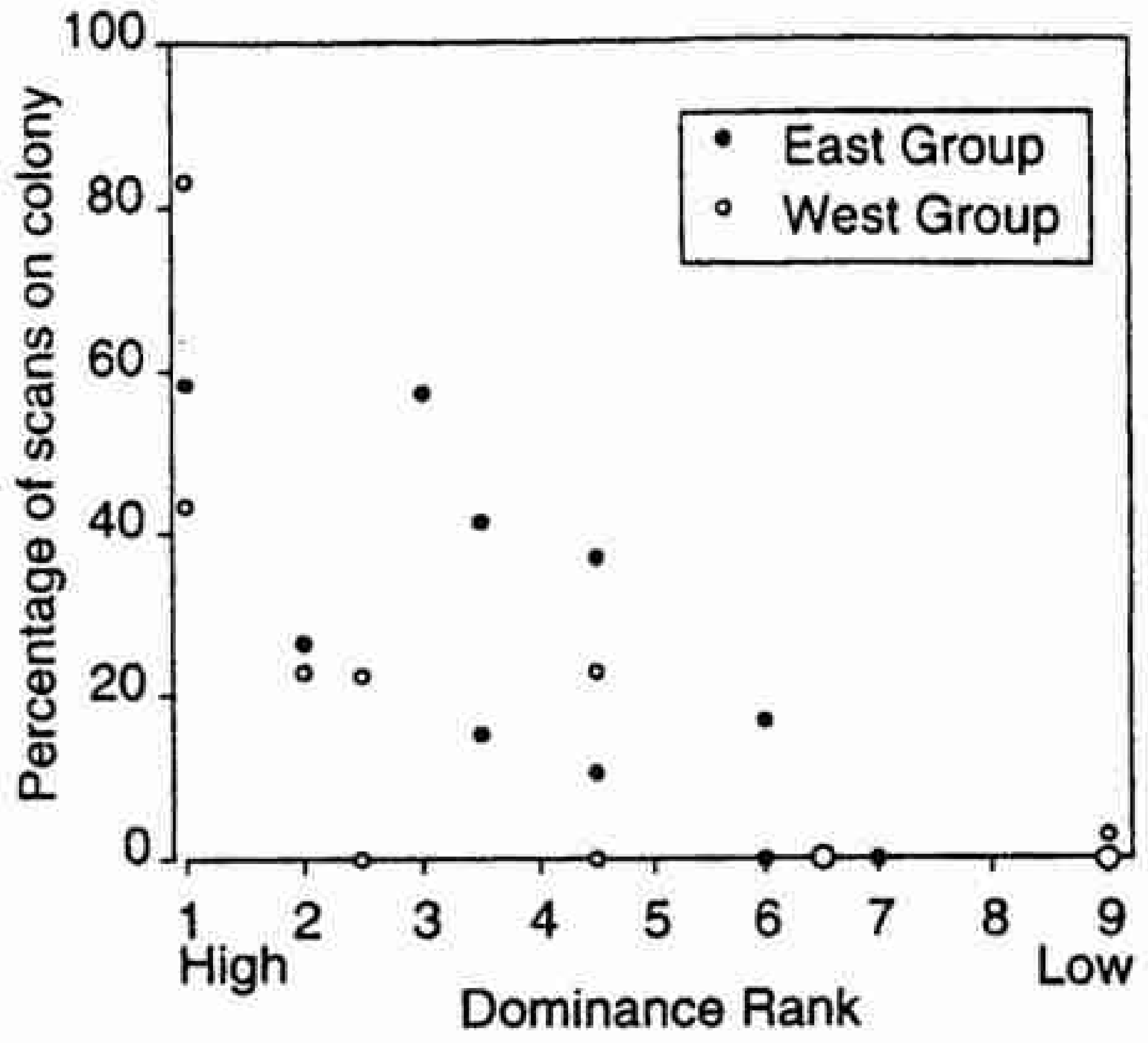

Fig. 5 Percentage of scans in which each male was observed in a colony of females for 22 males from two groups. *Large symbols* indicate coincident points from two males

$P < 0.01$). Third, the percentage of nests at the colony within a males' activity space was significantly correlated with dominance rank for the West group (Spearman's $r = -0.823$, $n = 7$, $P < 0.05$), but not when the males from the F2 colony were excluded ($r = -0.600$, $n = 5$, $P < 0.50$). For these analyses, relationships were significant when all males were included; as samples were pared into groups and then into colonies, some correlations became non-significant. The correlations between rank and access to colonies were not a consequence of high-ranking males occupying larger activity spaces; a male's rank and the area of his activity space were not correlated for the West group (Spearman's $r = -0.180$, $n = 7$, $P > 0.50$). For analyses of the area of males' activity spaces and the percentage of nests within males' activity spaces, sample sizes from the East group were too small for statistical tests (see Methods).

Exclusion of lower-ranked males

When two males appeared simultaneously in a scan sample, I determined which of the two was nearer the nesting colony and arranged these data in a matrix similar to a dominance hierarchy (Table 4). For each dyad of males for which I knew their dominance relationship, I determined which male of the pair was nearer the colony in more observations. Because some individual males appear in more than one dyad, dyads may not represent independent data points. I performed a randomization test (Manly 1991) to produce samples of independent data points. From the pool of dyads I observed, I drew a random sample of independent dyads (without replacement) and counted the number of dyads for which the dominant male was closer to the colony more often. This procedure was repeated 10,000 times, and the mean number of dyads (± SD) in which the higher-ranking male was closer to the colony more often was 6.5 ± 0.85 out of 7.6 ± 0.55 dyads, a significant difference from random (binomial $P < 0.04$). Therefore, I conclude that males that were near colonies simultaneously were not spaced independently of one another; higher-ranked males were more likely to be closer to the colony.

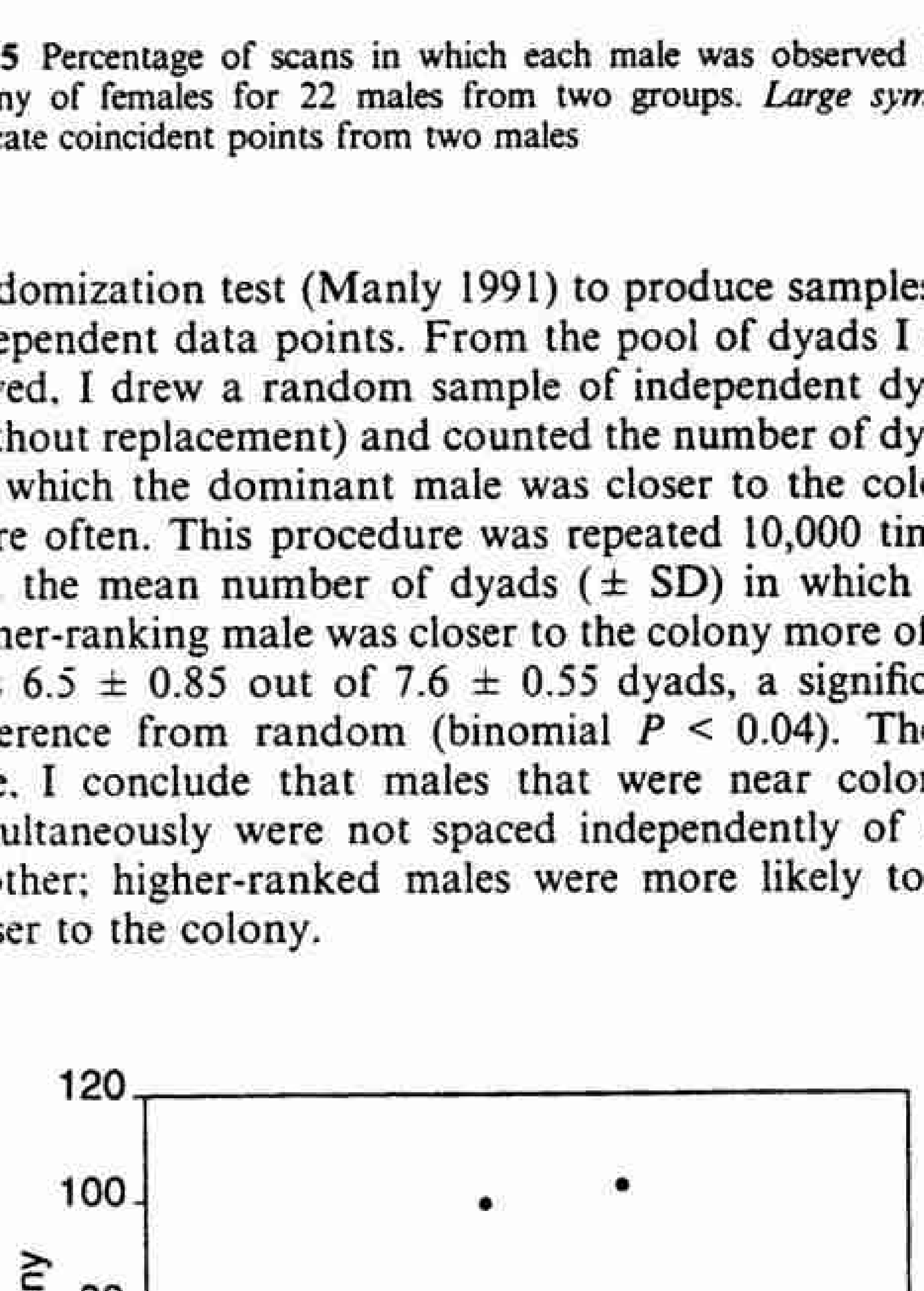

Fig. 6 Distance between the center of a male's activity space and the center of the colony of females increased with position in the hierarchy for 13 males. The centers of the three alpha males' activity spaces were within the colonies

Table 4 Matrix of the relative positions of pairs of males present simultaneously in relation to the colony. Entries in the table are the numbers of simultaneous observations for each dyad. Males have been arranged by dominance rank. Note that I do not know the dominance relationships between the 3 males ranked 5; they have been arranged to minimize the numbers below the diagonal

Closer to colony	Farther from colony							Rank
	A-RYY	-A	AG-BG	ARY-Y	RRR-A	ABB-B	ABR-R	
A-RYY	–		7		1	7	1	1
-A		–	2	1	5	5	2	2
AG-BG			–	2	3	11	2	3
ARY-Y			1	–	2	2	1	5
RRR-A		1	2		–	4	2	5
ABB-B			3		2	–	4	5
ABR-R		1				1	–	7

Discussion

Male boat-tailed grackles that competed for colonies of females formed linear dominance hierarchies. These hierarchies included males that interacted regularly and moved between colonies in response to the number of receptive females. Both mass and age were correlated with dominance rank. Thus, position in a hierarchy could be a result of fighting ability (as indicated by mass) or seniority (as indicated by age). It seems more likely that age and not mass determined dominance rank. First, the difference in mass for males in a hierarchy was only 5% of their total mass, and the difference between adjacent males in the hierarchy was even less than 5%. It seems unlikely that this small difference in mass could be responsible for differential fighting ability. Second, partial correlations revealed that age but not mass correlated with rank when the other was controlled. The relationship between age and rank (Fig. 3) was absolute: within a hierarchy males were never subordinate to younger males. Post (1992) similarly found that older males outranked younger males, but he found that high-ranking males were not heavier than low-ranking males. This difference between our studies could be because my measures of mass were based on a larger sample from each male: I made several measures of free-ranging individuals whereas Post measured males only once when he captured them.

Differences in mass could be a consequence and not a cause of differences in rank if dominance rank confers greater access to food. I did not observe dominance interactions at feeding areas, but Post (1992) observed that dominance relationships of males were the same at feeding sites in the winter as they were at breeding colonies in the spring. Our populations of grackles were non-migratory. The year-round interactions among males could promote the constancy of dominance relationships across time and location. I observed that dominance relationships were extremely stable, as would be predicted if males were members of a queue. Further evidence that males form queues is the observation of Post (1992) that when alpha males disappeared the beta males assumed the alpha position. Taken together, Post (1992) and this study provide strong evidence that male boat-tailed grackles form queues for access to colonies of females. The queues I observed contained at least 10–12 males, and the youngest alpha male of known age was 6 years old.

Out of six males in one queue, only the alpha male had a significant decline in mass during a breeding season. The energetic cost of escorting females away from colonies and chasing rival males (see Poston 1995) was probably responsible for his small loss of mass. Despite this loss, he maintained his position in the hierarchy. We need further evidence before concluding that alpha males are more likely to lose mass than other males. Nevertheless, this observation provides an interesting comparison with two other species of birds. McDonald (1989) found that male long-tailed manakins (*Chiroxiphia linearis*) at the head of queues for display perches in a lek lose more than 10% of their body mass during the breeding season (due to energetic courtship displays by males) and also maintain their position in the queue. In contrast, Robinson (1986a) found male yellow-rumped caciques (*Cacicus cela*) that defend females lose about 4% of their mass between seasons and subsequently decline in rank. Within a season male caciques that lose mass forgo breeding attempts until they regain weight (Robinson 1986a), a pattern that probably is rare among birds but is more common among ungulates that fast during the rut (see Clutton-Brock et al. 1982; Jarman 1979). Although a 4% decline in mass is sufficient to cause male caciques to lose dominance, similar losses in grackles or much greater losses in manakins do not induce similar declines in dominance as well. Caciques do not queue for breeding opportunities; younger males tend to outcompete older males (Robinson 1986a). Queuing, because it is a form of cooperation, could explain why loss of mass does not cause grackles and manakins to lose breeding positions (see below).

Spatial relationships of queuing males

A male's access to a colony depended on his rank in the hierarchy and thus his position in the queue. Males of higher rank spent more time in the colony, and they had activity spaces that overlapped more nests, than males of lower rank. Moreover, males of all ranks appeared to prevent lower-ranked males from approaching the colonies more closely than themselves. Because many copulations occur at a colony (Post 1992; Poston 1995; Poston, in press), access to colonies is an important component of mating success for males, and alpha males perform the majority of copulations in colonies (Post 1992; Poston 1995).

My analysis of males' activity spaces is based on a small number of males from two groups. Because males adjusted their activity spaces continually in response to receptive females, I could collect enough information to document activity spaces only at colonies that lasted for several weeks. Furthermore, the overlap between males' activity spaces required large samples for me to document their relative positions accurately. However, my analysis of the locations of males present simultaneously (Table 4) and the percentage of scans that individual males were on the colonies (Fig. 5) is based on observations of nearly all males from both groups. Post (1992) concluded that alpha males spend most of their time in a colony and lower-ranking males occupy locations peripheral to colonies. All evidence thus indicates that the positions of males in a hierarchy influence their spatial relationships.

Habitat characteristics could have influenced the size and spatial arrangement of males' activity spaces and hence their access to colonies. At Magnolia Gardens, males not in colonies or flying over them spent most of their time in the trees along the dike that surrounded the marsh. Perhaps males preferred these perches because they offered a view of the colonies near the dike. It is also likely that perches on the dike attracted males because females flew to the dike to gather nest material. Proximity of perches to colonies could have determined the proximity of males' activity spaces to colonies of females. The relationship between dominance rank and distance from the colonies has a more shallow slope for the West group than for the East group (Fig. 6), although the sample size for the East group is too small for statistical comparison. For the data in Fig. 6, males in the West group defended the I2 and F2 colonies near the dike, while males in the East group defended the A5 colony which was much farther from the dike (see Fig. 1). These observations also suggest that if preferred perches or sites of congregation by females had been distributed around colonies more evenly (instead of being concentrated on the dikes), males' activity spaces might have overlapped less. Boat-tailed grackles nesting in different habitats could exhibit different patterns of male activity spaces and association with females than documented in the present study. Habitat characteristics, the operational sex ratio (Emlen and Oring 1977), whether or not females leave a harem, and whether or not harems are mobile could all affect how males compete for females and whether males compete for proximity to females or remain in bachelor groups (see also Webster 1994). Perhaps males are more likely to compete for proximity to females when females leave harems frequently or predictably or when harems form near other harems.

Queues as reproductive decisions

Zack and Stutchbury (1992) and Ens et al. (1995) argue that site-specific dominance is necessary for queuing to be stable. It does not pay for individuals to wait in a queue if others do not need to establish site-specific dominance but instead can cut in line in front of them. Consequently, there is a tradeoff between the number of potential openings an individual can monitor and the likelihood that it will successfully acquire an opening; individuals queuing for a breeding position must concentrate their efforts on one or a few potential locations. In boat-tailed grackles, Post (1992) documented only one instance of a site-related reversal in dominance, and I observed no such cases. However, we rarely witnessed interactions among males from different queues. Two pieces of indirect evidence suggest grackles exhibit site-specific dominance over males from other queues. First, large colonies are sometimes controlled by two high-ranking males that defend separate ends of the colony. Second, when a male disappeared, the male below him in the queue, and not a male from another queue, ascended to his position. Therefore, it seems likely that when male boat-tailed grackles join a queue they establish site-specific dominance over males from other queues.

How males decide which queue to join remains unclear. The length of the queue and the potential payoff (number of females) are presumably important considerations for a young male (Wiley 1981; Wiley and Rabenold 1984; Ens et al. 1995). Stochastic events, such as the death of particular individuals, make it impossible for males to predict with perfect accuracy which queue will be the shortest. For example, in this study the second-ranking male in the East group was younger than the third-ranking male in the West group (Fig. 3). The East-group male became beta early in the 1992 season when the previous beta male disappeared. The similar slopes of the regressions of rank on age for the two groups (Fig. 3) suggest that males left the two queues (died) at similar rates. The nearly significant difference in intercepts suggests either that the East group had more males, or that this queue had been delayed about a year. Both queues had similar numbers of males (West group 12 males, East group 10 males), but the alpha male for the East group, of unknown age, held this position for 4 years (1991–1994), and the previous alpha male held it for at least 2 years.

Male boat-tailed grackles in their first year range widely and do not have well-defined activity spaces. Such males might compare queues before deciding which one to join. McDonald (1989) reached a similar conclusion for the lek-breeding long-tailed manakin. Like boat-tailed grackles, male long-tailed manakins are members of queues attached to one or a few sites, and young male manakins visit several groups' display sites (see also East and Hofer 1991 for a similar pattern in hyenas). Post (1992) suggested that some male boat-tailed grackles adopt an alternative strategy of displaying to females away from colonies. The relationships between males in a queue and males that are not in a queue for a colony are unknown. DNA fingerprinting reveals that females frequently copulate with males that do not attend their colony, presumably while females are foraging or collecting nesting material away from the colony (Poston 1995). Despite the fertilizations by males not in the queue, an alpha male sires more young than any other individual male. More work is needed to compare the relative success of male strategies and to determine if males form queues for reproductive positions away from colonies.

Queues raise several questions about the evolution of behavior. Queueing involves risks: males may die before they reach the head of the queue. The long tenures of alpha male boat-tailed grackles suggest that most males never acquire a harem of females (see also McDonald 1989, 1993b; Herrera and Macdonald 1993). Consequently, a perplexing question is, why do individuals not jump the queue? The possibility that individuals are ordered by their fighting ability seems unlikely (Maynard Smith 1983; Wiley and Rabenold 1984; see above). The most plausible explanation is that queuing is a form of cooperation in which the benefits are asymmetrical in time (Wiley and Rabenold 1984; McDonald 1989). Individuals low in the queue cooperate by not contesting higher individuals, and their payoff for cooperating comes when they reach the head of the queue. In addition, the reduced fighting that results from the cooperation could increase males' chances of surviving long enough to reach the head. Grafen (1987) suggests that seniority is a more stable asymmetry for settling disputes than other conventions, such as ownership, because all individuals have a chance of receiving the benefit of a seniority-based settlement scheme. Queues that are maintained by dominance behavior thus present an intriguing combination of cooperative and competitive behavior. An individual that tries to jump several positions in the queue may have to contest all of the individuals it surpasses, not only the one whose position it acquires (Maynard Smith 1983). Furthermore, if some individuals jump the queue, then the benefits to others of continuing to cooperate by remaining in the queue are removed and queuing breaks down (Wiley and Rabenold 1984). Queuing has received little attention from behavioral ecologists although it is probably more common than currently perceived (Maynard Smith 1983). Perhaps once more studies have considered age-specific reproductive decisions, queues will be found in more species.

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