THE WINTER SOCIETY OF THE OREGON JUNCO: INTOLERANCE, DOMINANCE, AND THE PECKING ORDER

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In an earlier paper the writer has described the assembly and integration of two winter flocks of the Oregon Junco (*Junco oreganus*), one observed in the Deep Springs Basin in Inyo County, California, and the other in Seattle, Washington (Sabine, 1955, 1956). Such winter flocks are stable in membership, with remarkably little absenteeism day by day, and the flock has a definite foraging circuit in which its members move, though the flock does not always move as a unit. The present paper is a study of close-up social relations between individual birds within the same two flocks or, in other words, of intolerance and dominance. The materials and methods used were those described in the earlier studies, the indispensable feature of the method being the color marking of the birds in such a way that each could be readily distinguished as an individual. A still earlier paper (Sabine, 1949) showed that intolerance and dominance in a winter flock of Slate-colored Juncos (*J. hyemalis*) are similar to those here described in the Oregon Junco though not in all respects identical with them.

The pattern of dominant and subordinate behavior displayed by foraging juncos has three main characteristics.

1. Even when the birds are not individually recognizable, casual observation shows a continuous display of behavior between pairs of juncos that in appearance is hostile—pecks and runs by one bird and retreat, avoidance, or occasional resistance by another. The words "peck" and "retreat" are used as shorthand expressions for a considerable variety of behavior, which will be described later. The bird which by pecking can induce another to retreat is said to be dominant to that bird, and the bird which retreats is said to be subordinate. As here used these words are meant to carry no presumption about the motivation of this behavior, of actual hostility or aggression or object-directed competition between birds related as dominant and subordinate. For reasons given later the writer believes that description of dominant-subordinate behavior in the junco may be distorted by any such presumption.

It is a distinctive feature of this behavior that it invariably takes place between two birds at a time and two only. The writer has never observed a case in which more than two birds appeared to be involved at once. Dominance-subordination in the junco is therefore a two-individuals relation within an assemblage of juncos. These twosomes hereafter will be referred to as "pairs" but nothing is implied regarding sex of either member.

2. When juncos are so marked as to be individually recognizable, it becomes apparent that the dominant-subordinate relation is, in a very large proportion of cases, permanent; the dominant bird of the pair is always dominant and the subordinate bird is always subordinate. It is true that in a winter flock of juncos a certain number of "reverse pecks" are observed; that is, cases in which a bird shown in a considerable number of contacts to be dominant is pecked by a bird that is generally its subordinate. As will be explained later, most such reverses occur sporadically and do not affect the relationship. But there are also a very few cases in which the order of the birds in a pair seems to be reversed, or in which the birds seem to be evenly balanced. These cases will be discussed later. In general, however, pair relations are fixed and stable. This fact was observed also in the case of the Slate-colored Junco (Sabine, 1949), and it has been noted in many species. It seems reasonable, therefore, to regard the permanent pair relation as an important factor in the social organization of the junco.

3. Within any group of wild, free-living juncos there is a linear order or ordinal

scale of dominance. As with some domestic birds the pair relations of juncos can be arranged in a pecking order of characteristically hierarchical or straight-line form. There is an alpha bird which can peck all others, a beta bird that can peck all but the alpha bird, and so on down to an omega bird that can peck no other. There are, to be sure, exceptions to this general rule, namely, triangular relations such that A pecks B, B pecks C, and C pecks A. These will be discussed later. The pair relations in these triangles are as permanent as those in the more common linear relations, though they violate the ordinal scale.

	ND	RN	CB	CR	OC	G	Y	AB	R	AO	CZ	NO	JO	PS	AD	BG	JD	GR	OG	CT	RS	LJ	JG	NJ	YJ	O	SA
ND		4	10	7	12	5	9	11	14	7	8	4	4	5		1		4	8	1			12	7	1	4	2
RN			6	25	15	16	7	6	12	3	16	3	2	5	7	4	2	2	2	1	1		3	5	2	12	6
CB	1^R	1^R		16	25	17	5	9	25	10	13	5	6	6		5	1	9	5	3		1	8	6	1	18	8
CR					19	17	12	19	24	12	20	14	5	16	4	4	3	5	8	2			6	15	5	14	8
OC						20	11	15	1	20	27	8	10	20	3	2	2		11	1	12	3	13	19	4	28	12
G							6	12	13	7	13	7		5		11	2	4	10	10	6	4	11	9	3	22	7
Y	1^R					1^R		17	7	6	9	2	3	6		2		1	3	1		4	3	2		10	
AB									12	5	9	17	7	16	1	7	3	36	15	7	2	1	4	17	6	39	22
R					26			2^R		19	22	6	9	5		2	3	1	5	1		2	6	7	1	18	6
AO								4			2	1	6	6		1		3	3	4	1		1	4	5	6	3
CZ				2^R		1^R		5	3^R			13	3	17	1	5	5		6	3	5		5	11	4	13	2
NO						1^R					3^R		4	18	7	3	2	1	6	3	8	6	5	3	7	18	5
JO									1^R					6	2	3	3		1	3	1	5	4	3	2	23	1
PS	1^R										1^R		1^R		5	11	2	23	13	16	11	9	12	19	9	7	19
AD						4					2					1	1	1	2	2		1	2				2
BG												1^R		1^R			1	5	5	3		5	3	1	14	11	11
JD													1^R	4		1		7	1	2	1		3	4	2	7	6
GR	2^R				12				21		10	12	11	1^R		1^R			11	3	7	3	5	17	8	32	5
OG										1^R						1^R				2	4	2	3	4	5		3
CT																1^R			1		18	9	9	2	15	16	12
RS									2						1							1	2	2	4	4	6
LJ							1^R						1^R			1^R							1	2	1	10	3
JG																								6	4	3	3
NJ						1^R					1^R	1^R	4			2	2^R				1	2			3	21	4
YJ																							3			9	3
O					3^R				1^R		3^R			24	5		1^R		17	8	2^R	1^R	12				19
SA						1^R														1^R							

Fig. 1. The scale of dominance for 27 birds of the feeding station flock at Deep Springs.

A linear pecking order is evidenced by a significant predominance of triplicate relations that fall into a transitive order over those which do not. There is no necessary relation between the permanence of pair relations and the possibility of arranging them in a linear hierarchy, though sometimes it seems to be assumed that there is (*e.g.*, Collias and Taber, 1951). A pecking order might exist such that every bird in it was involved in a triangle. Such a state, or an approximation to it, has been observed in a mixed group of free-living juncos and Tree Sparrows, *Spizella arborea* (Sabine, 1949), in a group of captive cocks (Masure and Allee, 1936), and in a group of hens of different breeds (Potter, 1949).

DESCRIPTION OF THE FIGURES

In deciding that an observed contact between two birds provided evidence of dominance or subordination, the following criteria were used. Every contact recorded was observably two-sided: the peck was a positive approach or gesture by one bird, taken to be dominant, and the retreat was a positive withdrawal by another, taken to be subordinate. One-sided contacts, in which the subordinate seemed merely to avoid, were frequent and commonly agreed with the evidence afforded by complete two-sided contacts. But what looked like avoidance might be merely a random movement made in foraging, and since the initial purpose was to establish with certainty the existence of a hierarchy, avoidance was not counted as a proof of the relation between two birds. For reasons to

	NW	RA	W	SO	QL	C	ZN	EN	CL	GA	YN	T	LB	CG	3X	RY	N	AT
NW		2	1	4		3	9	5	2		2	1	2				3	2
RA						2		1	1	2		1	3	1				
W				1			4		4	6	7			1	1	2		1
SO					2	7	8	7	4	2		6	12	4		1	2	3
QL						1	6	1	4	2		1	1				1	
C	1^R			1^R			5	5	7	5	3	8	2	1		2	3	2
ZN				1^R				7	10	5	3	3	14	1		2	2	1
EN									2	1		8	4			1	5	
CL	1			1^R	1^R		1^R	1		4	6	7	11	2	1	3	2	1
GA	1										16	9	27	3	9	7	1	4
YN									1^R			3	7	1	5	4		3
T	1			1^R	1			1^R					7				4	
LB														7	4	1	7	5
CG												1				2	1	
3X																2	1	1
RY			1										3					
N																		
AT																		

Fig. 2. The scale of dominance for 18 birds of the dairy flock at Deep Springs.

be given later this choice does not imply the conclusion that they were not indicative of the relation. No contact recorded in the figures was such that either the peck or the retreat could be regarded as inferential.

All contacts in which the outcome was not entirely clear to the observer were of course excluded. The ritualized fights usually fell in this category, because in the flurry of the event the two birds often could not be distinguished, or often both birds perched so that there was no clear evidence as to which was dominant. In some cases, however, a fight occurred between two birds whose pair relation was already well proved, and the subordinate left the station or the dominant returned to the feeding place where the fight started. If similar behavior was observed between two birds of unknown or not well authenticated rank, it was presumed to indicate dominance and was so recorded. Apart from relatively clear cases of these two kinds, fights were not counted. Fights of any sort made up an inconsiderable portion of the contacts observed.

The figures summarize the quantitative aspects of the data on pair relations and the pecking order, figures 1, 2, and 3 for the birds at Deep Springs and figure 4 for those at Seattle. The letters are symbols for the color markers (as R for red) and give the names of the individual birds. The top horizontal row of letters arranges the birds in the order of their rank in the hierarchy with the alpha bird at the left. The left-hand vertical column gives the same list with the alpha bird at the top. The Arabic numerals record the number of contacts observed. Thus, for example, figure 1 may be read from left to right as follows: ND was observed to peck RN four times, CB ten times, and so on across. Or the figure may be read down: SA was pecked by ND twice, by RN six times, and so on down. ND was regarded as having the highest rank because it pecked all the birds with which it came in contact and these included all the other high-ranked individuals. SA, on the other hand, was subordinate in all of its pair relations.

It is evident that in a figure thus constructed, all the numbers would fall in squares above a diagonal drawn from the upper left to the lower right-hand corner, if the pecking order were purely linear with no triangles or reverse pecks. Hence the numbers entered below the diagonal record irregularities, exceptions to a linear pecking order or possibly to the permanence of dominant-subordinate relations. It is convenient to refer to relations recorded above the diagonal as regular and those below as irregular. The occurrence of irregularities often makes it necessary to decide which of two possible arrangements gives the closest approximation to a smooth scale of dominance, since the position to which each bird is assigned is finally determined not only by its relation to adjacent birds but to all others. The principle followed in making the figures is that the arrangement to be preferred is that which gives the smallest number of significant entries below the diagonal.

Some numbers below the diagonal are marked with a superscript R to signify a reverse peck. It is intended also by the use of this symbol to indicate a distinction between data regarded as incomplete (roughly a quarter of the pair relations recorded in figures 1 and 2) and data deemed to be reasonably adequate to show which bird of a pair was probably dominant. The observer of free-living wild birds has no control over what is presented to him, and inevitably data relative to some pair relations are lacking or scanty. Moreover, to make trustworthy observations of contacts between small, swift-moving birds, the observer must focus his attention on a relatively small portion of the feeding station at a time; anything that happens outside that portion is lost. It is estimated that the contacts observed were probably about a quarter to a third of those that actually occurred at the station. If no contact was observed between two birds, the square in which that contact would have been recorded is blank. If the number of contacts observed was very small, the number was recorded but it was not regarded as conclusive.

	I ND	I RN	I CB	I CR	I OC	I G	I Y	II RA	I AB	I R	I AO	II NW	II W	I CZ	II SO	II QL	I NO	I JO	II C	I PS	II EN
I ND		4	10	7	12	5	9	2	11	14	7	8		8	3	2	4	4	1	5	3
I RN			6	25	15	16	7	5	6	12	3	4	1	16	2		3	2	8	5	3
I CB	1^R	1^R		16	25	17	5	6	9	25	10	3	7	13	5	1	5	6	4	6	6
I CR					19	17	12	6	19	24	12	3	2	20	2	1	14	5	10	16	4
I OC						20	11	3	15	1	20	5	1	27	4	1	8	10	6	20	4
I G							6	4	12	13	7	3	2	13	7	1	7		10	5	5
I Y	1^R					1^R		5	17	7	6	4	3	9	4	2	2	3	7	6	3
II RA				1^R	4		1^R		8					4			4	2	2	2	1
I AB										12	5	6	3	9	1	3	17	7	8	16	7
I R					26				2^R		19	5	2	22	7	1	6	9	2	5	3
I AO									4					2	1	1	1	6		6	1
II NW								2					1	2	4			1	3		5
II W		5	2^R		2				1^R	4	1			5	1			1			
I CZ				2^R		1^R		1^R	5	3^R		1			4	2	13	3	5	17	8
II SO									9					1^R		2	1		7		7
II QL																	1		1	1	1
I NO						1^R						5	2	3^R	1			4		18	2
I JO								3		1^R										6	2
II C							2^R		1^R	2		1^R			1^R					3	5
I PS	1^R												6	1^R				1^R			3
II EN														3^R							
I BG																	1^R			1^R	
I GR	2^R				12					21			3	10		1	12	11		1^R	
I OG											1^R										
I CT																					
I LJ							1^R											1^R			
I JG																1					
I NJ						1^R								1^R			1^R	4			
II ZN								1	3	11					1^R						7
II CL												1			1^R	1^R					1
II GA			1									1									
I YJ																					
I O					3^R					1^R		1		3^R						24	
II YN																					
II T												1			1^R	1					1^R
II LB			1^R																		
II CG							1														
I SA						1^R															
II 3X																					
II RY													1								
II N																					
II AT																					

Fig. 3. The scale of dominance for 42 birds of the total flock at Deep Springs.

I BG	I GR	I OG	I CT	I LJ	I JG	I NJ	II ZN	II CL	II GA	I YJ	I O	II YN	II T	II LB	II CG	I SA	II 3X	II RY	II N	II AT
1	4	8	1		12	7	10	5	1	1	4	2	2	1		2		1		2
4	2	2	1		3	5	1	12	8	2	12	2	2	1	1	6	1			2
5	9	5	3	1	8	6	3	15	9	1	18	2	1	10		8		3		2
4	5	8	2		6	15	4	10	5	5	14		1	4	1	8	1	1	2	5
2		11	1	3	13	19	9	9	13	4	28	3	2	5	2	12		1	2	6
11	4	10	10	4	11	9	2	7	14	3	22		5	4	2	7		3		3
2	1	3	1	4	3	2	6	12	5		10	3	3				1	1		
2	1	1	1		1	3		1	2	1	3		1	3	1					
7	36	15	7	1	4	17	1	6	8	6	39	10	8	17	4	22	1	4	5	5
2	1	5	1	2	6	7		5	6	1	18	2		3		6		1	1	4
1	3	3	4		1	4	1		2	5	6	3				3		1	1	2
		1		1	2	3	9	2		1	1	2	1	2					3	2
2			1	2	4	1	4	4	6	1	11	7			1	3	1	2		1
5		6	3		5	11	10	4	6	4	13	3	6	2	2	2			2	3
2	1	2			3		8	4	2	1	11		6	12	4	2		1	2	3
		1			1		6	4	2		2		1	1					1	
3	1	6	3	6	5	3		3	6	7	18	2	1	3		5	2		1	9
3		1	3	5	4	3	5	4	9	2	23	4		4	3	1		4		5
	1	5	2		5	1	5	7	5			3	8	2	1	2		2	3	2
11	23	13	16	9	12	19	6	6	13	9	7	8	4	9	1	19	2	3		4
	1	8	1		11			2	1	1	12		8	4		3		1	5	
	5	5	3	5	3	1		2	2	14	11	2	2	6		11		4	2	5
1^{R}		11	3	3	5	17	7	7		8	32		1	8		5	3	3	1	7
1^{R}			2	2	3	4	5		5	5		4	12	4	1	3	3		3	
1^{R}		1		9	9	2	1			15	16	1	1	11	6	12	1	5	1	1
1^{R}					1	2	2			1	10			1		3	1			
						6		9		4	3	6	.2	5	2	3	1	3		1
2				2			6	7	8	3	21	4		7		4	1	1	1	
1			2		6			10	5	2	9	3	3	14	1	1		2	2	1
1		10				2^{R}	1^{R}		4	3	7	6	7	11	2	9	1	3	2	1
	20	1^{R}	4	3	8					4	15	16	9	27	3	9	9	7	1	4
						3					9					3			1	1
		17	8	1^{R}	12			1^{R}				1	12	15	10	19	4	9	6	7
	3	1^{R}	1			1^{R}		1^{R}		1	3		3	7	1	8	5	4		3
					1									7					4	
			1^{R}							5					7	18	4	1	7	5
													1			2		2	1	
			1^{R}										2				1	2	4	
																		2	1	1
														3						
					1															

Fig. 3 continued. See opposite page.

The distinction was drawn between cases where 3 or more contacts were observed and those where 2 or fewer were observed, since inspection of the data suggested that this was a reasonable dividing point. Thus, if the number above the diagonal is 1 or 2 with no record below, or if the number above the diagonal is 0, 1, or 2 with 1 or 2 below, no symbol is inserted, but if as many as 3 contacts are recorded, reverse pecks are indicated by an R beside the number below the diagonal. For example, in figure 1, OG pecked CT twice while CT pecked OG once and no symbol is used, but JO pecked PS 6 times while PS pecked JO once, and the symbol R appears against the number 1.

A number larger than 3 below the diagonal with a small number of the corresponding square above the diagonal usually indicates the existence of a triangle or triangles. There are also a few pairs that call for special remark, which will be supplied beyond.

The number of contacts recorded is as follows:

	Number	Per cent
Figure 1		
Regular	2414	90.8
Irregular	245	9.2
Total	2659	100.0
Figure 2		
Regular	439	95.9
Irregular	19	4.1
Total	458	100.0
Figure 3		
Regular	3945	90.6
Irregular	410	9.4
Total	4355	100.0
Figure 4		
Regular	1954	90.1
Irregular	215	9.9
Total	2169	100.0

COMMENT ON THE FIGURES

The total flock at Deep Springs was formed by the amalgamation of two flocks that were originally separate (Sabine, 1955). One assembled at the feeding station at the end of the fall migration and was resident there throughout the winter (referred to as the feeding station flock). The other (referred to as the dairy flock because it was first seen near the dairy barn) originally had its own foraging circuit; but on December 7, 1948, it combined with the feeding station flock, abandoned its foraging circuit, and adopted that of the feeding station flock. The amalgamation was complete, with no show of hostility by the birds of one flock toward those of the other. The feeding station flock was thus in possession of the foraging circuit for a month or more before the dairy flock moved in. Figure 1 records the quantitative data on dominant-subordinate relations and the pecking order in the feeding station flock. In all, 30 birds were marked (Sabine, 1955, table 1); but three disappeared almost as soon as observations began. Of these one is known to have died and the others probably fell prey to predators. Figure 1 includes the remaining 27 birds. Figure 2 gives a similar record for the 18 members of the dairy flock. These data are relatively meager. For reasons explained in the earlier article, the color marking of these birds was delayed, and only about three weeks of observation remained before the beginning of the spring migration.

Figure 3 gives the scale of dominance for the birds of the total flock at Deep Springs. It consists of 42 birds rather than 45 because three birds (AD, JD, and RS) included in figure 1 had disappeared before the amalgamation took place. Figure 3 repeats the entries of figures 1 and 2 and adds the contacts between a bird of the feeding station flock and one of the dairy flock. To permit such contacts to be readily distinguished, a Roman I has been placed against the names of birds belonging to the feeding station flock and a Roman II against the names of birds belonging to the dairy flock.

	OR	TM	TW	W	YM	OW	YW	CG	Y	LC	C	LG	GP	L	P	GM	TR	CM	R	Q	YR	ML	OG	OC	TC	PR
OR		21	25	14	5	5	10	6	10	6	4	3	9	2	7	5	6	1	18	3	3	7	3	4	3	7
TM			13	33	5	9	6	12	10	11	3	7	15	4	15	4	2	3	9	9	1	6		3		12
TW				10	1	3	7	5	6	8	8	3	2	6	4	6	1	2	8	11	3	2	1	2	2	3
W					9	9	9	8	17	12	16	12	19	9	7	3	4	4	20	14	7	5	7	11	8	6
YM						8	1	5	4	3	1	1	3	1			4	2	1	3	1	2	2			2
OW					1^R		9	10	6	7	1		2	3	9	1	2		8	2		6	1	2	7	7
YW								4	14	1	7	7	4	7	9	8	7	1	4	2	5	3	1	5	4	10
CG							1^R		8	14	7	3		5	3	10	7		4	1	2		2		1	2
Y										8	7	7	11	5	14		4	1		9	1	3	3	4	6	7
LC						1^R	9		1^R		9	9	2	2	10		10	1	7	5		5	2	1	5	2
C					7							8	17	8	19	11	5		15		6		4	17	6	9
LG						4							14	8	14	17	7	1	27	9	11		4	20	14	9
GP								4	2^R	1				5	19	6	3	1	21	7	9	5	4	4	6	7
L													1^R		14		2	2	4	2	1		1	6	4	4
P					8	1^R			1^R							19	10	1	22	13	16	13	4	20	20	6
GM					11	16			6	6				5			9	1	7	8	2	9	3	7	5	1
TR						5								1				6	19	5	2		6	3	7	14
CM					1			2	1										1	1	3	3	1	5	1	2
R							1^R		23	1^R			1^R		1^R					7	7	9	3	5	1	1
Q											10			1					1^R		6	4		2	2	3
YR											2^R	1^R							1^R			3	3	6	4	
ML					2						8	4		12			5	1^R		1^R			1	6	5	3
OG																		3						3	1	2
OC													1^R						1^R						10	5
TC													1^R	1^R					9					2^R		5
PR														1^R		4			12					3	2^R	

Fig. 4. The scale of dominance for 26 birds of the flock at Seattle.

Figure 4 is a record of dominance and the pecking order for the 26 birds composing the flock studied at Seattle. The composition of this flock differed in two respects from that of the flocks at Deep Springs: (a) Since juncos at Seattle are resident as well as migrant, a distinction could be drawn between 12 birds that appeared to be residents and seven which appeared to be winter residents only (Sabine, 1955, table 6). (b) During a five-week period of heavy snow, seven additional birds apparently belonging to other flocks regularly frequented the feeding station but detached themselves as soon as the weather moderated. Hence, the amalgamation of these birds with the flock, though apparently complete while it lasted, did not continue throughout the flocking season as did that of the dairy flock with the feeding station flock at Deep Springs. It should be noted that the addition of this considerable number of visitors did not disturb the pecking order of the flock as it had been prior to their coming. Pair relations both among the visitors and between a visitor and a member of either of the other groups were permanent and fell into a scale that included all three groups. Indeed, the same was true even of casual visitors which were presumably migrants. Juncos display no hostility toward such visitors and their pair relations can be placed in the flock's scale of dominance.

The quantitative aspects of dominant-subordinate relationships in the several flocks are substantially similar. Since the data in figure 2 are relatively scanty, and since the data in figure 4 present few peculiarities and nothing at variance with the observations at Deep Springs, the following comments refer for the most part to the data in figure 1.

Of the pair relations in figure 1 of which the number of observed contacts was insufficient to determine which bird was dominant, nothing need be said beyond pointing out that the records of 4 birds (AD, JD, RS, and LJ) yield 58 of the 93 squares in which such an insufficient number appears. These birds disappeared early in December before many contacts had been observed. It can only be assumed that, if observations could have been extended, irregularities would have been found among these pair relations in about the same proportion as among those which were better authenticated.

Of the pair relations recorded as conclusively determined, those require special mention or comment where an entry below the diagonal indicates an exception either to the linear hierarchy (a triangle) or to the permanence of the relationship between two birds (a reverse peck). When the data recorded in the figures are supplemented by taking account of the dates at which contacts occurred, however, two additional types of exceptions seem to be revealed, that is, cases in which the relation between two birds may have changed permanently and cases in which two birds may have been so evenly balanced that the relation was fluctuating or variable. The following comments are devoted to these four types of exceptions, which probably occur characteristically in junco flocks.

1. Triangular relations.

The most conspicuous departures from a linear pecking order are triangular relations, which occur in junco flocks as in flocks of domestic birds. A triangle is a triplet of birds whose pair relations are such that one bird is dominant to a second and the second to a third which, however, is dominant to the first. This relationship is independent of any order in which the pair relations are arranged. But if the pair relations for a flock can be arranged in a generally linear order, a triangle brings it about that a bird of lower rank in the hierarchy pecks a bird of higher rank, the ranking of each bird being determined by its position in the whole network of pair relations. The pair relation between the lower ranking and the higher ranking bird is permanent, like pair relations that fall in the linear order.

For example, in figure 1, the entry below the diagonal shows that R pecked OC 26 times while the entry in the corresponding square above the diagonal shows that OC pecked R only once. Yet OC must be placed higher in the linear order than R since OC pecked G 20 times, Y 11 times, and AB 15 times, while these three birds pecked R, respectively, 13, 7, and 12 times. R pecked none of these birds except AB and then only twice as compared with AB's record of 12 pecks against R. The number of triangles thus produced can be counted by considering all the birds involved by threes. In the example chosen there are 3: R—OC—G, R—OC—Y, and R—OC—AB. It happens, also, in this example that the data are sufficient to establish conclusively all the pair relations. Where this was not true, the same level of significance was used as in placing the symbol R: no triplet was counted as a triangle if it included any pair having a probability below 0.125. Thus, for example, the triplet GR—OC—BG was discarded because the pair OC—BG was evidenced by only 2 pecks. Thus counted, the number of triangles represented by the data in the several figures is as follows:

Figure 1	29 triangles
Figure 2	0 triangles
Figure 3	88 triangles
Figure 4	64 triangles

The position assigned to any particular bird in the hierarchy depends upon its relation to all the other birds of the flock, and the existence of triangles may leave an exact order indeterminable. If a group of birds is selected from a flock, their order may not be the same as it would be when they are considered in relation to other birds not selected. Thus, in one instance in figure 1, triangles are so related that the ranking for three birds, if these were taken as an isolated group, would be opposite to the order to which they are assigned in the figure; it would be GR—R—OC instead of OC—R—GR. A similar instance occures in figure 4: in the arrangement YM—P—GM the order of P and GM could be reversed, since a triangle of adjacent birds would permit the order GM—L—P instead of L—P—GM; but the order YM—GM—P, if these three birds were isolated, would become P—GM—YM. Similarly, the addition of more birds to a flock may unsettle the order as determined from the data for the initial flock. In figure 2, ZN is clearly higher in rank than EN, so far as the data in that figure are concerned. But in figure 3, which gives the hierarchy for the total flock at Deep Springs, several birds of the feeding station flock have to be placed between ZN and EN, and in the total flock EN has to be given a higher position than ZN.

Uncertainties of this sort may be a serious hazard in experiments on hierarchy that use small selected groups of birds or that transfer a few birds from one flock to another. Consider, for example, the six birds which in figure 4 are placed in the order Y—C—GM—R—Q—ML. The pair relations of these birds make five triangles, and every bird is involved in at least one. Any order for these birds will include irregularities, and the order which seems best will depend largely on relations between these birds and others in the flock. An experimenter who had the records only of the 6 would probably choose the order GM—R—Y—Q—ML—C as giving the best approximation to a smooth hierarchy. This factor of inherent uncertainty in a hierarchy that includes triangles may account for the fact that the rank of a hen in one hierarchy permits no prediction of its rank when it is transferred to another flock (Douglis, 1948).

The dominant-subordinate pair relations which run counter to the order of the hierarchy are as well authenticated and as permanent as those which are in line with it. The number of contacts supporting pairs that occur in triangles is in general as large as that supporting pairs which do not. In figure 1, 10 entries below the diagonal run from 8 to 26 contacts and 4 from 4 to 5, the latter usually involving birds with short records (*e.g.*, AD and JD). The numbers in the corresponding squares above the diagonal are no larger than those marked as reverse pecks below the diagonal. Though some birds were involved in numerous triangles (for example, GR in 18), nothing was observable in their behavior that seemed to account for their ability to peck birds of higher rank. Both in their role as subordinate birds and as dominant to birds of higher rank they behaved in all perceptible respects like other birds in subordinate or dominant positions.

Experiments on hens have shown that the position of a bird in the pecking order can be raised by suitable doses of the male hormone testosterone propionate (Allee and others, 1939), and this suggests that a linear order may reflect quantitative hormonal differences between individuals. The normal occurrence of triangles in flocks of hens and juncos, however, shows that relations in the pecking order are not invariably transitive and hence cannot be explained solely by such quantitative differences. Since it has frequently been observed that birds as well as other animals have an advantage on their own ground, it is natural to suppose that prior occupancy may be a factor in determining the hierarchy as it appears at any given place. The evidence for the influence of prior occupancy in the junco flocks here studied will be given later. It should be noted, however, that if an approximately linear pecking order results from quantitative individual differences, this does not necessarily imply that the order itself is a mechanism by which the flock is integrated.

2. Reverse pecks.

Reverse pecks (marked in the figures with a superscript R) are contacts in which the normally dominant bird of a pair retreats before a peck delivered by the normally subordinate bird. Such contacts occur, though not with great frequency, and are violations of the rigid permanence of pair relations, but as a rule they indicate no instability in the relationship and no tendency to reverse the usual order of dominance between the birds concerned. In figure 1, the symbol R is set against 38 entries below the diagonal and in 5 cases there is an entry above the diagonal corresponding to an irregular entry below. In 33 of these instances there was one reverse peck, in 5 there were 2, and in 5 there were 3, or 58 in all. The sum of reverse pecks was about two per cent of the total number of contacts, but the number of pair relations thus momentarily modified was about 17 per cent of the total, and 18 out of 27 birds were involved.

Reverse pecks occur most frequently in periods of hurried feeding induced usually by severe weather such as high winds, snow, or extreme cold. Under these conditions the birds run along the brush seeking a place to eat; they hover, fight, snatch a seed, trill, approach closely and return persistently if pecked. They eat rapidly and have the appearance of being preoccupied with feeding and of taking little notice of one another. In such conditions the ratio of reverse to normal pecks may for short periods rise as high as 1 in 20. Of the 58 reverse pecks just mentioned, 52 occurred under such conditions of tension. The remaining six occurred at times of no unusual tension; but these also did not alter the relation between the birds, even though in one case the subordinate forced its dominant to retreat by a fight.

The observations suggest that most reverse pecks are delivered, so to speak, by accident or inadvertence. Since some aspects of the junco's dominant-subordinate behavior depend on individual recognition (Sabine, 1956), there seems to be no reason why errors of recognition should not occur. If the reverse peck is a form of resistance elicited by difficult conditions of feeding, it is less effective in giving access to food than persistent return. Yet the possibility cannot be excluded that a reverse peck may rarely be an attempt to reverse the relationship. In the first observed contacts between O and OC, for example, the latter retreated twice before strong drives by O and postured and sidled as a subordinate often does when eating close to a dominant. Yet the relationship was eventually well established; OC pecked O 28 times.

3. Fluctuating dominance relations.

Though the pair relations of juncos are almost always a clear case of dominance on one side and subordination on the other, it appears to be possible that pairs may rarely occur in which the members are so evenly balanced that the relationship is unstable. When the dates at which contacts occurred are taken into account, this turns out to be a possibility with the pairs YJ—NJ and AB—CZ (fig. 1). On November 30, YJ and NJ each behaved as dominant relative to the other. On December 15 and 17, YJ was dominant to NJ, and on December 19 and January 2 NJ was dominant to YJ. No other contact was observed between these birds since NJ disappeared on January 6. Fourteen unambiguous contacts were observed between AB and CZ. In these AB was dominant to CZ on November 26, December 16, 17, 20, and 25 (2 contacts), and on January 11 and 19. But CZ was dominant to AB on December 15 and 22 and on January 3 and 22. On January 18, there were two contacts, AB being dominant in one and CZ in the other. In addition to these unambiguous contacts recorded in the figure, on January 23, CZ appeared to avoid AB, and on March 3, shortly before their migration, AB twice appeared to avoid CZ. In no case were these variable contacts characterized by resistance on the part of the bird that took the subordinate role. In figure 4 the pair OC—PR behaved similarly: OC was dominant on December 30, PR on January 15 and 25, OC on January 27, PR on January 28, and OC on January 31 and February 4 (2 contacts).

The hypothesis that these relations exhibit a virtual equality of dominance is somewhat strengthened by the fact that YJ and NJ were adjacent birds in the pecking order, as were PR and OC. AB and CZ, though not so placed in figure 1, may also be regarded as adjacent, since AB, R, and OC formed a triangle of adjacent birds and could as well have been placed in the order R—AO—AB. The order in the figure was selected because, when the dairy flock was marked, some of the new birds fell between AB and CZ and also between NJ and YJ, suggesting that there was some degree of inequality between the birds. Nevertheless, the facts here presented suggest that two birds in a given flock may be substantially equal and that some factor in the immediate circumstances may control dominance in a particular contact. The observations, however, failed to reveal any peculiarity of circumstance that might be supposed to explain the shift of dominance in these contacts.

Among the contacts recorded in figure 3, between a bird of the station flock and a bird of the dairy flock that occurred after the amalgamation of the two flocks, there are two (RA—OC and RA—JO) which may be variable. In three contacts on December 10, OC was dominant to RA but RA was dominant in one contact before that date and in four thereafter. JO was dominant to RA on December 12 and 15, but RA was dominant on December 29 and January 2 and 4. The data seem too scanty, however, to warrant giving much weight to the record of these pairs.

4. Permanent change in pair relations.

When the data in figure 1 are supplemented by reference to the dates at which the contacts occurred, it appears possible that the order of dominance between two birds may in some cases change permanently. When such a change takes place, the initial contact or contacts observed may be regular, in the light of the hierarchy as finally determined, or *vice versa*. There are five pairs in figure 1 where such a change may have occurred.

(a) JO—NJ. This alone of the five started as irregular and became regular. On November 30, NJ pecked JO once; JO made a small retreat, was pecked twice more, and finally was chased several yards. This sequence identified NJ as clearly dominant at this time. But on January 2, JO pecked NJ and again on January 4 (2 contacts). NJ disappeared on January 6.

(b) PS—O. On November 21, PS pecked O twice. Between November 22 and 25, three fights occurred between these birds. In the first O remained, assumed a threat posture, was pecked and retreated but did not leave. In the second, O retreated but soon returned. The third encounter was unusually violent; O retreated but returned and PS made an avoiding movement. Six hours later O was pecked and retreated. On November 30, O had a series of contacts with four birds (including PS) all dominant to itself and all retreated before drives on O's part of unusual speed. Thereafter, O was permanently dominant to PS though its relation to the other 3 birds remained as before.

(c) CT—O. On November 21, in five encounters, CT pecked O ten times, twice with three pecks in quick succession, and O did not resist. On November 22, two fights occurred between the birds after which O retreated, and later O retreated after an ordinary peck, as it did again on November 25. But by December 13, O was dominant to CT and so remained.

(d) PS—JD. PS pecked JD on November 30 and on December 7. But two hours later on the second date, JD pecked PS, as it did twice on December 15 and once on December 18. JD disappeared on December 23.

(e) AB—AO. On November 29, AB pecked AO once and on December 3, four times, three in quick succession. AO, however, pecked AB once on December 16, twice on December 22 in an unusually decisive way, and once on January 5.

In figure 4 the pair TR—OW similarly changed from regular to irregular. OW pecked TR on January 17 and 18, but TR pecked OW on January 26, 28, and 30, and on February 1 and 3.

In two respects the behavior which accompanied these possible changes of dominance suggests a comparison with behavior reported for experimental birds. (a) Permanent pair relations between hens are frequently settled at the initial contact of the birds, which may be a fight. Prior to two of the changes here reported, O had a series of fights with PS and CT in which the latter birds appeared to be victors. But O was the dominant bird shortly thereafter. With wild birds it is impossible to identify a contact as initial but perhaps with juncos a series of fights may be decisive in initiating dominance. As always the fights between O and the other two birds were ritualized. (b) It has been observed that dominant hens sometimes peck subordinates with unusual vigor shortly before a change of dominance takes place. In three cases, notably vigorous pecking by the then dominant junco preceded its displacement.

DOMINANCE AND INTOLERANCE

As was remarked above, the peck-retreat sequence used to identify dominance includes a considerable variety of actual behavior. The peck of the dominant bird may be a long swift swoop from a perch, a low-flying drive, or runs of varying lengths and speeds with the bill pointed at the subordinate. At close range a peck may be a short lunge with wings spread or, most often, hops of from 6 to 24 inches with the bill pointed. Correspondingly, the subordinate bird may fly away or it may merely withdraw to varying distances, sometimes only a few inches. In such cases it often edges around and approaches from behind. Frequently it will avoid a dominant without being pecked, or it will rise in the air and alight behind the dominant, especially if the peck is long. Occasionally it will make a show of resistance in a momentary flurry of bill-biting or by making the head-raising gesture, but as a rule resistance means merely that the subordinate refuses to leave or persists in returning. The writer has never observed a situation which suggested that resistance between dominant and subordinate, or the peck-retreat sequence of junco behavior, might threaten to break up the gregariousness of the flock, as intraspecific hostility might be expected to do.

It is highly characteristic of this behavior that the whole procedure seems to be completely ritualized. In the writer's experience the pecks practically never make contact, and injurious pecking certainly does not occur even in the most violent encounters. In a fight the two birds rise straight in the air to a height of 8 or 10 feet, apparently in an effort of each to get above the other; when clawing and pecking occur they are formalized movements rather than literal attacks. Apart from the infrequent fights, the peck may be reduced to a mere gesture or to the head-raising posture. Especially in conditions of crowded feeding the gestures tend to be narrowed. A slight shift of position with a minute pecking motion, a mere nod or even an intense stare, may cause a subordinate to avoid or withdraw. These gestures are sometimes so slight that they would almost certainly be imperceptible to a human being at a distance of 6 feet. In the behavior of the junco ritualization has been carried to a point where overt hostility is practically nonexistent. Yet in spite of an almost endless variability of actual behavior, the peck-retreat theme remains recognizable as a criterion for distinguishing a dominant from a subordinate bird: an approach by the latter induces a gesture from the former and this in turn induces avoidance or withdrawal.

It is tempting to describe this theme in terms of intraspecific hostility, pugnacity or aggression, of attack and resistance, of threat on one side and submission on the other. This is a usual, perhaps the most usual, interpretation of the dominant-subordinate relationship and of intolerance both in birds and in other animals. The position is sometimes stated in very general terms, as if it were a principle of animal behavior: for example, "Within the concept of aggression, dominance is pugnacity with social, and more particularly intraspecific, reference, and territorialism is pugnacity with spatial or topographical reference" (Armstrong, 1947: 283). From this point of view the relation between dominant and subordinate is interpreted as competitive and is contrasted with cooperative social relationships. Thus, a hen's status in the hierarchy of a flock is reported to be settled by the victory of the dominant or the submission of the subordinate, often at their first encounter, and fighting for status is described as characteristic (Collias, 1943). It is not certain, however, how far this observation can be generalized. Hinde (1952: 29, 155) found little evidence of fighting among tits to settle relations of dominance.

In accord with the view that identifies dominance with aggressiveness, competition is regarded as directed toward the possession of some object of advantage, such as food, mates, or territory, and fighting is reported to increase with shortage (Collias, 1944). Precedence to food is regarded as an experimental index to dominance. Subordinate birds, if starved, are reported to feed avidly in spite of severe punishment by dominants; their behavior is interpreted as a result of the conflict between "fear of a despot and degree of hunger," and it is held that fear may be quantified by "days of food privation" (Collias, 1950: 1078). It would seem to follow that deprivation should increase fighting, and that the amount of an animal's fighting should measure its aggressiveness and therefore its place in a scale of dominance.

At the same time it has been pointed out that, in the case of some experimental animals, the evidence on this point is not consistent (Seward, 1945). Rats and mice, when deprived of food or water for considerable periods, were found not to be more aggressive than when satiated (Hall and Klein, 1942; Ginsburg and Allee, 1942). It has also been regarded as anomalous that fighting in such cases may be more severe in the absence of food than in its presence and that high-ranked animals in a hierarchy do not always behave aggressively, as measured by the amount of their fighting (Scott and Fredericson, 1951). The latter point strongly suggests that "aggressiveness" is too indefinite to serve as descriptive of actual behavior. In particular, it suggests that the term has been used to cover at least two factors in behavior that may vary independently: the capacity of one animal to displace another, which defines it as dominant, and the expression of this capacity in recognizably hostile reactions or such as evoke in the subordinate a reaction that issues in fighting.

To describe the behavior of a dominant junco toward its subordinate in terms of pugnacity seems to the writer to be definitely inappropriate. What seems to be most apparent is that the behavior of the one bird is reciprocal to that of the other. For descriptive purposes a term seems to be required that will apply as well to the withdrawal or avoidance of the subordinate as to the peck of the dominant. The writer therefore suggests that, in the case of the junco, the term "intolerance" should be so used. What intolerance seems to be most clearly directed against is simply the proximity of another junco; it appears to be a spacing device that has the effect of leaving to each bird, whether dominant or subordinate, an area of privacy which another bird does not invade. As was stated in the earlier article, the behavior of juncos relative to each other seems best explained as actuated by two mutually limiting drives. "The winter residents are gregarious but they are also intolerant of the close proximity of fellow members of the species. The limits of tolerable proximity are elastic and vary with environmental conditions, but a reaction of intolerance may be said to be released by a second bird which is tending in one way or another to invade the area of privacy which the reacting individual maintains about itself. A subordinate bird may show its intolerance by avoiding a dominant bird; the latter shows its intolerance by pecking at, or otherwise gesturing at, the subordinate" (Sabine, 1955: 89).

The tendency of birds to maintain "individual distance" has been reported for several species (Conder, 1949). Emlen has noted it in perching and nesting Cliff Swallows, *Petrochelidon pyrrhonota* (1952*b*) and has remarked that a negative reaction to crowding is widespread and is particularly conspicuous in birds (1952*a*). Hinde (1952: 19, 26) has mentioned similar behavior in the Great Tit (*Parus major*). Both of the latter writers seem to regard the phenomenon as indicative of intraspecific hostility. Emlen describes intolerance as "functionally the antithesis of gregariousness," and Hinde places his account of spacing in the tit under the heading of "disruptive factors" and explains it as "aggressive behavior concerned with food." In the behavior of the junco, however, there is no evidence that intolerance of proximity is antithetical to gregariousness in any sense other than that the two drives mutually limit each other. Functionally they seem to be complementary. Nor is there any evidence that intolerance of proximity is disruptive. It is of course true that in a foraging flock the approach to food is likely to be an occasion of proximity between two birds and thus can give to peck and avoidance the appearance of competition for its possession. It does not follow that this appearance is the cause, and peck and avoidance between juncos occur commonly in situations where no food is involved. Intolerance in the sense of mutual avoidance seems to be a factor in integration and a part of the flock's social structure.

The point of view just sketched, which distinguishes dominance from pugnacity, questions its relation to competition for food, and regards intolerance as a spacing device, can be supported by four main types of evidence derived from observation of winter flocks of juncos. (1) When observation is concentrated on the subordinate bird, its behavior cannot plausibly be described as merely submissive, and there is little or no reason to believe that it is at a disadvantage in its access to food. (2) In the yearly cycle of junco behavior, the peck-retreat sequence plays different roles at different times, and these cannot all be covered by a concept so vague as aggressiveness. (3) The behavior of juncos in a winter flock shows little or nothing that can be clearly identified as aggressiveness, either interflock or intraflock, and there is no apparent relation between rank in the hierarchy and a tendency to peck. (4) Intolerance of proximity varies with conditions of crowded feeding, and it decreases rather than increases as feeding situations become progressively more competitive. The observations that support these statements are given below.

1. In order to form an adequate idea of the dominant-subordinate relation in a winter flock of juncos, it is important to attend especially to the behavior of the subordinate bird. This is indeed less dramatic than the peck of the dominant, but it is quite as distinctive and is equally characteristic of the relationship. Indeed, the writer's experience prompts the conjecture that the avoidance of the subordinate may be even more revealing or informative than the peck of the dominant. Conjectural comments put into the field notes before the data on pecks were reviewed and assembled were usually right,

with some errors due to the idiosyncratic behavior of individual birds. As the investigation was conducted, it was at first directed toward confirming the existence of a pecking order, but if it were known in advance that a species had such an order, a generally correct judgment about relationships in a particular flock might be reached more quickly by observing avoidances than by concentrating on pecks. Much subordinate behavior indicates the relationship when no movement by the dominant can be perceived. This is one consideration which led the writer to the conclusion that identifying dominance with aggressiveness is a hindrance to observation.

Carefully examined, the behavior of the subordinate does not give the impression of being without initiative or as being describable as simply submissive and a response to attack. It might better be described as resistance, though if this term were retained, it, too, like aggressiveness, ought to be shorn of any implication of pugnacity. A subordinate bird continually resists in the sense that it acts with reference to a dominant in such a way that the dominant's behavior is modified and the subordinate gains access to food. If dominance be defined as "determination of behavior of given individuals by other individuals" (Collias, 1944: 83), observation gives as much support to the view that the subordinate's behavior determines the dominant's as *vice versa*. The subordinate waits and watches its chance to eat; it remains on the outskirts, approaches cautiously, and if necessary scrambles away; it creeps slowly through brush or other cover; it comes toward the dominant from behind; it sidles and turns its back; it avoids quietly and sometimes ostentatiously; it darts in and snatches a seed. Its head-raising gesture is similar to that of the dominant. It returns again and again at short intervals, and in the end these tactics are often successful: the subordinate eats. Its persistent return is an effective answer to the dominant's peck, though it rarely if ever leads to behavior that disturbs the pair relation between two birds. What it seems to do is to wear down the dominant's impulse to peck. Observation has shown repeatedly that by its persistence a subordinate succeeds in feeding, while contrariwise a dominant bird impelled to continuous pecking is distracted from feeding. It is at least not obvious that pecking is the more effective means of getting access to food, and in the bitter winter of 1948–1949 at Deep Springs, the writer did not observe that low-ranking birds were prone to starvation.

2. The peck-retreat sequence in the behavior of juncos clearly covers a spectrum of functions which vary according to their place in the bird's yearly cycle of behavior. Apparently the junco simply lacks any mode of expression other than the pecking gesture. It may of course be true that ritualizations originate in the course of evolution as surrogates for fighting (Moynihan, 1955). It would not follow that, in a species whose behavior is so completely ritualized as the junco's, they remain aggressive as elements in evolved social behavior. Moreover, the elements of behavior, or the inherent drives postulated to explain it, must be functionally adjusted as factors in the yearly cycle that the bird is set to run through, and they must manifest themselves in correspondingly different forms. They can vary in intensity, in the way they combine and inhibit or are inhibited by other drives, and in the actual responses in which they issue under environmental and other stimulation. A small repertory of inherent drives, variable in intensity, combination, and form of expression, can give rise to a great variety of actual behavior. To refer it all to some general category like aggressiveness would appear to have little explanatory value.

Thus, in the case of the junco, slow and gentle pecking gestures on the part of the male are a phase of their courtship behavior, a form of pecking that cannot plausibly be called hostile, and from such gestures the female does not even flinch. Between a mated pair the kind of pecking that maintains distance in a winter flock is rare but it can occur, though with changes. Of the pair in the Seattle flock, OR the male and LG the female, that retained the area of the feeding station as breeding territory, OR had been far higher than LG in the winter hierarchy (fig. 4), yet if he approached closer than 6 inches, LG could and at least once did peck him off. In the mating phase there seems to be nothing that evokes the peck of the dominant bird; approaches and withdrawals have a different significance from what they have in the winter flock. If dominance is said to be transferred in this phase from the male to the female, its underlying physiology must have changed with the progress of the cycle.

Again, the type of peck and retreat that shows dominance in the winter flock is clearly distinguishable from another type that begins to be manifested at the opening of the breeding season—the long runs and selective pecking by which breeding territory is established. The latter has been described in connection with the dispersal of the winter flock in Seattle (Sabine, 1955). It differs from pecking in the winter flock in two respects: (a) It is discriminatory, directed by birds of a mated pair against specific birds, presumably rivals for the territory. Even in these cases the behavior was not overtly aggressive. No fights were observed and the birds pecked offered no resistance beyond refusal to depart. The pursuing male seemed rather to escort the other bird out of the territory than to try to catch it, a kind of behavior noted also in the Great Tit (Hinde, 1953). (b) The new type of pecking is added to that which evidences dominance in the winter flock but does not wholly supersede it. As long as the Seattle flock stayed together, dominant-subordinate relations remained intact with a single exception: the female of the mated pair became dominant to birds that had formerly ranked above her in the winter hierarchy.

The new type of behavior seemed to emerge smoothly from dominant-subordinate behavior in the winter flock. Its most obvious feature was that the mated pair became greatly more intolerant of the proximity of some other members of the flock. Intolerance of proximity seems to be a factor in all phases of the cycle, but its mode of expression changes with the physiological progress that leads from the winter to the mating phase. A somewhat similar change took place in the behavior of OR and LG toward their young. As these matured to the point where they could crack a seed for themselves, OR and LG became less responsive to their begging gestures, and finally OR chased them much as he had chased mature birds at the beginning of the mating season. This was clearly preparatory to a second brood, but the loss of LG prevented this from eventuating, and OR, in spite of continuous singing over a considerable period, failed to attract a second mate.

It is interesting also to compare the behavior of the junco with that of the Song Sparrow (*Melospiza melodia*), which is intensely intolerant, is solitary in winter, and has obvious difficulty at the onset of the breeding season permitting even the approach of its mate. Apart from the relations of the mated pair, the heightened intolerance of the junco at the dispersal of the winter flock makes its behavior look much like that of the Song Sparrow in winter. What seems to tie these examples together is that they are all variations in the utilization of space for activities appropriate to a phase in the bird's yearly cycle of behavior.

3. Recognizably aggressive behavior plays practically no role in the integration of a winter flock of juncos, whether in the form of interflock or intraflock hostility. The feeding circuit of the winter flock is in no sense a "defended area" (Allee *et al.*, 1949: 412), though the flock remains as a rule within its limits; it seems rather to be an example of spatial routinism. The birds make no display of hostility toward a casual visitor, and nothing is perceptible in their behavior analogous to the disorganization described as occurring when the membership of a flock of hens is rotated (Guhl and Allee, 1944). Two distinct flocks of juncos can amalgamate, as happened at Deep Springs, with no apparent

tension between the members of the one and of the other and with no apparent interval of disorganization while the amalgamation is taking place. A considerable group of visitors may regularly frequent a flock's feeding area for weeks, as happened at Seattle, with no display of hostility either by the visitors or by the members of the occupying flock; yet the visitors remained in some sense outsiders since they detached themselves as soon as the period of difficult feeding ended. In all of these cases, dominant-subordinate behavior between members of the flock and dominant-subordinate behavior between a member of the flock and an outsider were identical so far as observation showed. Pair relations were stable, and as may be seen from figure 4, the visitors presented no special difficulty in constructing a scale of dominance. The integration of a winter flock of juncos does not appear to depend in any degree upon interflock aggressiveness.

It is true, also, that in the behavior of individual juncos, no relationship can be perceived between high rank in the hierarchy and frequency of pecking or any other manifestation of behavior that is recognizably aggressive. A high-ranking bird may peck infrequently while a low-ranking bird may peck with great frequency, even though it is able to peck relatively few birds. At times, the writer is inclined to believe, this reflects what might be called "mood": the same bird does not always behave the same. In part the difference between birds seems to be idiosyncratic or, so to speak, temperamental, irrespective of rank in the hierarchy. Some birds seem to have a strong impulse to peck and others a weak one, and some peck at shorter distances than others. Some have a strong tendency to avoid and some are "good mixers"; the latter join aggregations of birds and peck or take pecks. In the Deep Springs flock, for example, the alpha bird ND (fig. 1) tended to stay aloof, and its approaches might be described not inaptly as tentative. Yet ND was unquestionably dominant to every bird in the flock; when it made its way through the brush to eat at a tray the other birds fell back with conspicuous promptitude. CT on the other hand, the twentieth bird of the flock, behaved in what seemed a very aggressive manner. One might say that CT seemed to enjoy pecking. Though there were only seven birds of lower rank, CT delivered 81 pecks to them, or an average of 11.6 per bird, while ND, having 26 birds of lower rank and making contact with 22 of them, delivered 140 or 6.4 per bird. Actually the discrepancy was much greater than the figures indicate, since CT disappeared on January 17 while ND's record ran until March 12. AO, the tenth bird, had almost no drive to peck yet its place in the scale was never in doubt; the nine birds above AO in the hierarchy pecked AO an average of 9.9 times per bird, but AO pecked 14 birds below it only 3.3 times. It is true that figure 1 shows a relatively high average number of pecks by the top five or six birds among themselves, but the observer gained no impression of a state of tension such as has been mentioned in the literature (Lorenz, 1935: 361). If the pecking was selective the writer was never able to observe the cues by which selection was made. There is nothing in junco behavior that suggests "persecution" of the omega bird sometimes reported in other species. In general there appeared to be no reason to identify high rank with any kind of behavior that was recognizably aggressive.

4. The view that intolerance preserves an area of privacy around a foraging junco does not of course mean that a bird keeps a standard distance irrespective of conditions. The area is elastic in two senses: it varies with different birds and it contracts or expands with different conditions of feeding. In respect to the first, there are almost certainly specific differences: a Lincoln Sparrow (*Melospiza lincolnii*), for example, will normally keep another Lincoln Sparrow at a distance of about 3 feet though it will tolerate a junco at about half that distance. Among juncos there seem to be both varietal and individual differences. Under what might be called normal conditions of unhurried feeding, the race of *J. oreganus* observed at Deep Springs was tolerant beyond a radius of roughly 6 to

15 inches with the bird at the center, while the race observed at Seattle, under comparable conditions, was tolerant outside an area of 15 to 24 inches radius. The Slate-colored Juncos observed in Ithaca fell between these extremes, keeping a distance of roughly 10 to 18 inches. There seem also to be individual differences. ND in the Deep Springs flock, as was said above, tended to stay apart, but two other birds almost invariably pecked at a distance of 12 inches. The threshold of the pecking drive apparently differs in different birds.

Even to casual observation it is evident that juncos space themselves when a flock is foraging in the open, but this need not imply that spacing is maintained by competition for food. On the contrary pecking by a dominant or avoidance by a subordinate is often observed between perching birds or in places where there is no food. It is not unusual to see a dominant bird peck a subordinate that is not close to food when other subordinates are present and are close to it. The elasticity of the distance which the birds maintain, however, and also the strongest ground for not connecting the behavior with competition for food, is seen in conditions of crowded or difficult feeding. Under such conditions intolerance of proximity decreases though the situation becomes increasingly competitive. A similar fact has been noted also in the case of the Great Tit (Hinde, 1953: 209). Under extreme conditions a junco's intolerance of proximity disappears altogether, but this neither induces fighting nor increases pecking, and it does not destroy the permanence of pair relations. In short, dominance and intolerance can be dissociated, and this would seem to be a point of considerable importance in explaining the behavior of juncos in the dominant-subordinate relation. For the capacity of the dominant, under the drive of hunger, to displace a subordinate is unaffected by the disappearance of the drive which maintains ordinary spacing relations.

A decrease in the intolerance of proximity can be seen in any conditions that induce crowded feeding or merely by concentrating the food supply while other parts of a feeding station are left without food. If food is offered exclusively in trays in such a way that, in order to feed, a subordinate must approach within 6 inches rather than 12 inches, for example, a dominant bird will, as a rule, come in the end to permit the closer approach. It is true that under such conditions the number of pecks delivered is likely to be temporarily increased, but it is also true that the subordinate's tendency to persistent return increases, too, and this after a time seems to wear down the dominant's drive to peck. There appear to be two mechanisms by which crowded conditions of feeding operate to reduce the distance that intolerance maintains between foraging juncos: (a) an exhaustion of the dominant's impulse to peck by the persistence of the subordinate; and (b) a greater preoccupation of both dominants and subordinates with feeding and a diminished attention to one another when feeding conditions become difficult.

When feeding conditions are very difficult the distance at which dominant birds will permit subordinates to feed is markedly diminished. At Deep Springs in January, 1949, there were several weeks with temperatures below zero and severe ground blizzards. To test the effect on intolerance, a round tray of peanut butter 3 inches in diameter was added to the food supply and nailed to a support in such a way that there was no perching place other than the edge of the tray itself. Two birds would eat together with their heads less than 3 inches apart, while other birds waited for an opportunity to feed. Neither fighting nor pecking was observed between the waiting birds.

At about the same time, the writer was indebted to the intervention of a flock of Brewer Blackbirds (*Euphagus cyanocephalus*) for a quasi-experiment which showed that under conditions of near-starvation, intolerance might disappear altogether though dominance did not. The blackbirds usually foraged in a nearby alfalfa field but when the ground was covered with deep snow they invaded the feeding station and drove the juncos from it. A feeding tray a foot square and baited with grain that stood on a window ledge was at once taken over by the juncos. The tray was literally filled with birds, 8 to 12 feeding together with their flanks touching but without pecking. It is a suggestive fact that the alpha bird ND, which has been mentioned above as having a strong tendency to avoid, was never seen to eat at this tray. Nevertheless, dominant birds continued to be distinguishable and the permanent pair relations continued to hold. Dominants displaced subordinates simply by walking over the backs of feeding birds and taking their places. Under these conditions it might have been anticipated that high-ranked birds would monopolize access to food, but this did not happen. Each bird fed only for an interval of about three minutes. Perhaps crowding induces a tension that stops the hunger drive short of satiation. Whatever the mechanisms may have been, they operated to feed the many a little rather than to feed the few a lot. It seems probable that with scattered feeding high-ranked birds have no appreciable advantage in their access to food.

These observations suggest the following considerations relevant to explaining behavior in a winter flock of juncos. First, it seems clear that the kind of crowded and potentially competitive feeding here described, without pecking or fighting and without the exclusion of low-ranked birds from access to food, is not analogous to the situation produced in experimental flocks of hens by rotation of membership or by starvation. The observations suggest that these experimental conditions cannot be so simple as to be explained merely as competition for food under a generally aggressive drive measured by degree of hunger. The possibility can hardly be excluded that enforced crowding itself may have important effects on behavior or may even tend to induce aggressiveness which under normal conditions of flocking does not invariably occur.

Second, it seems clear that any explanation of the behavior observed in a winter flock of juncos should take account of the fact that the permanent pair relation which subsists between a dominant and a subordinate bird is not destroyed, or even obscured, by the disappearance of the specific reactions of peck or avoidance by which the relation is normally evidenced. Dominance, defined as the capacity of one bird to displace another, is not identical with intolerance, defined as a tendency to react to too close proximity in a manner which maintains distance. The specific reactions of peck and avoidance can be modified or even inhibited by the simultaneous presence of other specific drives such as hunger. In the subordinate the drive to eat can induce closer approach or persistent return and in the dominant it can weaken or supersede the drive to peck by raising the threshold at which the approach acts as a stimulus, with the result that spacing is closer without a corresponding increase of pecking. Dominance on the other hand seems to be a permanent capacity, like flying or hopping, which can be used in the service of specific drives, like hunger or maintaining distance. This suggests that dominance should be regarded as a natural endowment depending on the basic physiological, possibly hormonal, equipment of individual birds. And if this is correct it would seem to suggest that a pecking order provides no evidence of flock integration; migrants or visitors fit into it as readily as members. It seems unlikely that either observation or experiment could ever start with a group related merely by these physiological differences, since their expression in behavior seems to be modifiable by age, sex, familiarity, seniority, and the phase of the yearly cycle.

Third, the behavior of juncos in maintaining individual distance either by pecking or avoiding appears to be an instance of a very general property of behavior, namely territorialism, which seems in substance to be the property of limiting activities within spatial boundaries and of modifying this tendency according to the manner in which a given activity fits into the yearly cycle of activities by which life is maintained and reproduction is accomplished. Breeding territory, flocking, wintering territory, a common foraging circuit, and a common roosting territory if this exists, are all concerned with drives which operate to keep an area clear for carrying out an activity necessary in the total range of activities, and intolerance of proximity in a foraging flock appears to be another manifestation of this general property of behavior. In no phase of their yearly cycle do juncos display behavior that can be described literally as defense of territory; in all phases their behavior shows an inherent responsiveness to the spatial element in the environment—the restriction of activities to definable areas and intolerance of other juncos within the area, a tendency to develop spatial routines, and to be affected by familiarity. Combined with the drive to aggregate, which also is spatial, intolerance of proximity suggests an interplay of factors of attraction and repulsion, both always present and varying with conditions and with phase, and not incompatible with the integration of the winter flock.

PRIOR OCCUPANCY AND THE LINEAR HIERARCHY

The generally linear hierarchy found in a junco flock might be explained on the assumption of hormonal or other quantitative physiological differences between individual birds. Since, however, it has frequently been observed, with birds and other animals, that an individual has an advantage in its own territory, the hypothesis is suggested that familiarity with territory might be another factor influencing the hierarchy that is actually found in a given flock, if the birds composing it differed in respect to their periods of occupancy. The assembly of the junco flocks both at Deep Springs and Seattle, as described in the earlier article (Sabine, 1955), affords an opportunity to examine this hypothesis, since their history permits at least a rough grouping of the birds according to the time at which they occupied the territory. It is possible, therefore, to compare these groups in respect to their positions in the hierarchy of the total flocks.

At Deep Springs the order in which the birds of the feeding station flock were trapped shows that they divide into three groups: 7 birds trapped between October 24 and 28, 10 trapped between November 7 and 16, and 13 trapped between November 20 and 28, with intervals between in which no birds were trapped. From each of these groups 2 birds have to be omitted because their records were so short that they had few if any contacts with later arrivals. It seems fair to assume, for reasons stated in the earlier article, that the date of trapping was in general indicative of the time at which the birds arrived in the fall migration. Still later, on December 7, the dairy flock of 18 birds moved into the foraging circuit already occupied by the feeding station flock. Thus, the entire group of 42 birds can be regarded as made up of four groups, having respectively 5, 8, 11, and 18 birds, distinguished by the length of time during which the birds composing them had occupied the foraging circuit.

The flock at Seattle, where juncos are both resident and migrant, fell into three groups composed respectively of 12 birds plausibly regarded as residents, 7 that were winter residents only, and 7 visitors from other flocks that frequented the station temporarily and detached themselves after five weeks of occupancy. It may reasonably be assumed that the residents were prior occupants relative to the winter residents and that the latter in turn were prior relative to the visitors.

Table 1 shows the position that the birds of these several groups held in the scale of dominance for their respective flocks. The numbers on the left give the rank, from 1 to 42 in the Deep Springs flock and from 1 to 26 in the Seattle flock. Thus, the 5 birds trapped earliest at Deep Springs (Group 1) were respectively second, fourth, seventeenth, twenty-second, and twenty-third in the ranking of the whole flock; the birds trapped in the second period (Group 2) held the first, fifth, and so forth, positions, and

Table 1
Rank Positions of Comprising Groups within Two Flocks

	Deep Springs Flock Group			
Rank	1	2	3	4
1		*		
2	*			
3			*	
4	*			
5		*		
6			*	
7			*	
8				*
9		*		
10			*	
11			*	
12				*
13				*
14		*		
15				*
16				*
17	*			
18			*	
19				*
20		*		
21				*
22	*			
23	*			
24		*		
25			*	
26			*	
27			*	
28			*	
29				*
30				*
31				*
32		*		
33			*	
34				*
35				*
36				*
37				*
38		*		
39				*
40				*
41				*
42				*
Totals	5	8	11	18

	Seattle Flock Group		
Rank	1	2	3
1	*		
2	*		
3	*		
4	*		
5		*	
6	*		
7	*		
8	*		
9		*	
10			*
11	*		
12	*		
13		*	
14			*
15	*		
16		*	
17			*
18			*
19		*	
20	*		
21			*
22			*
23		*	
24	*		
25		*	
26			*
Totals	12	7	7

similarly for the birds trapped in the third period (Group 3), and for those of the dairy flock (Group 4). In the ranking of the birds at Seattle, the residents (Group 1) held the first four positions and so on; the winter residents (Group 2) ranked fifth and ninth and so on; and the visitors (Group 3) occupied the tenth position and so on down.

Inspection of these rankings shows no marked difference between the birds in groups 1, 2, and 3 at Deep Springs but a reasonably clear tendency of the birds in the dairy flock (Group 4) to rank low in the scale relative to the birds of the feeding station flock. But this is a tendency rather than a cause that regularly determines rank: a bird of the dairy flock held eighth place and a bird of Group 2 fell as low as thirty-eighth place. Yet taking the birds by groups, in each of groups 1, 2, and 3, more than half of the birds ranked above the middle of the scale, and in the three groups taken together 14 birds out of 24 are above the middle. But in the dairy flock, 11 out of 18 are below the middle of the scale. The impression gained from inspection of the table is supported by statistical analysis. Through the cooperation of Dr. D. W. Alling, of the Biometrics Unit, Cornell University, a Kruskal-Wallis test was applied to the data. Applied to the ranking of the birds of the Deep Springs flock classified according to group number, the result was as follows: $\chi^2 = 8.43$, d.f. $= 3$, $p < .05$. The same test applied to the rankings of the birds classified according to membership in groups 1, 2, and 3 or Group 4 gave the following result: $\chi^2 = 7.95$, d.f. $= 1$, $p < .005$.

In the Seattle flock it seems clear that the resident birds tended to rank high, all but three being above the middle of the scale, and that the visitors tended to rank low, all but one being below the middle. The winter residents were scattered pretty evenly over the scale though none is above the fifth place. A Kruskal-Wallis test applied to the rankings of the birds in the Seattle flock classified according to group number gave the following result: $\chi^2 = 6.73$, d.f. $= 2$, $p < .05$. The same test applied to the rankings of the birds according to membership in Group 1 or groups 2 and 3 combined gives the following: $\chi^2 = 6.38$, d.f. $= 1$, $p \sim .01$.

It seems likely that when the birds are grouped in the manner described, the grouping reflects a factor (probably prior occupancy) that is roughly related to higher rank in the scale of dominance. Familiarity with a given territory, it may be supposed, gives a bird a certain advantage but not an advantage that is always sufficient to settle the dominant-subordinate relation between two birds. The effects of prior occupancy thus appear to be unevenly distributed through the flock. If there is a factor (perhaps the birds' native hormonal endowment) that disposes them to be arranged in a linear order, prior occupancy might operate as a second factor influencing the position which a bird or group of birds actually occupies in the hierarchy.

The separation of the birds into groups distinguished by periods of membership in the combined flock suggested the possibility of examining also the question whether the mixing of originally distinct groups of birds affects the occurrence of triangles in the combined groups. Specifically it suggested comparing the number of triangles that occur between birds of a single group (called intragroup triangles) with the number that involve birds of two groups (called intergroup triangles). Accordingly triangles were counted for each of the groups and for the combined flock. The number of intergroup triangles could then be obtained by subtracting the sum of intragroup triangles from the number for the flock.

The difficulties of computation in this comparison proved to be formidable, especially for a number of birds as large as the total flock at Deep Springs. The help of Professor LaMont C. Cole, of the Department of Zoology, Cornell University, is most gratefully acknowledged, as well as that of Dr. D. W. Alling. The details of the statistical analysis applied to the data of this study will be published elsewhere by Dr. Alling.

The results of the comparison are shown in table 2.

In general, the conclusion indicated by these figures is that no signficant change in the proportion of triangles is demonstrated as a result of mixing groups, either in the Deep Springs flock or in the Seattle flock. In both cases the proportion of triangles was slightly increased in the mixed groups, and in the Deep Springs flock the increase approached statistical significance, suggesting that more investigation might show a significant effect of combining groups of birds originally separate. The result of the comparison in the case of the Seattle flock was wholly neutral.

The hypothesis that the configuration of a flock's hierarchy may reflect the condi-

Table 2

Comparison of Occurrence of Triangles Within Two Flocks

Deep Springs Flock

	Intragroup	Intergroup	Total
Number of triangles	2	86	88
Number of linear triplets	189	2439	2628
Total	191	2525	2716

$\chi^2 = 2.46, \quad p > .10$

Seattle Flock

	Intragroup	Intergroup	Total
Number of triangles	8	56	64
Number of linear triplets	168	924	1092
Total	176	980	1156

$\chi^2 = .20, \quad p > .50$

tions under which the flock has been assembled does not imply that the hierarchy is itself a causal factor in the flock's integration. Rather it suggests that the hierarchy is a pattern imposed on the flock by the causal influences that determine behavior and that consequently determine the permanent pair relation of dominance or subordination that subsists between the birds taken by pairs. An expression which describes the hierarchy as a "type of social organization" (Allee *et al.*, 1949:417) seems inappropriate and possibly misleading. For it suggests that survival value, and hence causal efficiency, can be attributed to the hierarchy; for example, the function of diminishing intraspecific hostility. But this function, if indeed it exists, would be performed by the permanence of pair relations, whether these could be arranged in an approximately linear series or not. If a flock in becoming integrated goes through a phase of "settling down" which diminishes fighting, it would seem that this must result from causal factors that lift the threshold at which the presence of another bird evokes pecking or other behavior that in turn evokes resistance. In the behavior of juncos there seems to be no reason to believe that the hierarchy itself should be counted as an integrating mechanism. The case of the visitors in the Seattle flock suggests that the pair relations of any assemblage of juncos can be arranged approximately in a hierarchy, whether the assemblage is an integrated flock or not. The configuration of the hierarchy appears to reflect merely a quantitative factor in individual physiological equipment modified by the effect of conditions under which the flock has been assembled.

CONCLUSIONS

1. The order of dominance between any two birds in a winter flock of juncos is, as a rule, permanent, though it is possible that the order may occasionally change or that dominance between two individuals, or in a "pair," may be so evenly balanced as to be unstable. Permanent pair relations exist between visitors and between visitors and flock members as well as between members of an integrated flock. Non-linear pair relations that occur in triangles are as permanent as those which are linear.

2. Intolerance in a winter flock of juncos is a spacing device which leaves to each bird an area of privacy maintained alike by the pecking of the dominant bird and by the avoidance of the subordinate. It does not jeopardize the integration of the flock but rather is a factor in the flock's social structure. Intolerance is not occasioned by competition for food, since it decreases under conditions of crowded feeding, and it is not explainable as pugnacity, since such conditions do not increase fighting or pecking. The changes that occur in the winter flock with different conditions of feeding, and also at different stages of the junco's yearly cycle of behavior, do not upset the stability of dominant-

subordinate pair relationships. Intolerance and dominance should be distinguished, intolerance like territoriality or spatial routinism being regarded as an aspect of the bird's utilization of space, and dominance being regarded as referable to differences of native (perhaps hormonal) endowment modified by the effect of familiarity with territory.

3. The dominant-subordinate pair relations in a winter flock of juncos can be arranged in a scale of dominance that is in general linear but with triangular irregularities. A reasonably smooth scale of dominance can probably be found in any assemblage of juncos, whether it is an integrated flock or contains a considerable number of visitors. The conclusion seems to be suggested that the ordinal scale has no causal efficiency tending to bring the flock together, to hold it together, or to segregate it from another flock, and that these are the functions of an integrating mechanism.

4. Though the hierarchy is not a flocking mechanism, its configuration—the position of a bird or group of birds in the hierarchy and perhaps the number of triangles—may reflect the conditions under which the flock has been assembled. Prior occupancy or familiarity with territory seems to be one factor that influences position in the hierarchy. In general later additions to a flock tend to fall into lower positions in the hierarchy.

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