

AGGRESSIVENESS, DOMINANCE AND SOCIAL ORGANIZATION IN THE STELLER JAY

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Aggressiveness and submissiveness are of primary importance in the motivation of behavior and as formative forces in avian social organization. In another paper (Brown, MS) their behavioral expression in the Steller Jay (*Cyanocitta stelleri*) is examined. In this paper their manifestations in the organization of a society of the Steller Jay are considered.

The evolutionary consequences of aggressiveness in birds are mediated through the ecological and physiological effects of aggressive and submissive behavior in natural populations. Despite this, the studies of aggressiveness as expressed in dominance hierarchies and similar types of social relationships in captive birds far outnumber the few studies of wild birds. Since the forms of social organization taken by a number of individuals of an avian species in captivity so often differ from those in the wild, studies in the wild state are basic to the understanding of social organization. The present study contributes to the relatively meager information on dominance hierarchies in wild populations of birds.

The social structure of the Steller Jay and other species, such as tits, in which dominance hierarchies in nature have been demonstrated, is excellently suited for observation of the causes and consequences of changes in aggressiveness in wild birds. Because of the regular presence of many individuals at particular loci and the possibility of determining their social rank, a sensitive index (rank) is available for the detection of slight changes in aggressiveness in a relatively large number of individuals and for the correlation of these with features of the environment and histories of individuals.

METHODS

The observations reported here were made in Indian Camp, Tilden Regional Park, Alameda County, California. The center of the 63.3 acre area was a picnic ground containing about 25 permanent picnic tables arranged in a rough linear sequence along both sides of a road for a distance of approximately 700 feet. This situation possessed several advantages not often found in populations of the Steller Jay. The birds were quite tame, allowing close observation and easy trapping. By contrast, in unpopulated areas Steller Jays can be so wild as to be virtually unobservable. Many birds in the study area had already acquired the habit of foraging on picnic tables; consequently, it became a simple matter to bait them to particular tables for observation. The area was relatively open, allowing birds from neighboring territories to observe when bait was available and to come to it with little delay. Furthermore, the breeding population was of sufficient density (19 pairs per 100 acres) to allow particular tables to be within the usual foraging range of several pairs.

One hundred and fourteen Steller Jays were color-banded for individual recognition in this area over a three-year period, but only about 30 of these were present in the area long enough to yield useful information. A few unbanded birds were encountered from time to time but the regular inhabitants of the area were almost all color-banded and the remaining individuals could often be identified by other means.

Sunflower seeds were found to be an efficient bait for Steller Jays in most seasons. Observations of dominance were made by placing a pile of sunflower seeds on a picnic table and then retiring to a distance at which notes could be taken without danger of inhibiting the activities of the birds at the table. Steller Jays did not come to the seeds

only to eat them immediately but at all seasons actively stored them. In fact it seemed that the vast majority of seeds taken were stored in the ground rather than eaten directly.

Since encounters in some months occurred rapidly, a tape recorder was sometimes used to record observations of encounters. In taking notes by hand it was usually necessary to concentrate on pairs of birds for which records on relationships were lacking.

DOMINANCE CRITERIA AND BEHAVIOR DURING ENCOUNTERS

The criteria used by different workers in judging dominance in various species have differed remarkably in some cases, ranging from simple avoidance to victory in an actual fight. Some of the criteria used by other workers would be quite misleading in the present situation. Before criteria of dominance are considered, it is necessary to understand some of the variables in an encounter between individuals.

A typical pattern most of the year for a dominant male jay taking seed from a table within his area of dominance was to fly directly to the table, often supplanting other birds if they were present, fill his mouth and bill with seeds, fly to an area used for storage, and store his seeds. He would usually not bother to chase other birds out of the area but merely supplanted them when they were in his way or too close. He sometimes fought with them, however, if they showed resistance. Occasionally he chased certain individuals away, although such chases were generally unpredictable.

A subordinate bird from another area typically flew to a tree near the table, watched until there were few or no dominant birds present, flew to the seeds, filled his mouth and bill, and returned to store the seeds in his own area of dominance. Sometimes, however, subordinates were not so cautious and would wait on the table a few feet away for the dominant to leave. When the dominant left, two or more subordinates might rush to the seeds and one supplant the other. It was common for two or more low-ranking individuals or mated pairs to take seeds from opposite sides of the same pile simultaneously without exhibiting aggressiveness. High-ranking birds rarely tolerated each other at such distances (about six inches).

Theoretically an individual, A, was judged dominant over another, B, in an aggressive encounter if B departed because of the approach and behavior of A. In practice, however, the observer could not always be sure whether B left because of A's behavior or for some other reason. For example, the appearance of a subordinate waiting for a dominant to leave, then quickly flying to the seeds had some resemblance to a supplanting encounter. It was even more confusing when a subordinate arrived in a threatening manner, giving indications that he would fight, just when a known dominant was leaving or about to leave of its own accord. The dominant bird if not ready to leave would fiercely attack and drive away a subordinate behaving in such a way, but when leaving to store his seeds he might simply fly away, giving a superficial appearance of being supplanted.

Another situation difficult to judge occurred with a bird which acted "nervous" upon arrival. If at that time another bird abruptly landed close behind, the first bird would leap up in the air and fly for cover regardless of whether the bird landing behind him were dominant or subordinate to him. Consequently, the bird which flew appeared to have been supplanted by the bird which landed; however, such uncertain cases were not utilized in this study if recognized. If the arriving bird was subordinate, the nervous bird usually returned and supplanted it.

Such ambiguities could be largely avoided by considering in addition to the arrival and departure of individuals their behavioral indications of perception of each other

and of subsequent predisposition to attack or escape. For example, if bird A flew or ran directly at B and especially if A gave an aggressive call, it was likely that A would have fought B if B did not leave. And if B had recently arrived or was apparently not preparing to leave for other reasons, and appeared by his posture and orientation to perceive the approach of A, then the probability was high that A's behavior was the primary cause of B's departure. Under these conditions A would be judged to have supplanted B.

SOCIAL RANK AND DISTANCE FROM NEST AREA

Aggregations of Steller Jays at any point in the study area exhibited dominance relationships which could be summarized in the form of hierarchies. Table 1 shows one such hierarchy; it is a summary of 637 encounters between banded jays at picnic table 7 from November of 1959, through March of 1960.

TABLE 1
AGGRESSIVE ENCOUNTERS IN WINTER AT PICNIC TABLE 7*

Winners	Losers																			Total				
	X-YY	VR-RR	XY-OO	YRY-X	O-RXR	VO-MVX	OOO-XRO	RXR-OR	XW-WW	XMY-YMY	OY-YX	MO-MXV	XW-YGY	MVM-VXM	RV-VRX	RY-YRX	XMR-RMY	RX-OGO	XY-YYY		XWW-RGW	XYW-YM	XOV-VY	
♂ X-YY		3	22	10	10	—	2	—	—	3	4	7	1	11	4	—	3	4	—	—	—	—	—	84
♂ VR-RR	1		10	8	4	2	1	1	5	3	4	3	—	2	1	2	2	2	—	1	4	—	—	56
♂ XY-OO	—	—		15	14	3	7	4	8	7	13	8	—	12	6	—	12	1	—	—	—	4	—	114
♂ YRY-X	—	—	—		7	6	4	2	3	3	7	9	—	7	2	—	4	2	—	—	—	1	—	57
♂ O-RXR	—	—	—	—		1	3	1	9	6	6	4	—	—	1	—	6	2	—	—	—	2	—	41
♂ VO-MVX	—	—	—	1	1		3	—	—	—	—	—	—	2	—	1	1	—	—	—	—	5	—	14
♂ OOO-XRO	—	—	—	—	—	—	—	—	4	—	3	1	—	6	—	2	—	1	1	1	—	—	—	19
♂ RXR-OR	—	—	—	1	1	—	—	—	6	—	1	—	—	—	—	—	—	—	—	—	—	—	—	9
♀ XW-WW	—	—	—	—	—	—	1	—	—	1	21	24	1	27	8	—	11	9	1	—	5	—	—	109
♂ XMY-YMY	—	—	—	—	—	—	—	—	—	—	5	2	—	1	—	—	—	—	—	—	—	—	—	8
♂ OY-YX	—	—	—	2	—	—	—	—	6	1	—	5	—	3	9	1	11	3	—	—	4	—	—	45
♀ MO-MXV	—	—	—	2	—	—	—	—	—	1	1	—	—	9	4	—	4	5	—	—	4	—	—	30
♂ XW-YGY	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
♀ MVM-VXM	—	—	—	—	1	—	—	—	—	1	4	—	—	—	5	2	7	4	—	—	—	—	—	24
♂ RV-VRX	—	—	—	—	2	1	1	2	—	—	2	1	—	4	—	—	—	3	—	—	1	1	—	18
♂ RY-YRX	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—	3
♀ XMR-RMY	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	—	—	3
♀ RX-OGO	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2
Total	1	3	32	39	40	13	22	10	41	26	71	64	2	88	40	8	63	37	2	3	31	1	—	637

* November, 1959, through March, 1960.

A principal factor in the structure of dominance hierarchies which has not been investigated in the numerous studies of captive birds is the distance from nest area of each bird. In figure 1 the nesting areas for each male in the spring of 1959 are shown together with their rank in the winter hierarchy shown in table 1. Paired Steller Jays generally retained the same nesting area at all seasons in successive years.

The dominant male in this hierarchy was the owner of the nest area in which the observations were made (X-YY). Similarly, in five other nest areas in which hierarchies

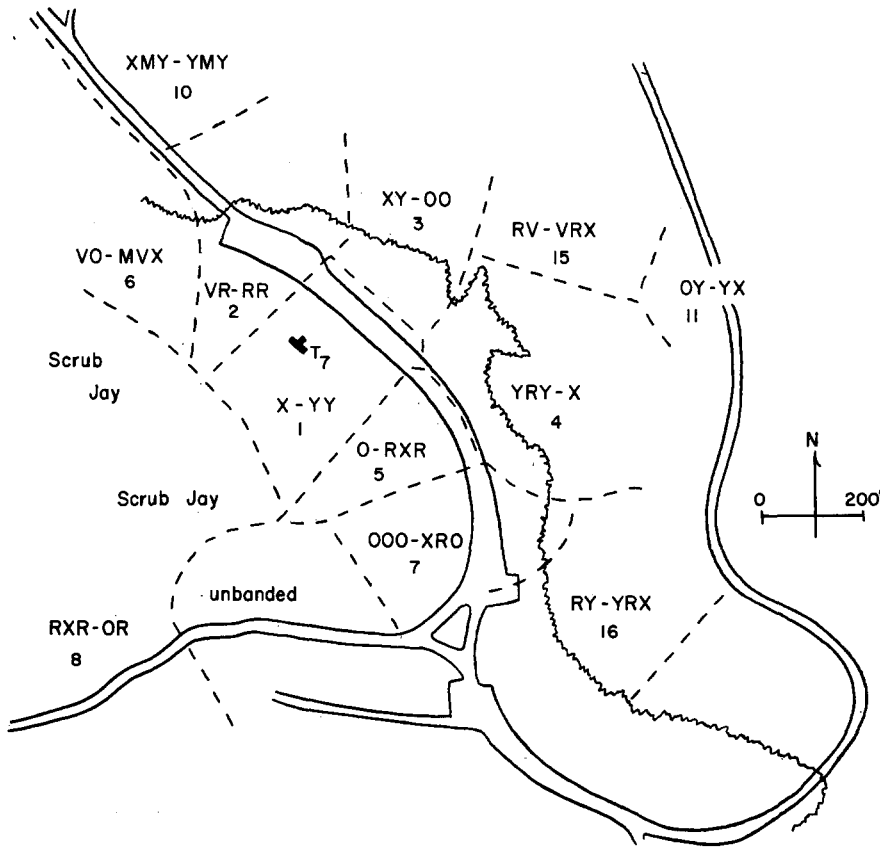


Fig. 1. Diagram showing ranks of male Steller Jays (*Cyanocitta stelleri*) in the dominance hierarchy of the winter of 1959-1960 at picnic table 7 in relation to nest areas of 1959. Approximate boundary lines between areas of dominance are indicated by dashed lines. See table 1.

were recorded, the male which had nested there was always the dominant jay at all seasons (figs. 2, 3).

Just below the owning male in rank were the male owners of contiguous nest areas (VR-RR, XY-OO, YRY-X, O-RXR, VO-MVX). And at the bottom of the male hierarchy were the owners of areas separated from the area of picnic table 7 by one or more intervening nest areas of other jays as seen in figure 1 (OOO-XRO, RXR-OR, XMY-YMY, OY-YX, RV-VRX, RY-YRX).

Among the females, XW-WW, the mate of the male owner, was dominant to all other females. Similarly in the five other nest areas in which hierarchies were recorded the mate of the dominant male dominated all other females. Just below XW-WW was the female from an adjoining nest area (MO-MXV), and at the bottom of the hierarchy were those females from farthest away. However, MVM-VXM was an exception, being higher in rank than some females whose nest areas were closer.

A direct correlation between rank in a dominance hierarchy and distance from nest area in winter has also been shown for the Black-capped Chickadee, *Parus atricapillus* (Odum, 1942), Blue Tit, *Parus caeruleus* (Colquhoun, 1942), and the Great Tit, *Parus major* (Brian, 1949).

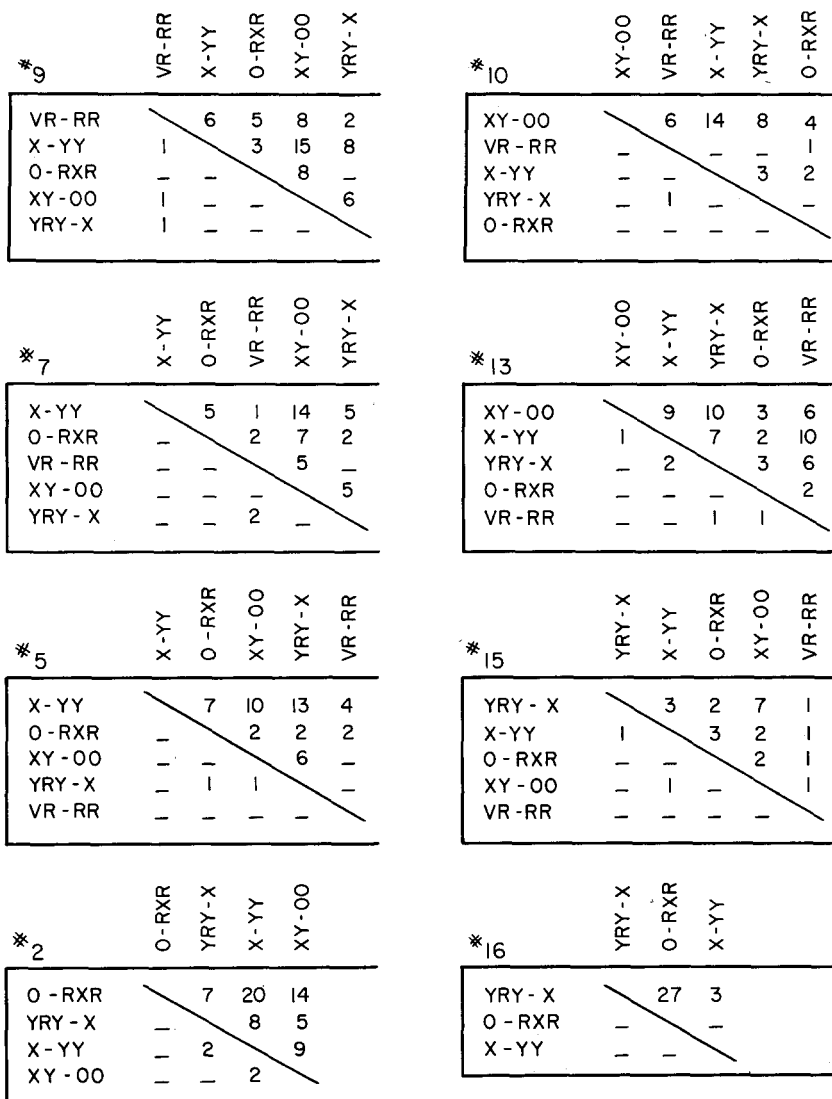


Fig. 2. Dominance hierarchies of male Steller Jays at different picnic tables, February 12 to March 9, 1959; supplanter at left, supplanter at top. See figure 3 for locations of picnic tables.

If the correlation just discussed between rank and distance from nest area is valid rather than due to chance, the same correlation should be found regardless of where the hierarchy is recorded. An objection sometimes raised against earlier studies of the correlation between rank and distance was that the study area may have been located by chance in the territory of a particularly aggressive bird. Furthermore, it is also necessary to demonstrate the change in rank of individual birds as the distance from the nest area increases.

In figures 2 and 3 the rank of five male Steller Jays may be examined in a number of different hierarchies obtained at picnic tables at varying distances from the nest area

of any one individual. Each of the five jays represented was dominant to all others in the area about his own nest at all seasons. The data show that the rank of each individual declined with increasing distance from its nest. For example, O-RXR ranked first at table 2, second at tables 5 and 7, and third at table 9 as the distance from its nest increased.

Only data for the period of February 12 to March 9, 1959, are shown. However, similar data showing the same relationships were obtained for the period of May 1 to 19, 1959. Thus, the phenomenon was not limited to winter but occurred also during the breeding season. Although not shown, the data for females indicated a similar decline in rank with increasing distance from the nest.

The importance of the nest itself in relation to dominance was emphasized by the effects of changes in location of the nests of males X-YY and O-RXR (shown in fig. 3). The nesting season of 1959 was an unproductive one in the study area and males X-YY and O-RXR (with mates) built four and three nests, respectively, each in a different location. Although the effects of these location changes on rank in hierarchies were not studied, the changes in the area dominated by each male were clearly evident, especially since the different nests were relatively far apart. The area of dominance of each male

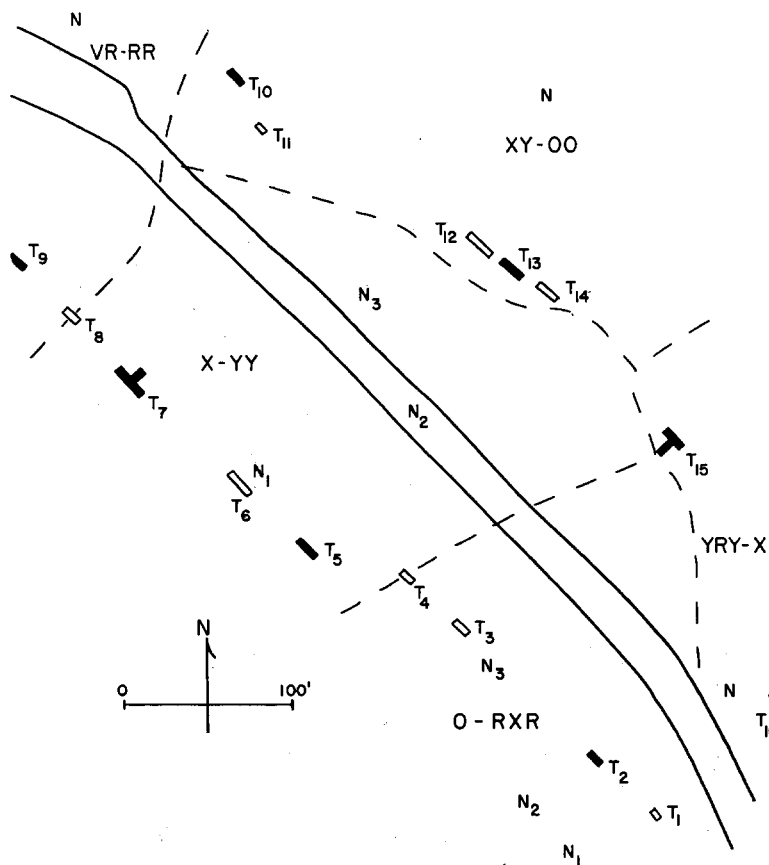


Fig. 3. Diagram showing locations of nesting areas of male Steller Jays in 1959 and picnic tables where dominance hierarchies were studied in the spring of 1959. Baited tables are represented by solid symbols; N = location of nest. See figure 2 for the corresponding hierarchies.

centered around the current nest, and its borders shifted in the direction of each change of nest site.

SOCIAL RANK AND STAGE OF NESTING CYCLE

The intolerance of male Steller Jays toward intrusions of neighbors increased during the spring courtship period to a peak just before incubation and then markedly dropped during incubation. When renesting, intolerance again increased during courtship and nest building, only to decline rapidly again during incubation. Both males and females did much calling, displaying, and active chasing of other jays during their courtship and nest-building phases; but they were especially quiet and inconspicuous when the female was incubating or brooding—a well-known trait of jays in general.

Evidence of such changes in aggressiveness and resulting dominance relationships between the neighboring males O-RXR and X-YY in 1959 is shown in table 2. Each

TABLE 2
SHIFTS IN DOMINANCE BETWEEN MALES O-RXR(O) AND X-YY(X)
CORRELATED WITH THEIR NESTING CYCLES*

Date	Wins/Losses for dominant male					Stage of nesting cycle				
	Table 2	Table 3	Table 4	Table 5	Table 7	O-RXR	X-YY			
February										
12	O	4/0				Courtship				
13	O	7/0								
19					X	2/0				
23	O	9/0								
24				X	3/0	X	3/0	Building; twigs N1		
March										
17		O 1/0	X 2/0			Building; mud	N1	Nest finished N2		
19		O = X				Building; mud	N1	Nest finished N2		
27				O	2/1	Building; lining	N1	Early incub. N2		
31			O-			Early incubation	N1	Incubation N2		
May										
1			O	8/0	O	2/0	Laying or incub.	N2	Between nests —	
7						X	1/0	Incubating	N2	Building; twigs N3
14		O 6/3	X 2/0					Incubating	N2	Laying N3
15			X 3/1	X	4/0			Incubating	N2	Laying N3
17						X	1/0	Incubating	N2	Laying N3
19				X	3/0			Brooding	N2	Building N4
June										
12				X	2/0			Incubating	N3	Late incubation N4
16						X	1/0	Incubating	N3	Late incubation N4
18						X	3/0	Incubating	N3	Brooding N4

* Wins and losses refer only to encounters between these two individuals.

of these males remained dominant to the other near the center of his area (picnic tables 2 and 7, respectively) throughout the year. But the border line, where neither was dominant to the other, shifted back and forth in correlation with the stages of the nesting cycles of each pair.

Between March 17 and 19, just before laying and incubation started in X-YY's nest, X-YY extended his border to picnic table 3, where on the 17th he had been subordinate. Eight days later, however, on the 27th, X-YY's female was incubating, O-RXR's nest was in a late phase of construction, and O-RXR had extended his boundaries to include picnic table 5, that is, well into the area normally dominated by

X-YY. In the first two weeks of May, X-YY reacquired picnic tables 4 and 5 into his area of dominance during a period of nest building and courtship while O-RXR's mate was incubating.

SOCIAL RANK AND SEX

Male Steller Jays averaged slightly but noticeably larger than females of a comparable age class. Most males were usually dominant to most females. The top several jays in every hierarchy were paired adult males, and the females were below. No female was ever observed to be the top bird in a dominance hierarchy.

Although females as a group always remained subordinate to males, the dominance relationship between the sexes varied with the season (see fig. 4). The proportion of

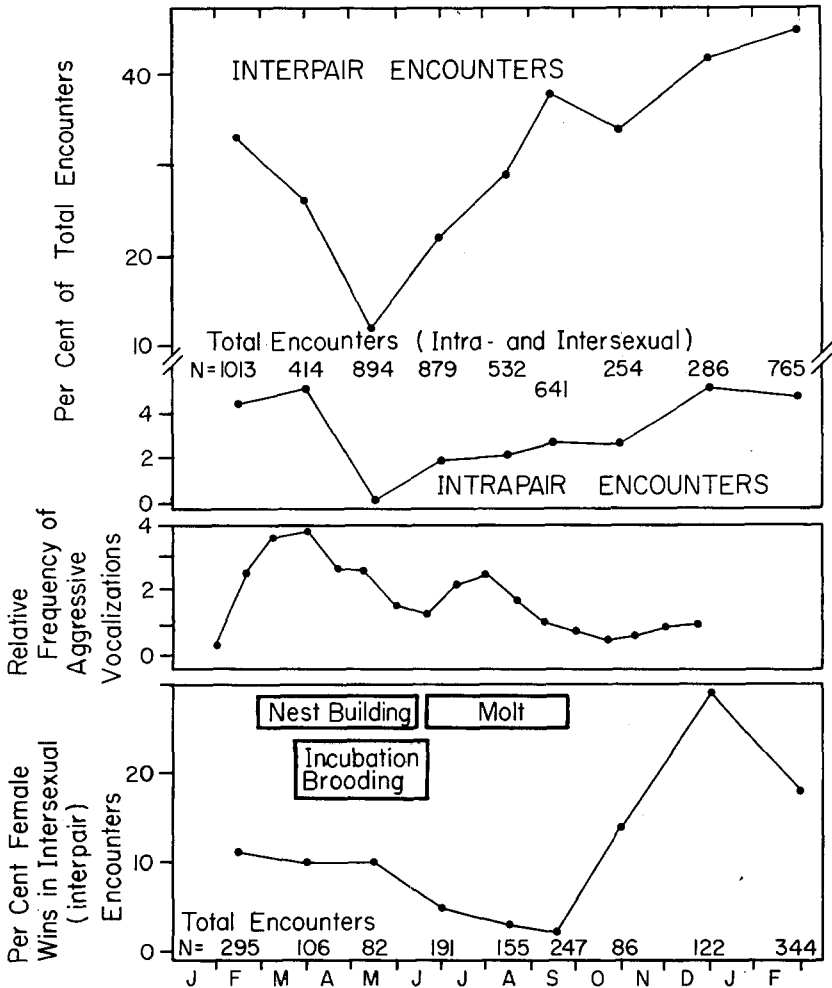


Fig. 4. Seasonal changes in relative frequency of intersexual aggressive encounters between color-banded Steller Jays, and relative success of females versus males throughout the year. Data are for all individuals of known sex except the unusually aggressive female XRR-RV (see text). Encounters were recorded at picnic tables throughout the study area, with one-half of them at table 7. Curve for relative frequency of aggressive vocalizations (Musicals) for comparison from Brown (MS). Dates for nest building, incubation, brooding, and molt represent the extremes for the population of the study area in 1959. See also table 3.

intersexual, as opposed to intrasexual, aggressive encounters was highest during the winter, reaching 49 per cent, and lowest during May, 12 per cent. The low coincided with the period when most females were incubating and when most males remained close to their nest areas. The winter period of greatest aggressive competition between the sexes (judging by the curve in fig. 4) occurred at a time when males and females were most often encountered out of their nest areas. However, the greater wanderings of males in winter cannot be the only factor responsible for the variation because the curve for encounters between members of mated pairs follows a pattern similar to that for interpair intersexual encounters.

The success of females in supplanting males not their mates reached a maximum of 29 per cent of the total number of such aggressive encounters in the winter period (fig. 4), when wandering of males outside their own areas was frequent. Since males away from their nest areas were less aggressive and ranked lower in hierarchies, they could more often be dominated by local females than when they remained closer to their home areas. Females were least successful during August and September, when they won only three per cent and two per cent, respectively, of all encounters with males. This lack of success by females coincided with the period of molt, and the subsequent steep increase in success of females occurred just after cessation of molt. Why females were so much less successful than males especially during the molt is, however, not known.

In contrast to their dominance relationships with other males, females were almost never seen to supplant their own mates, as shown in table 3; but their mates frequently

TABLE 3

INTRAPAIR INTERSEXUAL AGGRESSIVE ENCOUNTERS*

	1959											1960		
	F	M	A	M	J	J	A	S	O	N	D	J	F	M
♂ > ♀	45	17	0	0	2	12	10	17	1	3	13	1	23	12
♀ > ♂	0	4	0	0	1	1	0	0	0	0	0	0	0	0
Total encounters	1013	360	49	915	436	442	495	641	20	235	223	53	502	248

* Compare with figure 3; F = February, M = March, and so forth.

supplanted them. Thus, the curve in figure 4 for per cent intrapair aggressive encounters of total encounters represents essentially the seasonal variations in the relative frequency with which males supplanted their own females. Since mated pairs generally remained together on or near their nesting areas throughout the year, opportunities for intrapair aggressive encounters were always present.

Thus, females were least successful in avoiding supplantings by their mates during the season when they were most successful in supplanting other males (winter). Also the period in May when females were most successful in avoiding supplantings by their mates failed to coincide with the period of greatest success of females in interpair encounters (winter).

Supplantings of a female by her male were so common in most months that they were not always recorded if other more interesting encounters were occurring simultaneously; hence, the numbers in table 3 are somewhat smaller than actually observed. The maximum activity of males in supplanting their mates was reached during the winter.

In April, May, and June, however, aggressive encounters between members of a pair were practically absent, despite an intensive watch for them whenever a pair was seen together. Of 1400 supplantings recorded in these months within the areas of several different pairs, the male of a pair supplanted his female in only two instances, and both of these were in the last week of June. A total of 51 such supplantings would have been expected in the same period on the basis of observations at other times of the year (when 3.7 per cent of the recorded encounters were between members of a pair). In only seven of the 5632 encounters recorded over the whole period of study did the female of a pair supplant her mate (table 3), and only one of these occurred during the April-June period.

I conclude that indications of dominance within the pair at food sources normally disappears during April, May, and June, during the period of incubation and brooding. Although both sexes appeared definitely more aggressive in this period than in winter, no observations were made which would indicate dominance of either sex, either at or away from food sources.

Of the seven instances in which a female dominated her mate six were by one female, XRR-RV, which was unusually aggressive in comparison with other females (as revealed in dominance hierarchies). Also, her mate, RV-VRX, was unusually submissive in comparison with other males. Within the same period, March 6 to July 7, 1959, RV-VRX dominated the female on four occasions. These records suggest that during the season when male dominance of the mate subsided only one unusually aggressive female, of the seven pairs closely watched, attained even partial dominance over her mate. Whether the unusual relationship in this pair existed outside of the breeding season could not be ascertained because of the permanent disappearance of the female and subsequent remating of the male.

POSSIBLE CAUSES OF LOSS OF MALE DOMINANCE

Correlated with the absence of clear dominance relationships between the sexes in mated pairs from April through June was the occupation of the female in incubation and brooding. As shown in figure 4, the involvement of females in aggressive encounters decreased in terms of percentage of all observed encounters both in respect to their own mates and to other males. The frequency of encounters in general was also low during this period.

Despite the preoccupation of the females with parental matters, many opportunities for supplanting of one mate by the other occurred; and no such supplantings were seen (with the two exceptions just noted). Perhaps more important than mere absence of the female while she was on the nest were the facts that, during the brief and infrequent times when the female was off the nest, she was often fed by the male and that in general the male's efforts were oriented toward aiding the female and protecting her and the nest. Food was not scarce at those times, and the same mutual tolerance which allowed courtship feeding was apparently present in other contexts during that period.

Since females were most successful in supplanting males in the winter season, when they were least successful in avoiding being supplanted by their mates, an explanation based on variations in simple aggressiveness is insufficient. A special relationship with the mate not based purely on relative aggressiveness is indicated.

In captive Scrub (*Aphelocoma coerulescens*) and European jays (*Garrulus glandarius*) the situation was similar. In a pair of hand-reared Scrub Jays kept by the author, supplanting of the female by her mate ceased when nest building and courtship began. Similarly, in captive European Jays kept by Goodwin (1951) the male domi-

nated the female except during incubation and brooding. Transition periods of about three or four days occurred a few days before the laying of the first egg and when the young were 15 to 18 days old. Goodwin wrote (p. 612), "At these periods there are frequent fights . . . These fights are no mere token affairs. The birds spring up at one another like gamecocks and fall interlocked, screeching; pecking, and clawing and littering the aviary with the easily torn-out vinous-fawn body-feathers . . . In every actual fight that has been witnessed, G [female], heavy with eggs and soon exhausted, has unquestionably been vanquished, but her repeated aggressiveness appears to induce in P [male] a defeatism which shows itself first in a growing disinclination to defend himself and thus start a fight when attacked and finally in complete submissiveness to his mate."

While such fights between mates were never witnessed between wild or captive Steller or Scrub jays, it seemed likely that persistent resistance of the female to the mate's aggressiveness may have been involved in the dominance shift. Probably several factors combined to bring about the dominance shift. These seemed to involve primarily an altered relationship between the individual members of the pair rather than a significant change in aggressiveness of females relative to males in general.

For a brief review of dominance relationships between the sexes in other species of birds, see Thompson (1960).

SOCIAL RANK IN RELATION TO RANK OF MATE

In colonial Jackdaws (*Corvus monedula*) studied by Lorenz (1952) the rank of the female was determined by the rank of her mate; the pair cooperated in aggressive encounters and its members possessed the same social rank in the flock. The same could not be said for the Steller Jays. Although the male and female of a pair often foraged and perched rather close together during boundary disputes between pairs, at no time was one of the pair ever observed to intervene in an aggressive encounter involving the other.

If a male flew aggressively toward an intruder, the female would continue with her occupation of the moment and the male would soon return. Interest of the male in the success of aggressive encounters involving his mate likewise seemed absent.

For example, when two females (XWWW, MO-MXV) were involved for several minutes in a high intensity dispute with loud calling, aggressive sidling, displacement activities, and raised crests in their mutual border zone, the mate of MO-MXV (O-RXR) perched nearby much of the time apparently not noticing the encounter below him. Once he even supplanted a towhee (*Pipilo erythrophthalmus*) a few feet away and foraged where the towhee had been scratching (not redirection aggression). Another time O-RXR took sunflower seeds and stored them unconcernedly several times from a table top under which his mate and XW-WW were engaged in a similar prolonged dispute. In both of these cases XW-WW's mate was absent.

The correlation between the rank of a male among males and the rank of his mate among females at any particular place was not high. In all four pairs for which the ranks of females in the area of dominance of their mates could be determined, the female mate dominated all other females. Below the first rank, however, correlations broke down. Females were seen going to bait outside their nesting areas less often than males, and several of them were particularly reluctant to visit the bait in the presence of other jays. Therefore, a complete picture of the hierarchy for females was difficult to obtain. The number two and three positions in the female hierarchies were held by jays from adjoining areas rather than from more distant ones (table 1). But beyond this there

was no correlation. The principal factors in determining the female hierarchy seemed to be distance from the nest area and individual differences in temperament, the former factor accounting for whatever correlation occurred with the rank of the mate.

REMATING

The relationship of dominance status to pair formation was observed in one case. The stable and generally permanent pair bond in the birds observed precluded repeated observations of pairing. That a female's dominance to other females in her own nesting area did not depend on the presence of her mate was shown when female XW-WW lost her mate, X-YY, who was last seen December 9, 1959. Neighboring jays appeared to sense the disappearance of the dominant male, for they came afterward in greater numbers and less nervously to the bait in X-YY's former area of dominance. But XW-WW became, if anything, more aggressive and did not decline in rank in the hierarchy during the period in which she was widowed (December 11 to 21, 1959).

Although it was midwinter, XW-WW remated after about ten days with male RV-VRX, whose female had disappeared five months earlier. This was surprising because RV-VRX had been subordinate to XW-WW (table 1) in the former area of dominance of XW-WW's mate and because RV-VRX had only one leg. That she did mate with a male subordinate to her was probably facilitated by the absence of any other unpaired males which were dominant to her during that winter.

The only possible competitor was male OY-YX, who had been dominant to RV-VRX and subordinate to XW-WW, but who did little if any courting of XW-WW. He was principally a spectator who occasionally supplanted RV-VRX. Probably he also was unpaired, for in the subsequent breeding season he and his former mate both remated with other individuals. These observations suggest that XW-WW did not choose her mate on the basis of dominance but according to which contender most actively and persistently courted her.

During the process of losing her first mate (X-YY) and gaining a second (RV-VRX), XW-WW exhibited no change in rank in the dominance hierarchy at table 7. After the loss of her first mate she seemed more often involved in aggressive encounters, but this was probably the result of more frequent entrance of other jays into her area in the absence of the formerly dominant male (X-YY). Remating with RV-VRX did not appear to reduce the increased number of jays coming into XW-WW's area.

In the previous spring the nests of RV-VRX and XW-WW were about 600 feet apart and the nesting areas were not directly neighboring each other. In the winter, unlike most male jays in the study area, RV-VRX had not shown any marked attachment to his old nesting area. It was in a *Eucalyptus* grove, and it did not seem to be a good foraging area, judging by the paucity of jays seen there. Furthermore, his mate had disappeared in the preceding July. So RV-VRX foraged often in the areas of other jays until he paired with XW-WW. From then on he foraged mostly with XW-WW in her nest area.

The combined acts of pairing with XW-WW in December and assuming her nesting area as the center of his activities had few immediate effects on the frequency of aggressive encounters or rank of RV-VRX. He was reluctant to be involved in supplanting encounters and would usually flee from the arriving dominants well before they landed. Consequently, he was recorded in relatively few such encounters both before and after mating with XW-WW and had a low position in the hierarchy at picnic table 7 (table 1).

The degree of success of RV-VRX in aggressive encounters at picnic table 7 before

and after pairing with XW-WW is shown in table 4. Although XW-WW had regularly supplanted RV-VRX before pair formation, this failed to occur afterward. That RV-VRX became somewhat more successful with other individuals is shown by the numbers of wins and losses by RV-VRX against all opponents other than X-YY and XW-WW). He won 9 and lost 62 before the pair formation and won 14 and lost 10 after pairing ($P < 0.01$ with chi-square test). The change seemed to involve both males and females, although the sample sizes were too small to show a significant difference for females ($P < 0.01$ for males; > 0.20 for females).

TABLE 4
EFFECTS OF MATING WITH FEMALE XW-WW ON DOMINANCE
RELATIONSHIPS OF MALE RV-VRX*

Opponent	Results for RV-VRX in aggressive encounters				P	X ²
	Before mating with XW-WW Feb.-Dec. 18, 1959		After mating with XW-WW Dec. 19, 1959-March, 1960			
	Wins	Losses	Wins	Losses		
Males	2	48	8	7	< .01	21.5
Females	6	8	6	3	> .20	1.2
Unsexed	1	6	—	—		
Total	9	62	14	10	< .01	18.9
X-YY	—	18	—	—		
XW-WW	1	13	—	—		

* Data are for all supplanting encounters observed at picnic table 7 involving RV-VRX.

Although RV-VRX exhibited a slight rise in aggressiveness and rank after pairing and adopting the nesting and foraging area of his mate, he was still subordinate to several males at picnic table 7 and remained generally non-aggressive most of the time. However, after nest building was well underway, in April, 1960, he drove away all Steller Jays from table 7 and the area around his nest. Since his nest was almost over table 7, he was very aggressive there with the result that the encounters usually occurred before the intruding jays ever reached table 7. This meant that very few encounters could be recorded at table 7 and that RV-VRX's superiority, although real, could not be demonstrated in the form of a dominance hierarchy at table 7. He did, however, vanquish the formerly dominant male jay, VR-RR, in each of five encounters there and did not lose once to any jay during April, 1960.

Therefore, in the case of RV-VRX it was possible to observe the effects on aggressiveness of pair formation and the resulting site attachment separately from the effects of experience in the nesting season. Advancement from the unpaired condition with no site attachment to the paired condition with site attachment led to significantly increased aggressiveness in a subordinate male, but not by a conspicuous amount. Achievement of full dominance required the experiences (hormonal and behavioral) of the nesting season and presumably would not have occurred in the unmated condition.

DOMINANCE RELATIONSHIPS IN SPRING AND FALL

Although dominance hierarchies in nature have been demonstrated for various species in winter, for none has the persistence of such a hierarchy through the breeding season and into the fall been demonstrated. Generally the species previously studied ceased coming to the feeding station at the end of winter and restricted their activities to the vicinity of their nest areas. Most authors have felt that the existence of such

hierarchies was incompatible with the development of mutual intolerance and defended areas at the onset of the breeding season.

In the Steller Jay, aggressiveness and intolerance also increased in spring but not to an intensity sufficient to completely prevent outsiders from entering a defended area for food or nest materials. The areas belonging to each paired male were, however, significantly more strongly defended; and at the same time each male became increasingly hesitant to enter areas not his own or to leave his female.

The number and frequency of recorded aggressive encounters between Steller Jays varied not only with the intensity of defense of nesting areas but also with the availability of food. The season when it was most difficult to observe aggressive encounters at the sunflower seed bait on picnic table 7 was not during the breeding season but in October, when the acorn crop was being most actively eaten and stored by the jays. The total numbers of aggressive encounters recorded in each period of the year are shown in figure 4 and table 3. Although the length of time spent making such observations varied greatly from month to month, the scarcity of records in October is still evident.

The dominance relationships between banded jays for the period May 2 to 19, 1959, at picnic table 7 are shown in table 5. The dominant male then, in contrast to the rest of the year, was VR-RR. This exception occurred during the period when X-YY's nest was relatively distant from table 7. The top-ranking males in May were the same indi-

TABLE 5
AGGRESSIVE ENCOUNTERS IN MAY, 1959, AT PICNIC TABLE 7*

	♂	♂	♂	♂	♂	♂	♂	♂	—	—	♂	♂	♂	♂	♀	♂	♀	♂	♀	—	—	Total
	VR-RR	X-YY	O-RXR	RXR-OR	XY-OO	YRY-X	VO-MVX	OOO-XRO	X-	XOY-YO	RV-VRX	XRY-YR	OY-YX	XMY-YMY	XW-WW	RY-YRX	XYW-YM	R-OGX	XRM-R	YR-RGX	YO-OYX	Total
♂ VR-RR		7	1	1	10	—	6	7	—	1	—	—	—	1	—	2	—	—	3	2	—	41
♂ X-YY	1		2	1	8	—	7	4	2	4	4	6	3	—	3	2	—	—	2	—	2	51
♂ O-RXR	—	—		—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
♂ RXR-OR	—	—	—		—	—	5	—	4	—	1	—	—	1	—	—	—	1	—	—	—	12
♂ XY-OO	1	—	—	—	—	1	3	3	—	2	1	1	1	—	2	1	—	—	1	2	—	19
♂ YRY-X	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
♂ VO-MVX	—	—	—	—	2	—	—	—	3	3	4	—	3	3	—	2	—	2	5	1	—	28
♂ OOO-XRO	—	—	—	—	—	—	1	—	—	—	—	—	1	—	2	—	—	—	—	2	—	6
— X-	—	—	—	—	—	—	—	—	—	2	1	—	1	—	1	—	1	—	3	—	1	10
— XOY-YO	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	2	—	—	5
♂ RV-VRX	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
♂ XRY-YR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
♂ OY-YX	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2
♂ XMY-YMY	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	2
♀ XW-WW	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1	1	—	—	—	4
♂ RY-YRX	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	2
♀ XYW-YM	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
♂ R-OGX	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
♀ XRM-R	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
Total	2	8	3	2	20	1	26	14	11	10	15	7	9	10	2	12	5	6	16	7	3	189

* Winners at left, losers at top.

viduals and in approximately the same order as in the following winter. A comparison of tables 1 and 5 shows that VR-RR and X-YY were the top two birds in both May and winter. Directly under them in both seasons were the same males with adjoining nesting areas (XY-OO, YRY-X, O-RXR, VO-MVX), although the sequence of rank among them could not be established in every case because of the small number of observations. Beneath these males in rank were females and males from farther away.

In August (table 6) at the same picnic table the rank order became considerably jumbled. X-YY regained his usual dominance. The male who had been dominant in May (VR-RR) became subordinate to five males and lost more encounters than he won (20 losses, 17 wins). And XY-OO although dominant to the second-ranking male was subordinate to the third, fourth, and fifth. In addition to the regular visitors, individuals from farther away became more frequent, as reflected in the greater number of banded jays recorded which was not entirely due to increased banding effort.

In August juveniles entered the competition for food at the picnic tables. Table 6 shows that unbanded juveniles defeated jays of all ranks including even the high-ranking male (VR-RR). However, their supplanting attacks were sporadic and seemingly irrespective of individual recognition. Usually one of the dominant males if supplanted by a juvenile would immediately return and drive it away. The degree of success

TABLE 6

AGGRESSIVE ENCOUNTERS IN AUGUST, 1959, AT PICNIC TABLE 7*

	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	Juv.	♀	♀	♀	♀	♀	♀	♂	♀	♀	♂	—	
	X-YY	YRY-X	O-RXR	RXR-OR	VO-MVX	VR-RR	XY-OO	OY-YX	XMY-YMY	XOM-MY	XRY-YR	XWV-VR	MMR-MRX	XW-WW	MO-MXV	XYW-YM	XYY-YYY	RV-VRX	RX-OGO	RMR-RMX	R-OGX	Juv.	Other banded jays	Total	
♂ X-YY		2	7	4	15	6	18	1	15	9	1	4	10	3	12	11	5	3	6	4	12	9	6	163	
♂ YRY-X	—		1	—	4	1	1	—	1	1	—	1	2	10	—	1	—	—	—	—	—	1	—	24	
♂ O-RXR	—	—		—	6	2	4	—	2	1	—	—	6	4	1	2	1	—	—	—	—	3	7	2	44
♂ RXR-OR	—	—	—		1	1	7	—	—	3	1	—	—	1	—	—	—	—	—	—	—	2	1	4	34
♂ VO-MVX	—	—	—	—		1	12	—	5	4	1	4	—	7	3	2	2	2	3	—	—	5	1	5	57
♂ VR-RR	—	—	—	—	—		3	—	1	1	—	1	1	3	1	2	—	—	—	—	—	2	2	—	17
♂ XY-OO	—	4	—	—	3	3		—	11	6	—	—	1	23	6	5	—	7	—	4	10	4	16	103	
♂ OY-YX	—	—	—	—	1	1	—		—	1	—	—	—	—	—	—	1	1	—	—	—	—	—	—	5
♂ XMY-YMY	—	1	1	—	—	1	4	—		6	—	—	—	6	6	3	4	8	1	—	—	6	2	6	55
♂ XOM-MY	—	2	1	—	—	—	1	—	1		3	1	3	1	—	2	—	—	1	—	—	16	—	3	35
♂ XRY-YR	—	—	—	—	—	—	—	—	—		—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
♂ XWV-VR	—	—	—	—	—	1	—	—	—		—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
Juv. MMR-MRX	—	—	—	—	—	—	—	—	—		—	—	—	2	—	—	—	—	—	—	—	—	—	—	1
♀ XW-WW	—	—	—	—	—	—	—	—	—		—	—	—	—	3	1	—	—	—	—	—	—	—	—	2
♀ MO-MXV	—	—	—	—	—	1	1	—	—		—	—	—	—	—	1	—	—	—	—	—	—	—	—	3
♀ XYW-YM	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
♀ XYY-YYY	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
♂ RV-VRX	—	—	—	—	—	1	—	—	—		—	—	—	—	—	—	—	—	1	—	—	—	—	—	2
♀ RX-OGO	—	—	—	—	—	1	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
♀ RMR-RMX	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
♂ R-OGX	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Juveniles	—	—	—	—	—	1	—	—	2	3	—	—	6	—	1	—	—	—	—	—	—	—	4	1	—
Total	0	9	10	4	32	20	50	1	38	35	6	12	29	60	33	31	14	21	12	14	64	27	47	569	

* Winners at left, losers at top.

enjoyed by juveniles even with high-ranking individuals suggests that they did not necessarily enter dominance hierarchies at the bottom.

DOMINANCE RELATIONSHIPS IN SUCCESSIVE YEARS

For those banded males which were studied over three or two years no loss of the first rank in their own home areas occurred, although the boundaries of the areas where they were dominant shifted to a small degree. Similarly, no females in their own areas were observed to be subordinate to other females in any year. Below the top position in the hierarchy, individuals remained in roughly the same order, but specific inter-individual relationships were subject to change. A comparison of the top five ranking birds (all males) at picnic table 7 in February 1959 and 1960 is shown in figure 5. In 1960 only X-YY of the 1959 birds had disappeared. The newcomer in 1960 had not been banded in February, 1959, but probably was actually present then also. Figure 5

1959		1960									
A	X-YY	O-RXR	VR-RR	XY-OO	YRY-X	B	VR-RR	XY-OO	YRY-X	VO-MVX	O-RXR
X-YY		5	1	14	5	VR-RR		2	3	1	1
O-RXR	-		2	7	2	XY-OO	-		5	3	5
VR-RR	-	-		5	-	YRY-X	-	-		4	4
XY-OO	-	-	-		5	VO-MVX	-	-	1		1
YRY-X	-	-	3	-		O-RXR	-	-	-	1	

Fig. 5. Aggressive encounters among the top five Steller Jays at picnic table 7 in February of two successive years.

shows that the rank of no single individual was exactly the same in both 1959 and 1960; however, four of the five were among the top-ranking jays in both years. In both 1959 and 1960, the males whose nest areas were the closest to picnic table 7 ranked highest, and they were followed by their females and males and females from farther away in mixed order.

STABILITY OF DOMINANCE RELATIONSHIPS

In an idealized dominance hierarchy no individual would ever dominate another of superior rank, and no changes in rank would occur. In nature, however, many factors act to upset such stability. Inconsistencies in the records of dominance relationships in a group of Steller Jays were present at all seasons. They were attributable to at least three causes:

(1) *First encounters.*—When two jays met for the first time in a new location or after a long absence, a series of encounters was sometimes required before one recognized the other as dominant. In the beginning both individuals would win some encounters; but after the relationship had become established, the subordinate would no longer resist nor win any encounters. Although the observer could not be sure that such birds had not previously met, prior observation there and the birds' "uneasy" behavior made the assumption of first encounter highly probable.

(2) *"Mistaken identity."*—Some individuals were confident and relatively unreactive to loud noises and sudden events in the environment around the bait stations, while others would leap up and fly to the nearest cover at slight disturbances. Jays of

all ranks which were newly arrived on a particular day were especially sensitive. When a confident jay happened to land abruptly behind a sensitive jay or when a jay arrived in some other way which hindered individual recognition, the sensitive one sometimes flew away even though the newcomer might be a subordinate. Even after jays had become used to the surroundings, supplantings by subordinates of dominants sometimes occurred in cases where because of the positions and silence of the two individuals identification was difficult. Such cases were surprisingly few, however; and the ability for individual recognition was apparently excellent. A similar explanation of "reverse pecks" in the Oregon Junco (*Junco oreganus*) was invoked by Sabine (1959).

(3) *Changes in dominance.*—The most common causes of inconsistencies in the records were actual changes in the dominance relationships among individuals. The fewest changes were recorded during the winter, from November through March, 1959 (table 1), when the remating of RV-VRX and his subsequent rise in aggressiveness and rank caused the principal alterations. Aside from this event the commoner causes of dominance shifts were absent or minimal during winter. The relative stability of the winter period is well shown for XY-OO in table 7, where it may be seen that XY-OO's encounters with particular individuals were more consistently won or lost than in other seasons.

During spring and early summer frequent changes in dominance relations occurred as a result of changes in nest location and in phase of reproductive behavior. In summer and fall, differences in time of onset and completion of molt were correlated with some changes. And at any time of the year sickness or injury could probably cause a decrease in rank. All the sick and injured birds were low in rank, with the exception of RV-VRX.

TABLE 7
WINS/LOSSES OF XY-OO AT TABLE 7

	May	June	July	August	September	Winter	Total
X-YY	—/8	—/6	—/5	—/18	—/13	—/22	—/72
VR-RR	1/10	3/11	—/—	3/3	1/2	—/10	8/36
YRY-X	1/—	—/—	—/4	4/1	—/—	15/—	20/5
O-RXR	—/—	—/4	2/—	—/4	1/—	14/—	17/8
VO-MVX	3/2	2/5	4/1	3/12	8/5	3/—	23/25
RXR-OR	—/—	10/—	9/1	—/7	5/3	4/—	28/11
Total	5/20	15/26	15/11	10/45	15/23	36/32	96/157
Per cent wins	20	37	42	18	39	53	38

Monthly changes in dominance relationships for one male (XY-OO) in respect to the other high-ranking males at picnic table 7 are shown in table 7. The top-ranking jay in the hierarchy (X-YY) dominated XY-OO in every one of 72 encounters distributed through the year. With the second-ranking jay (VR-RR), XY-OO was almost as unsuccessful, but in one month, August, when VR-RR had sunk to sixth place, he succeeded in winning half the encounters. His relationships with the other four males during the non-winter months often changed. During the winter he won every encounter with each of them, but in June, July, and August he was subordinate to at least one of them, and in May and September he lost almost as many encounters to them as he won.

Triangles, or circular relationships in which a higher ranking bird was dominated by a lower ranking one, were relatively rare among the jays higher in the hierarchies.

Among most of the lower ranking individuals the number of records was not adequate to conclude that such relationships were rare; however, none was conclusively found.

An example of a triangular dominance relationship is shown in the hierarchy for August (table 6). Although XY-OO ranked sixth or seventh in the hierarchy at picnic table 7, he dominated the second-ranking jay (YRY-X) in 4 of 5 encounters.

In the monthly summary of XY-OO's wins and losses (table 7) the development and subsequent resolution of this triangle may be traced. In the preceding month, July, the hierarchy was linear and the circular relationship absent; YRY-X dominated XY-OO and XY-OO dominated O-RXR, VO-MVX and RXR-OR. In August XY-OO's dominance relations with each of these four males were reversed. Although XY-OO's success in aggressive encounters with these males was lower in August than at any other season and his rank fell from third in July to sixth or seventh in August, he nevertheless achieved temporary dominance over YRY-X. In September his success increased again; he regained incomplete dominance over VO-MVX and RXR-OR and rose to second place in the hierarchy. Thus, the duration of this triangle was only about a month.

The low position of XY-OO in the hierarchy during August was correlated with his slower progress in molt in comparison with the other jays. In the Steller Jay the fading of the old feathers on the head, neck, and body allowed easy differentiation in the field between old and new feathers. In mid-August, when all the dominance observations for that month were made, these areas were only 1/2 refeathered in XY-OO. But in the three males who achieved temporary dominance over him at that time the areas were 3/5, 5/6, and 9/10 refeathered for O-RXR, RXR-OR, and VO-MVX, respectively.

Another triangular dominance relationship, which involved a different development and resolution, is shown in figure 6. At picnic table 7 from June 16 to 24, 1959, female XRR-RV, who ranked

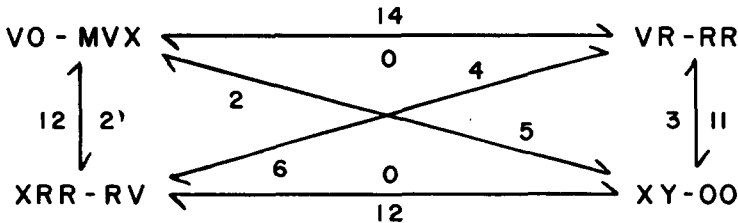


Fig. 6. A dominance "triangle" at picnic table 7, June 16 to 24 in 1959. Numbers indicate wins; split arrows show direction.

ninth in the hierarchy, dominated male VO-MVX, who ranked third. XRR-RV was dominated by two other males, both of whom were subordinate to VO-MVX. Shortly before this triangle developed XRR-RV was feeding her young in the nest and did not appear at picnic table 7 at all. Then all activities connected with the nest and young suddenly ceased, and XRR-RV and her mate (RV-VRX) began to appear regularly at table 7 to take the sunflower seeds put there. XRR-RV was exceptionally aggressive for a female at that time and attacked individuals of all ranks, achieving success with the lower ranking ones, but meeting with many defeats from the higher ones. With VO-MVX, however, she won 12 times and lost only twice. Her aggressiveness was not restricted to table 7 but manifested itself in the areas of dominance of other males in which bait was placed. The unusual dominance relationships created by XRR-RV's abrupt appearance ended early in July, when XRR-RV disappeared not to be seen again.

Both triangles just discussed arose during periods when the aggressiveness and dominance relationships of the individuals involved were undergoing a period of change. The development of the first (with XY-OO) seemed to depend on asynchrony in the course of molt; the second depended on the precipitous cessation of parental activities by XRR-RV. When changes of this sort no longer occurred in winter, triangles no longer occurred.

In contrast to the Steller Jay, triangles reported for winter flocks of Oregon Juncos were said to be as permanent as the more common linear relationships (Sabine, 1959).

SCRUB JAY VERSUS STELLER JAY

Although X-YY was dominant to all other Steller Jays at picnic table 7 and at other tables near his nest area, he almost invariably retreated when a Scrub Jay landed on the table. Only one pair of Scrub Jays lived close enough to table 7 to visit it for food, and they usually avoided the picnic area, seeming shyer than the numerous Steller Jays. However, when they came they arrived confidently and quickly supplanted all the Steller Jays nearby regardless of their rank. Only a few times, when the bait was almost directly under an active nest of X-YY, was he successful in driving away the Scrub Jays.

In 142 supplanting encounters between Scrub and Steller jays at picnic table 7 from June, 1959, to March, 1960, only the female Steller Jay, MVM-VXM, was ever recorded supplanting a Scrub Jay. She won over female Scrub Jays twice in December at a time when she was seventh or eighth in the hierarchy of Steller Jays. Although normally low-ranking and hesitant at table 7, she was at that time rebellious and became involved frequently in aggressive encounters. The general dominance of Scrub Jays over Steller Jays was not confined to this one pair in this one location but was frequently observed at other places in coastal California. On 15 occasions at places outside the Indian Camp study area, Scrub Jays were observed supplanting or chasing Steller Jays and on no occasions was the reverse seen. A stuffed Steller Jay placed ten feet from an active nest of a Scrub Jay was viciously attacked and pecked by the Scrub Jay.

AGE STRUCTURE AND DISPERSAL

The year of hatching of a Steller Jay can be determined only until its first complete molt, which occurs in its second autumn. First-year jays constituted a relatively unimportant part of the particular population studied. All of the Steller Jays mentioned in this paper (both text and tables) were adults unless specifically designated otherwise. Although almost 50 per cent (54 birds) of the banding sample of 114 birds for the Indian Camp study area were banded in their first year, the only two of these mentioned in the dominance observations reported in this paper (RX-OGO, RR-X) had by the time of the observations attained the ages of two and three years, respectively.

The major period of dispersal of first-year jays began about mid-September. Of the 54 first-year jays banded, from May, 1957, to September, 1959, the majority (40) were banded in the months of July, August, and September. All of the 40 birds-of-the-year banded in these months had disappeared by early October although they had been relatively common through mid-September. Exactly how long the dispersal lasted could not be ascertained, but the following data indicate that it was over by the following spring.

There was little evidence of a tendency for the first-year birds to return to the study area in subsequent breeding seasons. Of the 37 presumably locally reared young of the year banded in July, August, and September, 1958, only three were ever seen again in the study area. Two of these remained as nonbreeders through the following summer and one reappeared for a few days one year later. Seven others were reported from localities in the Bay Area from one to 22 miles away. These were in Oakland, Berkeley, San Pablo, Hayward, Richmond and El Sobrante. The localities were all either north or south of the study area in the range of hills running along the eastern edge of San Francisco Bay. Suitable habitat for Steller Jays is largely restricted to these hills in the East Bay Area.

The only jay banded as an adult which was later observed outside the study area was found on the University of California campus about 2.7 miles away. Since seven of the eight birds observed outside the study area were banded in late summer as first-year birds and since approximately 50 per cent of the banding sample were banded as adults, the dispersal of Steller Jays from the population studied appeared to be predominantly by birds-of-the-year rather than by adults.

Steller Jays banded during their first year in late winter and early spring (after the period of active dispersal) were in general more sedentary than those banded before October. There was no distinct group of jays which could be classed as winter residents. In proportion to the number banded, many more of them than of fall-banded jays remained in the study area for relatively long periods of time. Of the 14 such individuals banded through September, 1959, four were subsequently paired in the study area and these were known to have been building nests there. Five of the 14 remained in the study area for periods from 11 months to three years. In contrast, of the 40 individuals banded in their first year before October only two remained in the study area after October and neither of these nested while present in the area.

Adults were relatively sedentary in comparison with first-year jays. Of 44 jays banded as adults one year or more prior to cessation of field observations, 20 were observed later for periods of a year or more after the date of banding and nine for six to eleven months. Adult jays with nesting areas near the center of the study area were seen regularly all through the year, but those which nested farther away were seen less often, and some entered the study area only rarely. Consequently, the failure of 15 of the 44 banded adults to be observed again is probably attributable more to the distances from the study area to their nesting areas than to mortality, emigration, or migration. Of the 22 banded paired adults, male and female, whose nesting areas are indicated in figure 1 only two disappeared between April 1, 1959, and April 1, 1960; all of the 20 remaining individuals were seen in the study area virtually every month for the entire year. This population of the Steller Jays thus differed from that of the Blue Jay (*Cyanocitta cristata*), in which many adults regularly migrate (Laskey, 1958).

The survival rate for these 22 paired adults was at least 91 per cent for the year. This was considerably higher than the adult survivorship of 55 to 58 per cent reported for the Blue Jay (Hickey, 1952). However, the present sample was considerably smaller than the sample of Blue Jays and represented only one small population for one year. The sample of Steller Jays was further restricted to paired adults, whereas this was not the case for the sample of Blue Jays. Differences in degree of permanent residency and other factors may also have contributed to the discrepancy.

MATE CONSTANCY

Once paired there were rarely changes in mates among the banded Steller Jays unless one of the members of the pair permanently disappeared. Of the two banded pairs which could be followed through three breeding seasons, one remained together for the whole period and one broke up after two, and probably three, years due to disappearance of the male (X-YY) in December, 1959. The female (XW-WW) of this pair remated with RV-VRX about two weeks later. Of the six banded pairs which could be followed for two breeding seasons, four remained together. The male of one (RV-VRX) remated in December, 1959, after the disappearance of his female (XRR-RV) in July, 1959. Only one of the six pairs split up, with each member known to have remated to another individual. Not only were members of a pair together during the breeding season, but they were usually together or within communication of each other through-

out the year. The evidence agrees with the hypothesis that members of this population of Steller Jays generally mated for life.

"TERRITORY" IN THE STELLER JAY

The concept of "territory" is inadequate to express accurately the dominance relationships between individual Steller Jays in respect to the topography of the areas where they lived. According to the data already presented the dominance relationships of an individual Steller Jay may be conceived as a series of concentric zones of diminishing dominance rank from the center of the nesting area outward. The dominance relationships within the population may be better generalized as many such series of concentric zones each overlapping with many others (depending on population density) than as a mosaic of discrete territories.

This generalization held throughout the year. In every month of the year and at every phase of the breeding cycle it was possible to observe hierarchical dominance relationships at picnic table 7 and elsewhere. There was no real defense of an individual's central area except during the breeding season, and even then it was not consistent.

Inconsistency of defense was correlated with several factors. First, the males with bordering nest areas were more consistently and persistently chased out than were strangers and jays low in the hierarchy, as in the Blue Jay (Hardy, 1961). Second, because Steller Jays live in forested environments, they have few good lookout perches such as are used by Scrub Jays, which inhabit lower and more open vegetation. Steller Jays generally cannot see intruders in their entire area of dominance from any one perch. There was no patrolling of borders, no advertising song, and no "sentry duty." Jays giving certain calls, such as the *shook* or *tee-ar*, were sometimes answered by other jays throughout the study area but territorial proclamation did not seem to be the principal function of any song or calls.

During the peak period of courtship, resident pairs seemed almost to seek the stimulation of encounters with neighboring pairs. A pair would go to its mutual border with one or more neighboring pairs and all participating pairs would engage in vigorous threat calling and displaying (Aggressive Sidling) followed often by courtship (Sexual Sidling, Circling, Song) when the birds returned into their home areas. First-year and unmated jays were frequently onlookers at these gatherings but were generally not observed to take part. These gatherings had the superficial appearance of gregarious, communal courtship parties; but generally only threat display was observed in the group. In the simplest case involving only two pairs the males of each pair generally approached each other calling loudly (*shooks, waks, too-leets*) to within twelve inches while the females stayed either a little behind or beside them and also called. The males generally called and displayed at each other and the females probably also to each other. In these groups males did not generally display to females. As the threats died down the pairs would separate into their own areas and begin courtship (Sidling, Circling, Song).

At this time, generally in March and April, the females appeared to take the initiative and fly where they pleased; the males followed their mates closely. It is possible that this threat activity was motivated as much in defense of the mate as in defense of the nesting area, since such threatening bouts at mutual borders usually occurred in the presence of the females. However, when courtship was observed, it was always between members of a mated pair or a pair in the process of formation; no actual competition for females by courting males was observed in this context. An individual female was courted only by her mate, with but rare exceptions. No unmated females were ever recognized in the gatherings.

One pair watched during this phase in the course of an hour indulged in such group encounters with three neighboring pairs in succession. This resulted in great amounts of noise all around the extreme perimeter of the pair's area of dominance.

As already mentioned, during the incubation phase the male's area of dominance appeared to become smaller and the boundaries less intensely defended. It was not possible to make many observations during the phase in which young fledged, but no increase in area defense was noted while the young were being cared for. The peak intensity of defense correlated with the time of courtship rather than the time when the young were being fed.

NATURAL DOMINANCE HIERARCHIES IN OTHER SPECIES

The information available on dominance hierarchies of the Steller Jay differs in one important respect from that for other species. In the Steller Jay the rank order of individuals was found to be strictly dependent on the location where the observations were made, not only for the first-ranking individual, but also for others. Unfortunately, however, in none of the other species was rank order investigated quantitatively at more than one feeding station.

Brian's (1949:148) statement for the Great Tit that "each male could be said to possess a field of influence diminishing outwards from a locus in which he was most frequently present" shows her belief in the existence of a situation in winter similar to that of the Steller Jay; however, she made observations on dominance relationships at only one station and did not give quantitative data for other stations to support her statement. By moving the feeding station back and forth between the home areas of two neighboring males she was able to demonstrate a shift in dominance between those two individuals depending on location. This was also done with the Steller Jay, with similar results.

In a winter dominance hierarchy in the Black-capped Chickadee (*Parus atricapillus*) "the three top males were the ones that remained on or near the winter feeding range to establish territory and nest" (Odum, 1942:522). Although considerable attention was given to the winter flock, no attempts to demonstrate differences in rank order within the flock dependent on location were made. The possibility remains, therefore, that dominance in this species is dependent on locality in somewhat the same manner as in the Steller Jay.

In a stable winter flock of Blue Tits the rank of the top five individuals at one feeding station was inversely correlated with the distance from the feeding station to the areas in which they roosted and later bred (Colquhoun, 1942). Whether the birds lived in flocks of relatively constant composition and rank order during the day or whether the flocks were constantly changing in composition and rank order according to their location, as in Steller Jays, was not established.

In winter flocks of Tree Sparrows, *Spizella arborea*, Slate-colored Juncos, *Junco hyemalis* (Sabine, 1949), and Oregon Juncos (Sabine, 1959) linear hierarchies existed at the feeding stations but no systematic dominance observations were carried out elsewhere to ascertain whether the rank order was the same throughout the flock's foraging area. Evidence that dominance was related to topography was found in the low rank of the individuals which came to the feeding station from outside the flock, the relatively constant flock composition, and constant flock foraging area. However, dominance was not found to be related to topography in these species in the same way as in the Steller Jay, since there were in the Steller Jay no flocks of constant composition or constant foraging area. The composition of aggregations of Steller Jays depended primarily on the location and varied from place to place.

In a study of winter dominance relationships of White-eyes (*Zosterops lateralis*) in which much larger flocks were involved than in the other species studied (up to 500 individuals in mid-winter at one feeding station), the effect of "prior residence" soon became ineffectual as the flock size increased (Kikkawa, 1961). This species, therefore, because of its large flocks and probable lack of a strict dependence of the rank of each individual on topography is more similar in its dominance relations to the juncos and Tree Sparrows than to titmice and Steller Jays.

The species in which dominance hierarchies have been studied in nature differ prominently in degree of permanent residency and in constancy and integrity of flock composition. In the Slate-colored Junco, Oregon Junco, and Tree Sparrow, the winter flocks were of relatively constant composition and seemed to be composed entirely of non-residents; evidence for correlation of rank with distance from the home area was confined to whether or not an individual was an outsider to the flock. In the resident Black-capped Chickadee, Blue Tit, Great Tit, and Steller Jay the flocks tended to have less integrity, and the evidence indicated a close dependence of rank on distance from the nest area. Therefore, although natural dominance hierarchies have been demonstrated in all these species they differ importantly in dependence of rank order on topographical relationships. It appears that in species with a hierarchical social organization in winter the more use individuals of a species population make of their breeding areas, the more dependent rank order is on topography. Data on more species would be desirable to substantiate this assertion.

The data for *Zosterops* suggest that flock size and gregariousness may also tend to minimize the effects of area attachment on rank order. However, too few species have been studied for this to be generalized at present.

DOMINANCE HIERARCHIES AND TERRITORIALITY

The close relationship of dominance hierarchies to classical territoriality may be seen by considering the series from (1) the two species of juncos in winter, with probably only a little dependence of rank on area, (2) through the titmice and Steller Jay, with a combination of hierarchy and strong dependence of rank on area, (3) to the classical cases of year-round territoriality, for example, the Robin, *Erithacus rubecula* (Lack, 1953), and the Wren-tit, *Chamaea fasciata* (Erickson, 1938), in which aggressiveness is apparently usually too great even in winter for flocks or even temporary gatherings to form. A similar series of stages is found in the seasonal change from winter flocks to summer territories in juncos.

The existence of these series suggests a common element, aggressiveness, expressed to different degrees. Probably this common element will be found to be a composite of several factors, but at this stage of analysis in comparative avian sociology it seems useful. Viewed comparatively in this way, topographically oriented aggressiveness seems antithetical to gregariousness. Hinde (1952) expressed a similar view stemming from his detailed study of one species, the Great Tit. Davis (1959:220) presented data which he felt supported the similar hypothesis that "a continuum exists from situations that are exclusively territorial at one extreme to those that are exclusively rank." He also mentioned the importance of population density.

Sabine (1959) felt that the dominance hierarchies in the flocks of juncos studied by her were not so much an expression of aggressiveness as of "intolerance." The maintenance of the hierarchy despite the infrequency of actual fighting led her to doubt the importance of aggressiveness. In the hierarchies of Steller Jays, however, aggressiveness was definitely related to the rank order. Aggressiveness was highest in a male's home

area, where he also had priority at all food sources, natural and artificial. Sabine's "intolerance" would appear to be the combined result of aggressiveness in individuals and the awareness of it in other individuals, that is, avoidance.

The rarity of actual fighting in Sabine's junco hierarchies is a characteristic of all stable avian dominance hierarchies which have been studied and is to be interpreted not as a lack of aggressiveness but as a result of the hierarchical organization. Probably threat behavior would have been found to be more common than actual fighting in Sabine's birds, as it was in the Steller Jay, but this was apparently not studied by Sabine.

SUMMARY

Dominance relationships and social organization were studied for three years in a color-banded population of Steller Jays in a public park near Berkeley, California. Paired males and females were permanently resident in the same nesting area. Dispersal was accomplished through movements of first-year birds in late autumn and early winter.

The dominance relationships of the Steller Jays which visited any point in the study area could be summarized in the form of hierarchies. Unlike earlier studies of other species, these hierarchies were shown to exist in every month of the year and not to break down during the breeding season. At each feeding station the rank of each individual bore a direct relationship to the distance from the nest area of that individual. In addition it was shown for the first time in any species that in a linear series of feeding stations the rank of any given individual decreased with increasing distance from its nest area.

These data indicate that the dominance relationships of an individual Steller Jay may be conceived as a series of concentric zones of diminishing dominance rank from the center of its nesting area outward. Consequently, the dominance relationships within the population may be better generalized as many such series of concentric zones each overlapping with many others (depending on population density), than as a mosaic of discrete territories.

Males held the top positions in the hierarchies at all seasons. Encounters between the sexes were least frequent in relation to intrasexual encounters during the breeding season. At that time supplanting encounters between members of mated pairs ceased to occur. Females were most successful in supplanting males in the winter but were least successful at avoiding being supplanted by their mates at the same time. They were least successful in encounters with males during the period of molt in August and September.

The rank of the male and female members of a pair were not invariably related to each other when outside their own nesting area. In the pair's own nest area the male dominated all other males, and the female, all other females. Males did not help females in encounters with females, nor did females help males in encounters with males.

The hierarchies were generally linear. Inconsistencies in the records of wins and defeats occurred during the initial phase of establishment of dominance of one individual over another, during cases of mistaken identity, and during actual changes in dominance. Triangular dominance relationships were uncommon; most resolved themselves into a linear order within a month or two.

Scrub Jays were generally dominant to Steller Jays in all parts of the study area in all seasons, except directly under an active nest of a Steller Jay.

During winter the hierarchies were stable; but in spring, summer, and fall the relative ranks of individuals changed fairly often, although not usually by very much. In the course of over a year's observations of dominance at one location numerous small

changes in rank occurred, but only one large change occurred. The latter resulted when a male ranking in the lower third of the hierarchy mated with the dominant female at that location; he then gradually rose to the dominant position over a period of three months. The small shifts in rank among the other individuals were correlated with such events as changes in nest location, phase of the nesting cycle, and stage of molt.

It appears on the basis of comparative studies that in species with winter hierarchies the more use individuals make of their breeding areas in winter, the more dependent rank order is on topography. The close relationship between hierarchical and territorial behavior is emphasized.

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