DOMINANCE-SUBORDINATION RELATIONSHIPS IN MOUNTAIN CHICKADEES

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Dominance-subordination relations have been recognized as a principle of organization of vertebrate societies for several decades, and recently (Wynne-Edwards, 1962: 139) they have been accorded added significance as a factor in the control of population levels. The social system described for the domestic fowl (*Gallus gallus*) by Schjelderup-Ebbe some 40 years ago was based upon unilateral despotism, but a less rigid social structure was found in pigeons (*Columba livia*) and shell parakeets (*Melopsittacus undulatus*) by Masure and Allee (1934*a*; 1934*b*). This second system, one of reverse pecking in which a relative dominance was determined by the number of contests won, was termed "peck-dominance" in distinction to the "peck-right" system found in chickens. Subsequently Allee (1942) recognized that in pigeons, ring doves (*Streptopelia risoria*), shell parakeets and canaries (*Serinus canarius*) the outcome differed according to the site of the encounter. Equivalent terms for this reversible dominance, "bidirectional pecking" (Guhl, 1961:1241) and "partial dominance" (Etkin, 1964:15), have been proposed, the latter apparently without recognition of Allee's qualification. Ritchey (1951) showed the influence of territoriality on peck-dominance in pigeons, and concluded that territorial relations blocked the formation of a rigid peck-right hierarchy. Castoro and Guhl (1958:62) supported her conclusion.

Social hierarchies based upon dominance-subordination have been found in free-living flocks of wild birds, especially in winter flocks of titmice and chickadees, *Parus* spp. (Colquhoun, 1942; Odum, 1942; Hamerstrom, 1942; Brian, 1949). Since each of these hierarchies was described from observations at a single feeding station, Marler (1955:115) questioned the interpretation of peck-right relationships. In a more general context Allee (1942:144) had indicated that observations at one point could lead to erroneous interpretation of peck-right relationships in a group that actually exhibited peck-dominance. Marler's query was prompted by the observation of Brian (1949:144) that the degree of dominance shown by individual Great Tits (*Parus major*) was inverse to the distance from the feeding station to the center of the subsequent breeding territory. The observations reported beyond were made with the view to clarifying the nature of dominance relationships in one species of this genus, the Mountain Chickadee (*Parus gambeli*).

METHODS

During the winter months of 1962–1963 observations were made from an automobile at feeding stations adjacent to a ski lift at an elevation of 7300 feet, some 30 miles by road northeast of Logan, in Cache County, Utah. Some of the chickadees under observation had been color banded 15 months previously, and their histories were followed in the subsequent breeding season. Each feeding station consisted of a walnut with parts of the shell removed, suspended by a wire so that only one bird could feed at a time. The plumage of most individuals was painted ("Magic marker" on body feathers, airplane "dope" on rectrices) to facilitate recognition. The data on flock organization were augmented by following the birds into adjacent conifer and aspen woodland on snowshoes. Temporary removal of some individuals sometimes was attempted, but the disruption caused by this trapping appeared unimportant.

TABLE 1

INTRAFLOCK RELATIONS OF THE WEST FLOCK AT ALL STATIONS OF OBSERVATION, DECEMBER 1, 1962, TO MARCH 2, 1963*

	1M	4M	1F	4F	Total
1M	—	48	15	4	67
4M	–	—	23	19	42
1F	–	–	—	16	16
4F	–	–	1	—	1
					126

* The number of contests won by individuals listed at the left may be read in horizontal columns.

Data were gathered during some 18 hours spent when chickadees were present at the feeding stations on 11 days between November 23, 1962, and March 23, 1963. Supplementary observations were continued into April. The data were tape-recorded and transcribed later.

Criteria of dominance-subordination used in this study were (1) supplanting attacks (Hinde, 1952:22) in which one individual displaced another either from food or from its perch, or (2) chasing of an individual from the vicinity of the food; (3) retention of the perch by a bird despite an attempted supplanting; (4) withdrawal upon detection of an approaching individual several yards distant; and (5) obvious waiting by one individual until another had completed its feeding and left. The avoidance aspects of these encounters (criteria 4 and 5) were perhaps more readily recognized in the chickadees than in Oregon Juncos, *Junco oreganus* (Sabine, 1959: 112) because the chickadees perched farther apart and flew to reach the food. All the criteria were combined in tabulations of encounters (tables 1–3).

THE SUBJECTS

Chickadees are exceedingly active birds and seldom remain in one site for more than a few minutes, even though food may be abundant there. For example, one male seen at a feeding station at 11:46 a.m. on December 1, was released at a trap 200 yards away at 12:12 p.m., and was back at the feeding station at 12:40 p.m.

Observations were concentrated in an area occupied by several individuals that were judged to be adults by the progress of their annual molt (Dixon, MS) when first marked in August, 1961. Two known adult males, 1M and 2M, and a third male, 3M, of uncertain age when banded in December, 1961, formed a flock in the winter of 1961–1962 and were ranked in the order listed. The mates of the first two, 1F and 2F, were the only other members of this flock. In the breeding season of 1962 the alpha male (1M) utilized the western part of the study area, the beta (2M) the eastern, and 3M the northern portion. Their breeding territories were exclusive but contiguous. In August, 1962, pair 1M–1F was joined by 4M, adult when banded on August 28, and by 4F, immature by skull condition (Miller, 1946) when banded on December 1. This quartet is referred to as the West Flock. The pair 2M–2F was joined by 5M, an unsuccessful breeder in 1962. This trio is designated as the East Flock. The third pair (3M–3F) remained on its breeding territory as a pair and is termed the North Pair. These flocks were fairly cohesive units and occupied circumscribed ranges that overlapped only slightly.

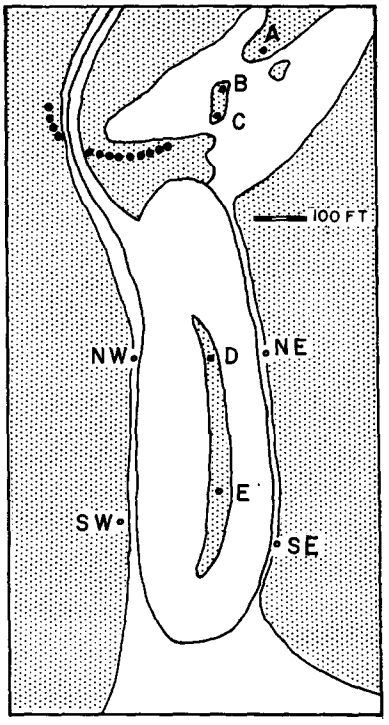

Fig. 1. Map of the study area, showing stations mentioned in the text. Dotted pattern denotes wooded terrain.

INTRAFLOCK DOMINANCE

In table 1 intraflock observations are summarized for all stations at which the West Flock was observed (NW, D, E, SE on map, fig. 1). The data indicate that a linear ranking was found wherever the birds traveled, and that the relations among flock members were of a peck-right type. A similar conclusion was drawn from the records of the East Flock. The rank order reflected precedence to food since low-ranking individuals could feed only when higher ranked ones were absent.

Background information on the individuals comprising these flocks, and the behavior of the subordinate flock members, leads one to stress seniority on the area as a factor influencing social positions. In the temporary absence of the alpha male (oldest resident) of the West Flock at station D on February 21, the beta male, 4M, supplanted the alpha's mate, and within a few minutes he assumed the bold, direct approach to the food and the "confident" manner of the alpha male. This pugnacious attitude was dropped when the alpha male reappeared following his release from temporary captivity.

A first-year male, 6M in table 2, was an irregular visitor from a flock that was situated 0.8 miles to the north. He was noted in the area mapped only on December 1 and 31, January 19, and February 21. The few contests involving this bird are difficult to evaluate, but the records to the left of the diagonal line indicate the instability caused by the appearance of an outsider. Although he visited the feeders, 6M was not assimilated into either the West or East flock. This first-year male was fairly aggressive and was the beta male of his "home" flock.

TABLE 2

SUMMARY OF ENCOUNTERS OF MOUNTAIN CHICKADEES AT STATION NW, NOVEMBER 23, 1962, TO FEBRUARY 28, 1963 (4 HOURS OF OBSERVATION ON 7 DAYS)*

	1M	4M	1F	4F	2M	5M	2F	6M
1M	—	19	3	–	1	–	–	2
4M	–	—	18	11	–	–	1	1
1F	–	–	—	1	–	–	–	1
4F	–	–	–	—	–	–	–	–
2M	–	–	–	–	—	1	–	–
5M	–	–	–	–	–	—	–	–
2F	–	–	–	–	–	–	—	–
6M	–	1	3	1	–	–	–	—

* The number of contests won by individuals listed at the left may be read in horizontal columns.

These observations, admittedly quantitative in only one sector of the flock range, suggest that flocks of Mountain Chickadees in the wild are organized on the basis of peck-right relationships. Similarly a peck-right organization was found within winter flocks of the Carolina Chickadee (*Parus carolinensis*) in Texas (Dixon, 1963).

INTERFLOCK RELATIONS

East and West flocks.—The first observed contact occurred at station SW (fig. 1) on November 11. Chickadee 2F was taken in a wire mesh trap three feet above the ground and was being harassed by her mate (2M) while their flockmate 5M foraged nearby. When 2M was accosted by 4M, the beta male of the West Flock, he became silent and withdrew a few feet but did not flee. An hour later at station E, 1M attacked 2F, again a captive, without challenge from 2M. The latter asserted himself with louder calls than those given by 4M in a vocal exchange immediately afterward. The comportment of these birds gave the impression that the order of dominance at station E was 1M, 2M, 4M. The withdrawal of 4M in the presence of 2M at station E on January 19 supports that impression.

Similarly 4M was supplanted twice by 2M at station SE on December 1, but no interaction of the two was observed at SE on December 31. Both 1M and 1F avoided station SE when members of the East Flock were present. On December 31, however, 1M foraged to the east of SE after the East Flock had departed. Thus the dominance of the alpha male of the West Flock (1M) appeared to extend farther east (to E, in the "island" of woodland) than that of the beta male, 4M, but station SE appeared to be the property of the East Flock.

At station NW (table 2) the members of the West Flock clearly prevailed. When the East Flock visited this feeder on November 23, 1M repulsed 2M. The only other visit by the East Flock occurred on February 28, while 1M was being held captive temporarily. At this station and at D on February 2 (tables 3 and 4) the two flocks alternated in their use of the site.

The West Flock was not detected at station NE as a group on any occasion. Attempts to lead the East Flock from NE to NW were not successful.

A feeding site was established at point D on January 19, and observations were begun on January 24. The two rival despots were noted together there only on February 2 and 12. On these dates, 2M (alpha of East Flock) clearly was dominant,

TABLE 3

SUMMARY OF ENCOUNTERS OF MOUNTAIN CHICKADEES AT STATION D, JANUARY 24 TO MARCH 2, 1963 (9 HOURS OBSERVATION ON 7 DAYS)

	1M	4M	1F	4F	2M	5M	2F
1M	—	20	6	4	–	1	–
4M	–	—	13	12	–	–	1
1F	–	–	—	8	–	–	–
4F	–	–	–	—	–	–	–
2M	5[1]	4	–	–	—	1	10
5M	–	–	1	1	–	—	1
2F	–	–	1	–	–	–	—

[1] 1M and 2M were present together only on February 2 and 12; however, on March 23, 1M won 5 contests from 2M and lost none.

putting 1M to flight and feeding unchallenged as though oblivious of his presence. The beta male of the West Flock also was subordinate to 2M (table 3), but data for other interindividual encounters are sparse.

The pattern of visitation at station D can be illustrated (table 4) by the events of February 2, a date when trapping was not attempted. In general, the two flocks alternated in their use of this food source. On three occasions, however, members of the West Flock arrived after the East Flock had vacated the site. In contrast, the East Flock approached the site three times while members of the West Flock were feeding and put them to flight. The pattern of site use by the West Flock recalls their avoidance of station SE when the East Flock was present on December 31.

Unexpectedly on March 23, the situation at D clearly was reversed. The pair 2M–2F was opposed by 1M, and the latter supplanted 2M four times; 2M withdrew in 1M's favor once. The female 2F was supplanted by 1M twice, and 1M gave the appearance of trying to keep himself between the food and the rival pair. After 1M had returned to the west side, 2M and 2F remained and fed, but they were not seen again at this feeder, although members of the West Flock fed there on April 3 and 13.

The circumstances underlying the change in proprietorship at station D may be

TABLE 4

DETAILS OF VISITS OF MOUNTAIN CHICKADEES AT STATION D, FEBRUARY 2, 1963

Flock arriving	Time interval of visit	Individuals present	Feeder vacated upon departure
West	8:40–8:45	4M	
East	8:45–9:10	2M, 2F, 5M; unidentified	Yes
West	9:13–9:35	1M, 1F, 4M, 4F	
East	9:33–9:45	2M, 2F, 5M; 4M	Yes
West	9:46–9:54	1M, 1F, 4M, 4F	
East	9:53–9:55	2M, 2F, 5M; 1M, 1F, 4M, 4F	Yes
East	9:57–10:05	2M, 2F; 1F[1]	Yes
West	10:08–10:13[2]	4F	

[1] 1F and 2F arrived simultaneously, and the former was driven away by 2F.

[2] Observations discontinued at this time.

explained by events on preceding days. Only members of the West Flock had appeared there on March 18 in the interval from 8:30 to 9:45 a.m., and the activity of the East Flock appeared to be centered several hundred yards to the east. On March 23, 5M left the area and was seen moving north past a feeding station 0.8 miles north of D. The arrival of chickadees that had wintered elsewhere further signalled changes in patterns of winter behavior (Dixon and Gilbert, 1964:62). The pair 2M–2F was seen in their more easterly area on April 3 and 13, and the shift in dominance at station D might have reflected 2M's disuse of that portion of his range.

Thus, during the winter period the East Flock appeared to "hold" the east side of the area and the north end of the "island" of woodland (station D), while the West Flock was dominant on the west side and at E. The influence of the alpha male of the West Flock was extended with the onset of the breeding season. He excluded 2M from the food at D in late March, and later he also incorporated the east side of the area into his domain.

West Flock and North Pair.—The boundary between the ranges of these groups extended along the dotted line on the map (fig. 1). On separate occasions on March 18, 1M and 4M flew downslope to feeding station A. This station was situated within the area frequented by the North Pair, 3M–3F. On each of these sorties the invading male, upon seeing the station occupied, veered toward the west while in flight and returned to its flock area. Later that day (March 18) the pendant walnut was moved upslope 100 feet to station B, in the lowermost aspen of a linear grove extending to C. During our next visit to the area, on April 3, the North Pair was found feeding on the walnut at this site. The food subsequently was moved upslope 20 yards to C. Within 2 hours an altercation between 3M and the members of the West Flock developed to the west, and the participants moved toward C. The male 3M perched between the invaders and the food, but 1M proceeded to feed from the walnut without challenge from 3M. Possibly the latter was preoccupied with the beta male, 4M. A skirmish followed that did not involve 1M for certain, but this male appeared dominant to 3M at station C.

After about 4 minutes the food was moved downslope to B. By this time 3M had retreated halfway to A, but he flew to B and fed unchallenged by either 1M or 4M. Male 3M then supplanted 4M and chased 1F and 4F in extended flights. During this interval 1M did not approach station B, although 4M fed while 3M was chasing 1F. Encounters between 3F and the invading females were not noted, although 3F was pursued by an invading male, 4M. During the skirmishing at B, which lasted for 20 minutes, 3M was silent, in contrast to the aggressive calling of 4M. At the close of the encounter, 3M held his perch on the walnut as both 1M and 4M made unsuccessful aerial passes at him before withdrawing from the vicinity. Thus "dominance" clearly was reversed over a distance of 20 yards, a sharper cognizance of boundaries than the 80-yard distance which was noted in one instance between two male Great Tits by Brian (1949:148). Further, this series of encounters involved a feeding site (C) to which none of the individuals had been conditioned prior to that morning.

DISCUSSION

The intraflock and interflock encounters in Mountain Chickadees in winter represent two categories or manifestations of dominance-subordination relations. The contests between individuals of the same flock reveal the existence of a hierarchy of precedence to food, based upon "peck-right" responses. These intraflock contests thus correspond to "winter fighting" or fighting over food (Hinde, 1952:20–30; Lockie,

1956:187–188), as distinguished from reproductive fighting. Although the interflock encounters appeared similarly related to food, the aggressive behavior that was exhibited differed in several respects. The interflock contests included: (1) prolonged and strenuous pursuit flights in which the female and subordinate males were chased by males of the opposing flock; (2) challenges of the bird perched on the pendant feeder (an activity seldom seen within one flock); and (3) obvious attempts of the "defending" male to stand between his adversaries and the food. Further, the interflock meetings reflected the spatial relationships that had been established among the three alpha males during the previous breeding season. This awareness of boundaries was manifest in the avoidance of trespass if a feeding station in the range of another flock was occupied.

Certain evidences of the intolerance that characterizes the breeding season were not found, however. Notable among these was the absence of the flute-like song notes. Also, during the winter (= flocking) period the alpha male directed his hostility toward all members of the intruding flock rather than against the rival male alone. The level of intolerance appeared intermediate between that seen within flocks under winter conditions and the interpair rivalries that were characteristic of the period after flocks disbanded in late April.

The interflock responses were principally the activity of the alpha males. Our data are not adequate to clarify the relationships to one another of subordinate members of the same sex from different flocks. Attempts to remove temporarily the two alpha males met with no success, although the beta male 4M appeared to take the initiative in the encounter with the North Pair (3M–3F) on April 3, and he challenged 3M independently of the alpha 1M on that date.

Since the outcome of a meeting of Mountain Chickadees from different flocks was dependent upon the site of the encounter, the behavior fits the concept of "peck-dominance" as modified by Allee (1942:143–144) to include the location of the contestants. In this study the awareness of previously established territorial boundaries seemed especially significant. It should be emphasized that this "peck-dominance" in Mountain Chickadees was not exhibited among members of a natural group but occurred where two such groups (each with its internal peck-right system) met. Thus we find systems resembling both "peck-right" and "peck-dominance" operating simultaneously in a single species.

Peck-dominance was characterized by Marler (1956:72) as a form of territorial behavior, and Guhl (1961:1241) noted overlap between the two phenomena. In support of Marler's contention it should be noted that a group exhibiting peck-dominance must be organized on a territorial basis in which the tendency of one individual to attack another differs from site to site. This fact is evident from Ritchey's (1951) study of pigeons.

The principal ecological consequence of such a system of site-related dominance is the reservation by the individual of an area for his own use. The exclusiveness of the individual's area was noted by Pitelka (1959:253) as a significant characteristic of the territory, and it results in the apportionment of the available resources among members of the population. The same end is achieved in the reversible dominance in pigeons ("perch-right," Castoro and Guhl, 1958). In many interflock encounters of Mountain Chickadees an alpha male excluded his rival males from a food source situated within the boundaries of his flock's range. In that exclusion he obtained access to the food (which also was used by the subordinate members of his flock).

Even though the behavioral manifestations of this "peck-dominance" differed from those of breeding season territoriality the resulting exclusion was comparable.

However, site-related dominance systems may not be equated with territoriality in every instance. In the Steller Jay (*Cyanocitta stelleri*) Brown (1963:483) described the dominance relations of the individual in terms of "a series of concentric zones of diminishing dominance rank from the center of its nesting area outward." While the territorial boundaries are not sharply defined, the ecological consequences of reservation of area are comparable to the situation in the Mountain Chickadee. Permanent flocks of constant membership are not formed in the Steller Jay.

The concept of "peck-dominance" has borne the connotation of an organizing principle in social groups. However, Etkin (1964:15) noted that there was little effectiveness in this respect. Reversible, site-related responses between individuals would hardly promote group action or unity. The only examples of such a system known to me are those reported from studies of confined subjects or those found on an interindividual or intergroup basis in free-living Mountain Chickadees and Steller Jays. Since these "peck-dominance" relations appear to have little relevance in the formation or maintenance of stable, permanent groups the continued use of the concept seems questionable.

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SUMMARY

Observation of color-marked individuals of Mountain Chickadees (*Parus gambeli*) at feeding stations in northern Utah in winter revealed that these chickadees traveled in small, cohesive flocks that exhibited linear or peck-right dominance relations. Interflock encounters were characterized by more pronounced hostility and more persistent challenging than were intraflock contests. The outcome of interflock encounters depended upon the site of the contest in relation to the territorial boundaries established by alpha males during the previous breeding season. These interflock contests fit the concept of "peck-dominance," but achieved results similar to territorial responses because the male that was dominant at a particular feeding station excluded members of the other flock from that site. The alpha males and their mates thus respond to existing territorial boundaries throughout the year, but tolerate additional individuals as "winter" flockmates. Since "peck-dominance" has not been demonstrated as a form of internal organization in unconfined groups of vertebrates, continued use of the term is questioned.

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