PATTERNS OF DOMINANCE AND AGGRESSIVE BEHAVIOR IN BLUE JAYS AT A FEEDER[1]

KEITH A. TARVIN[2] AND GLEN E. WOOLFENDEN

Department of Biology, University of South Florida, Tampa, FL 33620 and Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862

Abstract. We studied interactions among Blue Jays (*Cyanocitta cristata*) visiting a feeder in south-central Florida over a 4-year period to examine the influence of sex, time of year, and body size on dominance and aggression, describe changes in dominance among individuals over time, and test for the presence of linear dominance hierarchies. Males dominated females throughout the annual cycle, and in all 24 of the male–female significant dyads. We cannot reject the hypothesis that male dominance over females results from the larger body size of males. We infer that males also were more aggressive than females because they were involved in more interactions than expected by chance. Females became more, and males became less, aggressive immediately prior to the breeding season, but fluctuations in aggression did not lead to shifts in intersexual dominance. Dominance relationships among a few high-ranking males were intransitive and changed over time. Dominance hierarchies, characterized by reversals, circular triads, and unknown relationships, were not linear. Whereas linear hierarchies have been shown to exist in New World jays that live in small, stable social groups, we suspect the variable constituency and instability of flocks precludes the emergence of strictly linear hierarchies in the genus *Cyanocitta*.

Key words: aggression, Blue Jay, Cyanocitta cristata, *dominance hierarchies, New World jays, seasonality, sex-biased dominance.*

INTRODUCTION

Although the Blue Jay (*Cyanocitta cristata*) is a common and familiar eastern North American species, remarkably little is known about its basic ecology and social behavior, including dominance relations. Only Racine and Thompson (1983) have reported on dominance in Blue Jays, and although they found that rank order of jays visiting a feeder was constant over a period of a few weeks, they did not provide information on other features of dominance relationships in their study population. Here we report on Blue Jay dominance and aggression as it relates to sex, time of year, and body size, describe changes in dominance relationships among individuals over time, and test for the presence of linear dominance hierarchies. Analysis of the influence of site on dominance was outside the scope of our study.

The basic social unit of Blue Jays is the breeding pair. These pairs often share space with other pairs and individuals, and these pairs and individuals often coalesce into flocks to forage

or engage in social interactions (Hardy 1961). However, the flocks vary in membership and are spatially and temporally ephemeral (Cohen 1977). These social patterns hold for the non-migratory population in south-central Florida, which we have studied since 1990. Our present study of dominance and aggression at a feeder is relevant because members of different pairs often have the opportunity to interact and do so as they encounter each other on more or less "neutral" ground when foraging or harvesting acorns. Because Blue Jays do not defend or maintain exclusive territories, individuals encounter many other individuals from within and beyond the local neighborhood, and perhaps engage with them in competition for food, nest sites, etc. Thus, although attracting jays to an artificial food source to observe interactions may quantitatively enhance levels of aggression or frequency of interactions, it probably does not change the quality of the interactions because it mimics the social and spatial mileu within which Blue Jays normally exist.

For the congeneric Steller's Jay *Cyanocitta stelleri*, Brown (1963) reported dominance as site-dependent, rather than dependent on fixed social relationships (sex excluded). In contrast, many other New World jays live in small stable groups apparently organized around families.

Linear dominance hierarchies have been reported in three group-living jays for which dominance is related to sex, age, and breeding status of group members (Florida Scrub-Jay *Aphelocoma coerulescens,* Woolfenden and Fitzpatrick 1977, Mexican Jay *A. ultramarina,* Barkan et al. 1986, Pinyon Jay *Gymnorhinus cyanocephalus,* Marzluff and Balda 1992). However, an analysis of the degree of linearity of hierarchies has yet to be performed on *Cyanocitta* using recently proposed methods (Appleby 1983, deVries 1995). A color-marking program where numerous individual Blue Jays were sexed and measured provided the opportunity to examine correlates of dominance and aggression in a population of resident Blue Jays in south-central Florida, and to compare patterns of dominance in this species with those found in other New World jays.

METHODS

STUDY SITE

We studied dominance interactions among individually color-marked Blue Jays at a feeder at Archbold Biological Station, Highlands County, Florida (27°10′ N, 81°21′ W), from June 1991 through December 1994. The feeder was located in human-modified parkland with scattered large slash pines (*Pinus elliottii*), surrounded by native scrubby flatwoods and sand-pine scrub habitats (Abrahamson et al. 1984). We determined that adult Blue Jays at Archbold are year-round residents, and that birds in their first year tend to wander during autumn (unpubl. data). Virtually all the jays we observed at the feeder were banded, and unbanded immigrants that became regular visitors were captured and marked within a few days of their arrival. Although many jays marked at the feeder were not seen again, a core set of marked jays was seen in most months during each season of each year, and many of these core individuals were present for more than one year. Most observations were of these frequent visitors, and our use of significant dyads (see below) ensured that we did not unduly weight interactions of drifters and stragglers. The number of jays visiting the feeder during an observation session ranged from 1 to 5 in autumn to 10 to 20 in spring and summer.

We captured jays in a 4-cell Potter trap placed on the feeding platform by using a string to drop the door from a remote and essentially concealed position within a nearby house. By manually operating the trap, which was otherwise locked open when baited, we were able to catch focal jays, yet allow other jays to enter and leave the trap. Because we rarely attempted to capture jays (especially marked ones), jays rarely responded to the trap with apprehension. Furthermore, those jays that were captured usually fed again from the feeder within a day or so of their capture.

MORPHOLOGY AND SEX DETERMINATION

For most captured jays, we measured bill depth and width at the anterior margin of the nares, bill length from nares to tip, culmen, head length from occiput to tip of upper mandible, tarsus, primary 7, central rectrix, and mass. Feather measurements were estimated to the nearest mm; remaining linear measurements were to the nearest 0.1 mm. Mass was estimated to the nearest 0.1 g. Multiple measurements of the same individual taken after the jay had reached its second calendar year were averaged.

We determined sex of many Blue Jays by presence of a brood patch (females only), laparoscopy, or, in one case, by behavior at nests. Other jays were sexed using a logistic regression analysis. The logistic regression procedure correctly classified 88% of 124 Blue Jays of known sex, and calculated the probability that each bird of unknown sex was a female based on length of the head and central rectrix. The procedure made no classification errors within the 15% tails of the probability distribution when it was applied to the sample of Blue Jays of known sex. When the probability of being female was ≥ 0.85 or ≤ 0.15, we classified individuals of unknown sex as female or male, respectively. Individuals with intermediate probability scores were categorized as unknown sex. Twelve males and one female were sexed using this procedure. We were unable to assign sex to 13 jays.

ASSESSMENT OF DOMINANCE

From within the house we observed Blue Jays as they interacted at the feeding platform placed about 15 m in front of a window. A Potter trap centered on the platform and locked open contained about 30 g of commercial bird seed or a slice of bread that could be obtained by only a few jays simultaneously. Blue Jays quickly learned to associate the presence of food with a characteristic whistle that we emitted as we bait-

ed the feeder, and food (and concomitant observations of interactions) usually lasted no longer than 15 min. Limited access to a small amount of food and the whistle alerting jays to its presence combined to concentrate jay activity within a short time span, and thus promoted agonistic interactions used to assess dominance.

Observation periods usually were conducted 1–3 times per day, typically in the early morning and around noon. Observation periods were initiated on most days during the study period, except when we were away. During August through November, the responsiveness of jays to the whistle and to food provided by us sharply declined as a result of the jays' attention to harvesting and eating acorns. During that period, we usually did not attempt to initiate new observation periods if food remained on the feeder from a previous observation period. However, we were attentive to the activities of the jays in the area, and when we saw them around, we attempted to entice them to the feeder with the whistle and new food. Thus, our effort toward observing interactions was generally constant throughout the year, although it was modified somewhat during the acorn season in accordance with the responsiveness of the jays. Because we observed no aggressive interactions of jays at the feeder during September and October, those months were deleted from our analysis of seasonal patterns in aggression.

We considered a dominance interaction to have occurred when one jay either supplanted another that was feeding or standing on the feeding platform, or successfully resisted a supplantation "attempt" from another jay. In the first case, the supplanter was considered the winner of the interaction; in the second case, the resistor was the winner. During rare extended interactions, distinct supplantations were considered independent. We made no attempt to assess the intensity of interactions, and the rare interactions with ambiguous outcomes or apparently reflecting tolerance among individuals were not considered in our analyses. Because our view of the area surrounding the feeding platform was restricted by the window frame, we did not record the presence of individuals that perched near the feeder but did not visit it. We included in our analyses only interactions that occurred between jays that had reached or surpassed their second calendar year of age (AHY; ages were inferred from the color of the greater upper primary coverts and presence or absence of bars on the greater upper secondary coverts following Dater [1970] and Bancroft and Woolfenden [1982]).We considered one bird dominant over another only when the win:loss ratio within the dyad (the summary of interactions between members of a pair) differed significantly from random as determined with a two-tailed binomial test. A binomial probability ≤ 0.05 reflected a significant dominance relationship (henceforth "significant dyads;" see Barkan et al. 1986).

INFLUENCE OF SEX ON DOMINANCE AND AGGRESSION

To test the influence of sex on dominance, we considered only significant intersexual dyads, and used the two-tailed binomial test to determine whether the proportion of those dyads dominated by jays of one sex differed from that expected by chance. To determine how the propensity to interact differed between males and females, we calculated for each year the probability that a given interaction would involve either a male or a female, considering that each interaction involved two participants, and considering the mean number of males and females present during months for which interactions were recorded. We calculated the total number of observed participations (= 2 times the total number of interactions) and tallied the number of times members of a given sex participated in interactions, regardless of the sex of the birds with whom they interacted or whether jays of the focal sex won or lost. We used the two-tailed binomial test to determine whether the observed proportion of sex-specific participations differed from that expected by chance. We likewise examined the propensity of each sex to be involved in significant dyads. Our method of calculating expected frequencies of sex-specific interactions would be improved by considering the mean number of males and females present during each observation period. However, because we recorded number of individuals visiting the feeder during each month, rather than during each observation period, we are unable to generate more precise expected values.

We determined how the propensity of males and females to interact varied throughout the annual cycle by comparing the monthly distribution of sex-specific participations with that of total interactions, each summed over all 4 years.

We used a χ^2 goodness-of-fit test to determine whether the distributions of sex-specific participations matched that of total interactions.

We tested whether birds of a given sex were more likely to be involved in significant dyads with birds of the same or opposite sex. When a female is involved in a significant dyad, the probability of her being in a dyad with a male is

$$(N_{males})/[(N_{males}) + (N_{females} - 1)]$$

where N_{males} is the total number of males that may potentially interact, and $(N_{females} - 1)$ is the total number of females that may interact minus 1, because the focal female cannot interact with herself. The two-tailed binomial test was used to assess whether the proportion of female–male dyads was greater or lesser than expected by chance. We used the same procedure to determine whether the proportion of male–male dyads was greater or lesser than expected by chance.

INFLUENCE OF SIZE ON DOMINANCE

Within a sex, body size may influence dominance relationships (e.g., Searcy 1979). We used the Wilcoxon matched-pairs signed-ranks test to examine the influence of body mass and tarsus length, features commonly used as indices of relative body size within bird populations (Freeman and Jackson 1990), on the outcome of male–male significant dyads. Male Blue Jays are slightly, but significantly, larger than females at Archbold (unpubl. data), and therefore dominance of males over females, or vice versa, could be an effect of size. If size *per se* is an important influence of intersexual dyadic outcome, then it should similarly influence the outcome of intrasexual dyads. However, the conclusion that size of a given character is not an important influence of dominance within intersexual dyads is valid only if it is unimportant for intrasexual dyads in which the size differential between members is at least as great as the mean size differential between members of male–female dyads. Therefore, we tested for effects of body mass, tarsus length, head length, and length of the central rectrix (the latter two characters were most useful in distinguishing males and females using logistic regression analysis) on dominance in male–male dyads when the size differential for selected characters was equal to or greater than the mean size differential observed in male–female dyads.

DOMINANCE HIERARCHIES

We analyzed annual dominance matrices composed of jays that were involved in at least one significant dyad. This criterion served to cull from the matrix transients and other individuals that interacted only rarely, thereby reducing the number of uninformative unknown relationships (i.e., empty cells) within the matrix and increasing the likelihood that we detected linearity if it existed. Within dominance matrices, we considered one bird to dominate another only when the dyad was significant (Barkan et al. 1986). We followed deVries' (1995) procedure and evaluated linearity of hierarchies within each year by calculating d, the number of circular triads within a dominance matrix, and h, Landau's (1951) index of linearity, as described by Appleby (1983). Appleby's d and h were then transformed as described by deVries (1995) to derive the unbiased estimates d' and h', respectively. The parameters d' and h' are preferred over d and h because Appleby's technique is overly conservative when matrices contain unknown relationships (deVries 1995). The exact significance of d' (i.e., the significance of linearity) is generally determined via randomization tests. However, based on a series of randomization tests, deVries (1995) concluded that when the probability of Appleby's d is less than 0.01, the P-value associated with deVries' d' is less than 0.05, and the hierarchy is significantly linear at $\alpha = 0.05$. Likewise, if the probability of Appleby's d is greater than 0.15, deVries' d' is greater than 0.05 and the hierarchy is not significantly linear.

RESULTS

From 1991 through 1994, 48 Blue Jays were involved in 1,263 interactions. Over the 4-year period, 27 individuals were involved in at least one of 63 significant dyads. Of these 27 jays, 11 were males, 8 were females, and 8 were of unknown sex.

INFLUENCE OF SEX ON DOMINANCE AND AGGRESSION

Table 1 presents significant dyads grouped by sex of dominant and subordinate. Males consistently dominated females. Of 316 interactions involving both a male and a female, fewer than

TABLE 1. Blue Jay dominance interactions and significant dyads tallied over 4 years, grouped by sex of both members.

Direction of dominance	Total interactions	Significant dyads[a]	Number of individuals involved in significant dyads[b]		
			Dominant individuals	Subordinate individuals	Total individuals[c]
Male over male	493	14	5	10	11
Male over female	313	24	7	8	15
Female over female	99	4	2	3	4
Female over male	3	0	0	0	0

[a] Number of significant dyads tallied over all 4 years does not correspond with analyses presented elsewhere for which dyads are tallied within single years.
[b] 17 males and 15 females were observed in dominance interactions, but only 11 males and 8 females were involved in the 42 significant dyads for which sex of both members was known.
[c] Total individuals may be less than the sum of dominant and subordinate individuals because an individual may be dominant to some birds, while subordinate to others.

1% were won by the female, and the male was dominant in all significant intersexual dyads (two-tailed binomial test, $n = 24$, $P < 0.001$).

Males exhibited a greater propensity to interact than females. When controlling for the number of males and females present, males were involved in far more, and females in far fewer, interactions than expected by chance in each of the four years (Table 2). However, the pattern held in only two years when considered at the level of the significant dyad (Table 3). In 1992, the observed proportion of female–female versus female–male significant dyads was unexpected by chance, with females more likely to be involved in dyads with males than with other females (two-tailed binomial test, $n = 4$ female–female and 16 female–male dyads, $P = 0.02$). Sample sizes were insufficient for this test in other years. Males were involved in significant dyads with other males more often than expected by chance in one of three years for which sample sizes were sufficient (two-tailed binomial test: 1992, $n = 8$ male–male and 16 male–female dyads, $P = 0.31$; 1993, $n = 6$ male–male and 0 male–female dyads, $P = 0.04$; 1994, $n =$ 7 male–male and 5 male–female dyads, $P = 1.00$).

Dominance interactions were not distributed evenly throughout the year, and the propensity of either sex to interact throughout the annual cycle could not be predicted from the distribution of total interactions (Fig. 1). Males interacted more frequently than expected during May and June, and slightly less frequently from December through March (Fig. 1a). Females interacted more frequently than expected in March and less frequently in April, May, and July (Fig. 1b). Feeder visits, and therefore interactions, by females were especially uncommon during April and May when they were incubating and brooding. To account for the absence of females during the breeding season, we removed April and May interactions from the data set. Males still interacted significantly more frequently in summer and less frequently in winter and spring. The pattern for females was reversed (Fig. 1c and d).

INFLUENCE OF SIZE ON DOMINANCE

Neither body mass, tarsus length, head length, nor length of central rectrices significantly influ-

TABLE 2. Propensity of male and female Blue Jays to participate in dominance interactions.

Year	$\bar{x}$ number of individuals present per month[a]		Expected proportion of participations[b]		Number of actual participations[c]		z[d]	P[d]
	Male	Female	Male	Female	Male	Female		
1991	6.5	8.3	0.44	0.56	140	84	5.51	<0.001
1992	5.2	5.4	0.49	0.51	467	343	4.89	<0.001
1993	6.8	4.6	0.59	0.41	255	33	10.13	<0.001
1994	5.7	3.4	0.62	0.38	440	54	12.35	<0.001

[a] Based on months during which interactions were recorded.
[b] Calculated under the null hypothesis that each sex shares an equal propensity to participate.
[c] Regardless of wins or losses.
[d] Two-tailed binomial test. The normal approximation, corrected for continuity, was used because sample sizes were >25 (Siegel 1956).

TABLE 3. Propensity of male and female Blue Jays to be involved in significant dyads.

Year	Probability male is involved in dyad when sex of both members is known[a]	Number of dyads for which sex of both members is known (number of positions)[b]	Observed number of positions occupied by males	P[c]
1991	0.44	3 (6)	6	0.01
1992	0.49	28 (56)	32	0.28[d]
1993	0.59	6 (12)	12	<0.01
1994	0.62	12 (24)	19	0.09

[a] Based on ratio of mean number of males and females present at the feeder per month. See Table 2.
[b] Each dyad is composed of two positions (i.e., a dominant and a subordinate or 2 jays of equal status).
[c] Two-tailed binomial test.
[d] $z = 1.09$.

enced dominance within male–male dyads (Table 4). For body mass and head length, size differentials were as great or greater than the mean size difference of intrasexual dyads in only two male–male dyads. In these cases, the dominant had the larger feature in one dyad and the smaller feature in the other. No male–male dyads existed in which the tail length differential was as great as the mean differential among male–female dyads. The difference in tarsus length between members of nine male–male dyads was as great or greater than the mean difference in tarsus length calculated from male–female dyads. The male with the longer tarsus was dominant in six of those nine dyads (Wilcoxon matched-pairs signed-ranks test: $z = -1.16$, $P = 0.25$).

DOMINANCE HIERARCHIES

Dominance hierarchies (Table 5) among the Blue Jays we studied were characterized by reversals (a subordinate wins an interaction against a typically dominant individual; Brown 1975), circular triads (e.g., A is dominant to B, B is dominant to C, yet C is dominant to A; Appleby 1983), and unknown relationships (lack of a clear dominance relationship between individuals arising from a lack, or insufficient number, of observed interactions between them; deVries 1995). Consequently, none of the hierarchies we constructed was linear (Table 6). Throughout our study, four or five males seemed to be of substantially higher rank than the remaining jays, but dominance relationships
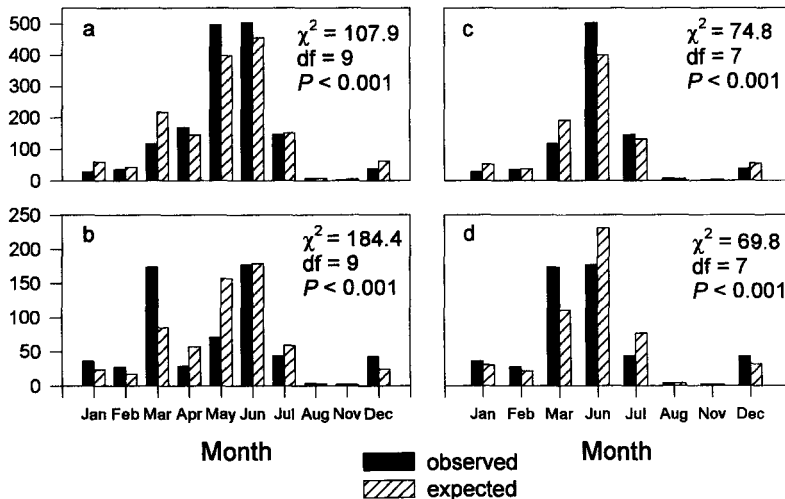

FIGURE 1. Distribution of interactions of male and female Blue Jays throughout the annual cycle (a and b). In (c) and (d), data from the major portion of the breeding season (April and May) are deleted. Male interactions are represented in graphs a and c; females in graphs b and d. Note the difference in the scale of the Y axis for males and females. We never observed interactions in the months of September or October; consequently those months were not considered when calculating goodness-of-fit tests.

TABLE 4. Relative size of selected characters of dominant and subordinate members of significant male-male dyads.

Character	Mean (SD)		n	z^a	P^a
	Dominant	Subordinate			
Body mass[b]	74.5 (1.0)	74.3 (5.2)	12	−0.24	ns
Tarsus[c]	35.1 (0.5)	34.6 (1.3)	12	−1.10	ns
Head length[c]	56.7 (0.5)	56.3 (1.0)	12	−0.94	ns
Tail length[d]	122.3 (3.4)	120.5 (3.2)	11	−1.16	ns

[a] Wilcoxon matched-pairs signed-ranks test.
[b] Measured to nearest 0.1 g.
[c] Measured to nearest 0.1 mm.
[d] Measured to nearest 1.0 mm.

among these high-ranking males changed through time (Table 7).

DISCUSSION

Although our study design encouraged jays to interact within a restricted space for a brief period, the social context within which the observed interactions occurred probably mirrors that of other encounters among the marked jays at our study site. The fundamental social unit of the Blue Jay is the breeding pair, yet a pair shares most of its home range with other jays (Hardy 1961, Cox 1984). Therefore, most Blue Jays when foraging or harvesting acorns potentially encounter all the other individuals residing within the neighborhood, as well as transients. Although the particular site at which observations are recorded may influence the order of the hierarchy obtained (Brown 1963), it should not affect the influence of sex or season on dominance or aggression, nor the degree to which hierarchies approach linearity within a single year.

The most conspicuous pattern in our study was the unwavering dominance of males over females. Such a pattern is consistent with those found in other studies of New World jays (Brown 1963, Woolfenden and Fitzpatrick 1977, Barkan et al. 1986, Marzluff and Balda 1992), as well as many other passerine species (e.g., Ketterson 1979, Piper and Wiley 1989; but see Samson 1977, and Belthoff and Gauthreaux 1991 for converse patterns in the genus *Carpodacus*). Contrary to reports from a few studies (Smith 1980 and references therein), dominance relationships between male and female Blue

TABLE 5. Blue Jay dominance matrix from 1992[a]. Hierarchy constructed following Brown (1975), except only birds involved in at least one significant dyad were included. Wins are in rows, losses in columns. Numerals above each column correspond with those adjacent each individual jay in the far left column. Sex of individuals identified at the top of each column: m = male, f = female, u = unknown sex.

	Jay	m 1	m 2	m 3	m 4	u 5	m 6	f 7	u 8	f 9	u 10	f 11	f 12	u 13	f 14	f 15	u 16
1	P-PS		14[b]	21	44	5	6	6	14	5	2	2	12	4	5	13	3
2	P-BS	—		9	1	2	5	2	5	14	—	1	7	2	10	1	—
3	G-RS	—	—		12	1	1	2	6	4	2	3	8	—	2	1	4
4	G-GS	—	16	2		9	—	9	11	14	2	5	23	5	19	—	2
5	G-OS	—	6	—	—		1	2	1	2	—	4	4	—	2	—	—
6	P-GS	—	—	2	—	1		2	1	6	—	—	5	2	3	3	10
7	R-YS	—	—	—	—	—	—		4	14	1	1	23	3	2	1	—
8	O-PS	—	—	—	—	—	—	—		13	1	—	6	—	4	—	—
9	L-BS	—	—	—	—	—	—	—	—		6	9	16	—	3	—	—
10	R-GS	—	—	—	—	—	—	—	3	—		1	1	—	—	—	—
11	BB-S	—	—	—	—	—	—	—	—	1	—		—	—	1	—	—
12	GG-S	—	—	—	—	—	—	—	1	—	—	—		—	1	—	—
13	P-AS	—	—	—	—	—	—	—	—	—	—	—	—		1	—	—
14	O-WS	—	—	—	—	—	—	—	—	—	—	—	1	—		—	—
15	-RGS	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—
16	GAS-	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

[a] Dominance matrices from other years of the study are available from the authors.
[b] Boldface values indicate number of wins within significant dyads.

TABLE 6. Characteristics of dominance hierarchies among Blue Jays visiting a feeding station at Archbold Biological Station, 1991–1994. One bird was considered dominant over another only when the win:loss ratio within the dyad differed significantly from random. Hierarchies were constructed using only birds involved in at least one significant dyad.

Year	Total number of interacting birds	Number of birds involved in significant dyads	Number of significant dyads	Linearity statistics		
				d'^b	h'^c	P^d
1991	29	5[a]	4	—	—	—
1992	25	16	38	114.9	0.325	ns
1993	23	10	14	24.5	0.406	ns
1994	15	9	13	17.1	0.434	ns

[a] Linearity statistics for the 1991 matrix are omitted because a hierarchy containing fewer than six individuals cannot be shown to be significantly linear (Appleby 1983).
[b] d' is an unbiased estimate representing the number of circular triads present within a dominance matrix, and it is significant when fewer circular triads occur than expected by chance based on the number of individuals in the dominance matrix. A dominance hierarchy cannot be linear when d is not significant (Appleby 1983). $d' = d - 0.25u$, where d is the number of circular triads derived via Appleby's (1983) method, and u is the number of unknown relationships in the dominance matrix (deVries 1995).
[c] h' is an unbiased index of linearity that ranges from 0 to 1, with 1 indicating perfect linearity. $h' = h + (6/[N^3 - N])u$, where h = Landau's index of linearity (Landau 1951, Appleby 1983), N is the number of individuals in the dominance matrix, and u is the number of unknown relationships in the matrix (deVries 1995).
[d] P-values derived for Appleby's d were > 0.15 for each dominance matrix. When P values derived for d are greater than 0.15, d' is not significant at $\alpha = 0.05$ (deVries 1995).

Jays did not shift during the breeding season. Because our data included few examples of male–male dyads exhibiting size differentials equal to or greater than the average differential within intersexual dyads, we cannot reject the hypothesis that male dominance over females is an effect of body size. However, male and female Blue Jays in our study population differ by less than 5% for the several characters we measured, and such slight sexual dimorphism is generally not considered to be an important influence on dominance (Smith 1976).

In addition to being dominant, male Blue Jays were more aggressive than females (see Wool-

fenden and Fitzpatrick 1977, Barkan et al. 1986, Marzluff and Balda 1992, for similar patterns in other New World jay species), as indexed by the relatively high propensity of males to interact overall, and by the low frequency of observed female–female interactions and significant dyads. Interestingly, even during the period of high female and low male aggression shortly before the breeding season, females were consistently subordinate to males. The overall rarity of female–female interactions, and the fact that females seem more likely to interact with males than with other females, suggests males may initiate interactions as is the case in Florida Scrub-

TABLE 7. Stability of relationships among 5 high-ranking male Blue Jays present in at least 3 of the 4 years of the study. Arrows indicate a significant direction of dominance unless otherwise noted. "—" denotes neither bird won more than 3 interactions. "≈" denotes at least 8 interactions were observed, but the win:loss ratio was not significant. "A" denotes Bird B not observed in interactions in that year.

Jay A	Jay B	Year				Overall relationship	Stability of relationship through time[a]	Number of possible interyear comparisons	Changes observed
		91	92	93	94				
G-GS	G-RS	—	<	—	<	<	NC	1	0
	P-PS	>	<	>	>	≈	C	3	2
	P-GS	—	—	>	A	>	NC	0	—
	P-BS	—	>	≈	A	>	C?	1	1?
G-RS	P-PS	—	<	>	>	≈	C	2	1
	P-GS	—	—	>[b]	A	≈	?	0	—
	P-BS	—	<	<	A	<	NC	1	0
P-PS	P-GS	—	>	—	A	>	NC	0	—
	P-BS	—	>	<[b]	A	>	C	0	—
P-GS	P-BS	—	<	—	A	≈	?	0	—
Totals:								8	4

[a] NC = no change; C = change; ? = evaluation of change equivocal.
[b] $P < 0.063$, therefore not included in the summary of possible interyear comparisons and changes observed.

Jays (Woolfenden and Fitzpatrick 1977) and Mexican Jays (Barkan et al. 1986).

We suspect the decrease in male, and the concomitant increase in female, aggression prior to the breeding season is a function of the nesting phenology and consequent energy demands of the jays, as suggested by Smith (1980). Most Blue Jays at Archbold are nesting by early April, and offspring from first nests fledge by early to middle May. However, as nesting success is relatively low and replacement nests consequently are common, many jays continue to nest through May and June (pers. oberv.). Heightened aggression of females at food sources in March may reflect their attempts to obtain the extra calories and nutrients needed to produce eggs. Similarly, heightened male aggression in May and June may reflect the energy demands of nestlings, which are fed by males until about a week before fledging. However, we did not directly test these ideas.

Although sex strongly influenced the outcome of intersexual interactions among Blue Jays visiting our feeder, factors influencing dominance relationships among males are complex. Body size, or some correlate of body size, may influence the outcome of interactions to some degree, but body size alone cannot fully explain the relationships we observed. This is best evidenced by the intransitivity of dominance among males over time, a pattern that precluded a strictly linear relationship between size and rank. The importance of the relationship of body size to dominance varies among bird species, and is probably strongly influenced by other features of the biology of those species such as mating system and social organization. Other factors not measured by us probably are better predictors of Blue Jay intrasexual dominance than is size. Such factors may include location of nests (Brown 1963, Wechsler 1988), familiarity with the study site (Glase 1973, Dhindsa et al. 1989), health (Weatherhead et al. 1995), variation in plumage signals (Holberton et al. 1989), age (Woolfenden and Fitzpatrick 1977), and degree of relatedness of participants. Unfortunately, most of the high ranking males in our study were banded as unknown age birds in 1990; consequently, we do not know whether age or site-familiarity differences existed among them. Likewise, we knew where few individuals nested, and were thus unable to examine effects of nest proximity on dominance. Brown (1963)

found that shifts in dominance of male Steller's Jays at particular sites corresponded with relocation of nest sites during renesting attempts. The significant changes in dominance over time among high-ranking male Blue Jays in our study may have reflected similar shifts in nest sites in different years.

The social ranks of Blue Jays visiting our feeder were not organized linearly. In a species with a social organization characterized by ephemeral flocks of varying constituency (Hardy 1961), such as the Blue Jays at Archbold, the numerous circular triads, reversals, and shifts in dyadic dominance of high-ranking males over time would be expected (Brown 1975). This conclusion is supported by the findings of Racine and Thompson (1983), who reported the rank order within a flock of wintering Blue Jays visiting an *ad libitum* feeder in Massachusetts was relatively stable over short (several weeks), but not long (several months), periods of time. Racine and Thompson (1983) also found both reversals and circular triads, a pattern consistent with our observations. Our criterion that dominance is ascribed only when the outcome of dyads is significant may be considered overly conservative. However, had we simply considered an uneven win:loss ratio as indicating dominance, we would have been forced to include far more individuals in our matrices than just those involved in at least one significant dyad. The result would have been far more unknown relationships in the matrices, and consequently, even lower degrees of linearity than were observed.

The dominance matrices compiled by Brown (1963) for the congeneric Steller's Jay are strikingly similar to those we compiled for Blue Jays, in that they include reversals, circular triads, and many unknown relationships. Brown (1963) ascribed inconsistencies within dominance matrices to first encounters, mistaken identities, and true changes in dominance among individuals, and we agree that such occurrences probably are common in species that do not live in stable groups. Neither Brown (1963) nor Racine and Thompson (1983) explicitly tested whether the dominance hierarchies they observed were linear. Although Racine and Thompson (1983) did not provide actual dominance matrices, we analyzed those in Brown (1963) using the same technique we employed for Blue Jays. The three matrices in Brown (1963) that contained more

than 5 individuals did not exhibit significant linearity (Brown's Table 1: $n = 22$ jays, $d' = 371.8$, $h' = 0.160$, $P > 0.05$; Table 5: $n = 21$, $d' = 330.8$, $h' = 0.141$, $P > 0.05$; Table 6: $n = 21$, $d' = 315.1$, $h' = 0.182$, $P > 0.05$).

In contrast to the unstable flocks of *Cyanocitta*, linear dominance hierarchies occur in stable groups of Florida Scrub-Jays (Woolfenden and Fitzpatrick 1977) and Mexican Jays (Barkan et al. 1986). Analysis of dominance hierarchies has been published for only one other New World jay, the Pinyon Jay (Marzluff and Balda 1992), a species that lives in relatively stable, but huge groups (> 50 individuals). Using Appleby's method, Marzluff and Balda (1992) found that a dominance hierarchy involving 14 of the highest ranking males in the flock was significantly linear. However, they did not employ significant dyads as indicators of dominance. When we reanalyzed their dominance matrix (Marzluff and Balda 1992, Table 10) using the more conservative significant dyad criterion and deVries' method to account for unknown relationships, we found no significant linearity ($n = 14$ jays, $d' = 81$, $h' = 0.29$, $P > 0.05$). Based on the available analyses, linear dominance hierarchies appear more likely to arise in New World jays when group membership is stable and group size is relatively small. Together, these group characteristics provide a milieu within which dyadic relationships may solidify over time (Brown 1975).

ACKNOWLEDGMENTS

LITERATURE CITED

ABRAHAMSON, W. G., A. F. JOHNSON, J. N. LAYNE, AND P. A. PERONI. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Fla. Sci. 47:209–250.

APPLEBY, M. C. 1983. The probability of linearity in hierarchies. Anim. Behav. 31:600–608.

BANCROFT, G. T., AND G. E. WOOLFENDEN. 1982. The molt of Scrub Jays and Blue Jays in Florida. Ornithol. Monogr. 29:1–51.

BARKAN, C. P. L., J. L. CRAIG, S. D. STRAHL, A. M. STEWART, AND J. L. BROWN. 1986. Social dominance in communal Mexican Jays *Aphelocoma ultramarina*. Anim. Behav. 34:175–187.

BELTHOFF, J. R., AND S. A. GAUTHREAUX, JR. 1991. Aggression and dominance in House Finches. Condor 93:1010–1013.

BROWN, J. L. 1963. Aggressiveness, dominance and social organization in the Steller Jay. Condor 65:460–484.

BROWN, J. L. 1975. The evolution of behavior. W. W. Norton, New York.

COHEN, S. M. 1977. Blue Jay vocal behavior. Ph.D. diss., Univ. Michigan, Ann Arbor, MI.

COX, J. A. 1984. Distribution, habitat, and social organization of the Florida Scrub Jay, with a discussion of the evolution of cooperative breeding in New World jays. Ph.D. diss., Univ. Florida, Gainesville, FL.

DATER, E. 1970. Dorsal wing coverts of Blue Jay (*Cyanocitta cristata*): guide to age. EBBA News 33:125–127.

DEVRIES, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50:1375–1389.

DHINDSA, M. S., P. E. KOMERS, AND D. A. BOAG. 1989. The effect of familiarity with an environment on the dominance relationships between juvenile and adult Black-billed Magpies. Ornis Scand. 20:187–192.

FREEMAN, S., AND W. M. JACKSON. 1990. Univariate metrics are not adequate to measure avian body size. Auk 107:69–74.

GLASE, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. Living Bird 12:235–267.

HARDY, J. W. 1961. Studies in behavior and phylogeny of certain New World jays (Garrulinae). Univ. Kans. Sci. Bull. 42:13–149.

HOLBERTON, R. L., K. P. ABLE, AND J. C. WINGFIELD. 1989. Status signalling in Dark-eyed Juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. Anim. Behav. 37:681–689.

KETTERSON, E. D. 1979. Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. Wilson Bull. 91:371–383.

LANDAU, H. G. 1951. On dominance relations and the structure of animal societies. I: effect of inherent characteristics. Bull. Math. Biophys. 13:1–19.

MARZLUFF, J. M., AND R. P. BALDA. 1992. The Pinyon Jay: behavioral ecology of a colonial and cooperative corvid. T. & A. D. Poyser, London.

PIPER, W. H., AND R. H. WILEY. 1989. Correlates of dominance in wintering White-throated Sparrows: age, sex and location. Anim. Behav. 37:298–310.

RACINE, R. N., AND N. S. THOMPSON. 1983. Social organization of wintering Blue Jays. Behaviour 87:237–255.

SAMSON, F. B. 1977. Social dominance in winter flocks of Cassin's Finch. Wilson Bull. 89:57–66.

SEARCY, W. A. 1979. Morphological correlates of dominance in captive male Red-winged Blackbirds. Condor. 81:417–420.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

SMITH, S. M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. Auk 93:95–107.

SMITH, S. M. 1980. Henpecked males: the general pattern in monogamy? J. Field Ornithol. 51:55–64.

WEATHERHEAD, P. J., K. J. METZ, D. SHUTLER, K. E. MUMA, AND G. F. BENNETT. 1995. Blood parasites and dominance in captive blackbirds. J. Avian Biol. 26:121–123.

WECHSLER, B. 1988. Dominance relationships in Jackdaws (Corvus monedula). Behaviour 106:252–264.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1977. Dominance in the Florida Scrub Jay. Condor 79:1–12.