INTERCOVEY SOCIAL RELATIONSHIPS IN THE VALLEY QUAIL

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SOCIAL barriers between members of different coveys of Valley Quail (*Lophortyx californica vallicola*) have been observed and studied under natural conditions at Davis, California since 1936 (Emlen, 1939). In these studies it was noted that birds which wandered beyond the limits of their own covey range were strongly attracted to other groups of quail which they happened to encounter. Wanderers that attempted to mingle with a strange covey on its home range, however, were quickly singled out and driven off by the residents at each approach. Thus, in a mixed covey, alien birds were almost invariably found a few yards from the main body of natives.

Because of the possible significance of intercovey social barriers to problems of quail dispersion and distribution and to the general question of social organization in bird populations, it seemed desirable to obtain further information on intercovey relationships by experimentation. Accordingly a series of experiments was performed at Davis, California during the winter of 1939–40.

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EXPERIMENTAL

Experiments were conducted on three covey ranges (B, C, and D of Figure 1) where conditions for observation were particularly favorable. Additional birds for some experiments were obtained from three other ranges (A, E and F) in the neighborhood. Range B, although it had been occupied by a covey during the four preceding winters and was apparently in excellent condition, was vacant in 1939–40. This provided a site for two introduction experiments (Nos. 9 and 10).

All quail on the observation areas were labeled with showy field markers visible at a considerable distance; dyed chicken feathers "imped" (spliced by means of a corroded needle [Wright, 1939]) to clipped rectrices and a similarly colored celluloid band on the left leg designated covey membership; two celluloid bands of various color combinations on the right leg identified individuals within a covey.

The experiments were of three types: (1) those in which birds, singly or in groups, were transported from their native range to that of another covey; (2) those in which birds, singly or in groups, were temporarily withdrawn from their native range to be returned after varying periods of time, and (3) those in which birds from two sources

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were introduced together into an unoccupied range. Observations on experimental coveys were made almost daily in the early morning and

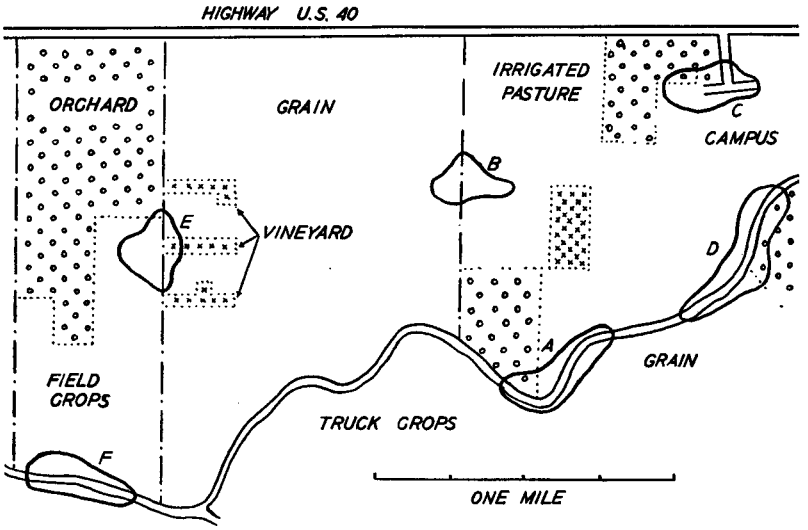

Figure 1. Covey ranges of Valley Quail.

late afternoon when activity was greatest. Ten experiments involving 29 experimental birds were completed before the breeding season (Table 1).

Results

Observations may be summarized under the following headings:

1. *Homing behavior was poorly developed in the quail under observation.* Of twenty-six birds transported from ½ to 2 miles from their native covey ranges, only two (Experiments 4 and 5) found their way back during the experimental period. These two homing records, furthermore, may have resulted from random movements rather than from a "homing sense," for in both cases the local distribution of cover favored movements in the direction of the original range. The low incidence of homing behavior of either a directed or a random type may be due largely to the strong and persistent attraction that an established covey exerts on a stray bird or group of birds (see next paragraph). The movement of the male in Experiment 4 may have been facilitated by a reduction in the flock bond, for this bird was already mated (see Experiment 3).

2. *Birds on a strange range were attracted to any group of quail they encountered.* During the winter season each quail covey at Davis

TABLE 1

OUTLINE OF EXPERIMENTS ON INTERCOVEY SOCIAL RELATIONSHIPS

Experiment	Bird	Experimental Procedure: Experimental treatment	From: Territory	From: Date	To: Territory	To: Date	Subsequent Behavior (Numbers in italics refer to days after start of experiment)
1a	♂	None (Natural movement)	A	1–9	D	1–10?	*6* to *16*, attacked frequently by native ♂♂, remains 5 to 10 ft.+ from covey (*9*, threatens a native ♀ attacking ♀ of expt. 1b); (*15*–, frequently attacks ♂ of expt. 2); *17* to *25*, attacked less frequently, approaches closer; *26* to *34*, not attacked by natives, still remains slightly apart from covey; *35*–, completely assimilated.
1b	♀	None (Natural movement)	A	1–9	D	1–10?	*6* to *16*, attacked by native ♀♀ and by ♀ of expt. 1c, remains 5 to 10 ft.+ from covey with ♂ of expt. 1a; *17* to *25*, attacked less frequently, approaches closer; *26* to *34*, not attacked, nearly assimilated; *35*–, completely assimilated.
1c	♀	None (Natural movement)	A	1–5±	D	1–6?	*10* to *20*, attacked by native ♀♀, dominates ♀ of expt. 1b, remains 5 to 10 ft.+ from covey, generally near ♂ and ♀ of expts. 1a and 1b; *21* to *28*, rarely attacked, nearly assimilated; *29*–, no further records (killed?)
2*	♂	Artificial transplant	C	1–23	D	1–23	*1* to *8*, attacked by native ♂♂ and ♂ of expt. 1a, remains 5 to 10 ft.+ from covey, roosts alone; *9* to *30*, attacked less frequently, approaches closer, roosts with covey (*26*, attacks ♂ of expt. 6a); *31* to *35*, not attacked, nearly assimilated; *35*, artificially removed for expt. 3.
3*	♂	Artificial transplant	D	2–26	C	3–1	*1* to *3*, attacked by native ♂♂, remains at considerable distance from covey; *3* to *14*, (paired) remains at considerable distance from covey with mate; *15* to *33*, associates quite freely with pairs of covey; *35*, artificially removed for expt. 4.
4*	♂	Artificial transplant	C	4–4	D	4–5	*1* to *3*, remains at distance from covey, calls much, dominates ♂ of expt. 6a as in earlier period of residence (expt. 2); *6*, has returned to territory C.
5	♂	Artificial transplant	D	2–7	C	2–7	*1*, runs to covey immediately on release, attacked by native ♂♂ after few seconds delay, retires and remains 20 ft.+ from covey; *3*, has returned to territory D.
6a	♂	Artificial transplant	E	2–17	D	2–17	*1*, attacked by native ♂♂ and by ♂ of expt. 2, retires, leaves territory; *33*, reappears, attacked by native ♂♂ (subsequent behavior confused by mating activity).
6b	♀	Artificial transplant	E	2–17	D	2–17	*1* to *15*±, attacked by native ♀♀, remains 5 to 10 ft.+ from covey; *16*± to *42*, not attacked but still incompletely assimilated; *44*, completely assimilated.
7	♂	Temporary withdrawal	D	1–23	D	1–24	*1*, released 50 ft. from covey, merged with them after 30 minutes, completely assimilated.
8a	♂	Temporary withdrawal	D	2–1	D	2–8	*1*, released 75 ft. from covey, merged with covey in 8 minutes and completely assimilated.
8b	♀	Temporary withdrawal	D	2–1	D	2–8	*1*, same behavior and reception as ♂ of expt. 8a.
9a	5♂♂ 6♀♀	Artificial introduction	F	2–15 & 16	B	2–16	Accept and remain on new (vacant) territory into nesting season.
9b	♂		E	2–15	B	2–16	*1*, (released with 11 birds of expt. 9a), not attacked but tended to remain apart from covey, roosts alone; *2*, not attacked but generally apart from covey; *5*, alone on territory; *7*, accepted by ♂♂ of expt. 10a, occasionally attacked by ♂♂ of expt. 9a, remains apart.
10a	3♂♂	Artificial transplant	E	2–21	B	2–22	*1*–, occasionally attacked by ♂♂ of expt. 9a, generally apart and scattered.
10b	2♀♀		D	2–21	B	2–22	*1*–, occasionally attacked by ♀♀ of expt. 9a, but generally accepted, tend to remain apart and scattered.

* Experiments 2, 3 and 4 all involved the same male bird. No other birds were used in more than one experiment.

acted as a focus of attraction for all quail entering its range. Birds appearing on a strange range (through natural wandering or experimental transplantation) approached and persistently followed the native covey for as much as a month or more, often in the face of active opposition (see next paragraph). Groups of 3 to 14 aliens were less strongly attracted to native coveys than were single individuals (Experiment 10; also Emlen, 1939: 120).

3. *Strange birds, alone or in small groups, were quickly recognized as aliens and forcibly excluded from intimate association in an established covey.* Members of established quail coveys at Davis were intolerant of strange birds appearing in their midst. Aliens, introduced or wandering onto an established covey range, invariably found their approach to the covey challenged by the natives. Aliens were never seen to resist these attacks and usually fled at the slightest display of animosity by a native.

4. *The active exclusion of aliens by members of an established covey gradually diminished and eventually disappeared.* Attacks on aliens were, in general, most frequent and vicious on the first day or two of association. Thereafter the intolerant attitude gradually diminished, falling off particularly after about two weeks. By the end of the fourth or fifth week attacks on aliens were rare, although one male in the spring of 1937 was still actively repulsed after the fifth week (Emlen, 1939).

5. *Quail from separate sources did not merge completely until they had "become acquainted."* Alien quail (single individuals or small groups) tended to remain somewhat apart from natives in their roosting and occasionally their feeding activities for several weeks after hostilities had subsided. This may represent a gradual trailing off of the initial native-alien antagonism, or it may be quite independent of it and indicate a hesitancy in these quail to mingle intimately with strangers until an "acquaintanceship" has become established. The latter interpretation is supported by observations in Experiments 9b and 10 in which two groups, established side by side on a range strange to both, demonstrated aloofness from each other with very little of the active antagonism of a native-alien relationship.

6. *Recognition of individuals as covey members was not affected by absences of a week, but was influenced by an absence of 38 days.* Birds withheld from their home coveys for periods of one day and 7 days in Experiments 7, 8a and 8b were immediately assimilated upon being returned. The male in Experiment 3, however, upon being returned to his native covey range after an absence of 38 days was treated as an alien. His acceptance into the covey was apparently more rapid than is usual with aliens, but this reaction may have been complicated by pairing behavior. After being returned to the range

of his second residence where he had become nearly assimilated in Experiment 2, this same bird was again treated as an alien, showing a considerable loss of recognition after an absence of 39 days (Experiment 4).

7. *Alien quail in a covey actively dominated birds of subsequent introductions.* When a succession of introductions was made into a single covey (Expts. 1b, 2, 6a, 6b) alien groups of longest standing attacked later arrivals much as they themselves were attacked by natives. This belligerent attitude toward newly introduced birds often seemed more vicious in partially assimilated aliens than in the established natives. The effect of this behavior was to establish an order of active dominance among the partially assimilated groups in a covey based on seniority of residence on the range. This order was modified in Experiments 4 and 10a where previous social relationship was apparently "remembered" and carried over.

8. *Aliens in a covey were attacked only by members of their own sex.* This feature of behavior, overlooked in the 1937–38 season, was checked almost daily on experimental birds in the present study. Only one instance of attack upon a bird of the opposite sex was noted, and this incident was of very brief duration. Observations did not start until mid-January, only a little over a month before traces of pairing behavior were detected, and it is possible that a low level of sexual activity was already present. Intra-covey fighting is rarely observed in midwinter at Davis, but when it has occurred (7 records in the past 4 years) it has always been between members of the same sex. In one instance (Dec. 4, 1937) a crippled female was repeatedly attacked by female covey mates but was not bothered by the males. These observations suggest that members of this sexually dimorphic species may be capable of sex recognition at all seasons of the year.

Discussion

Because of the difficulties involved in marking and observing under field conditions, very little is known concerning the inter-flock relationships of free-living wild birds. The phenomenon of a closed flock with domination of strangers, however, has been observed in wild Jackdaws, Rooks (Lorenz, 1931) and Chickadees (Odum, 1941: 118; Wallace, 1941: 53) as well as in the Valley Quail herein described. Similar behavior, furthermore, has been noted in flocks of a wide variety of captive animals. An initial attitude of intolerance towards newcomers by an established flock is well known to breeders of Valley Quail, Bobwhite Quail, Pheasants and other game birds; it has also been noticed in captive Song Sparrows (Nice, 1939: 260), White-crowned Sparrows, Spotted Towhees (Tompkins, 1933: 100) and various aviary species (E. C. Kinsey, personal communication). Domestic fowl, especially cocks, persecute new-comers, and precautions are often needed to pre-

vent the killing of an introduced stranger. A comparable initial domination of strangers occurs in herds of sheep, hogs, cattle, horses and various other herbivorous and carnivorous mammals (Alverdes, 1935: 195); it is also reported in wild Howling Monkeys (Carpenter, 1934: 100–104), and is characteristic of many human societies, both primitive and modern. Among invertebrates, ants (Wheeler, 1910: 182) and bees (Root, 1940: 52) are notably intolerant of strangers. A careless attempt to merge two bee hives by placing one upon the other without a separator may result in a conflict and "quarts" of dead bees (J. E. Eckert, personal communication).

When an encounter between strangers takes place on the home range of one of the contending parties, residents often hold an initial advantage over tresspassers (Nice, 1941: 469). In the Valley Quail studied at Davis, natives were invariably successful in their skirmishes with aliens. Differences in age, weight or physical condition definitely were not involved. It seemed rather that a quail on strange territory, and in the presence of strange birds, developed an attitude of subordinance which was quickly detected and capitalized upon by the natives. Three possible explanations for this behavior suggest themselves.

1. *Majority dominance.*—In all the observed instances of intercovey contact, the native group was larger than the alien group. It is thus conceivable that the assumption of dominance by natives was purely a matter of numbers. If this were the case, a large group of quail introduced into the range of a small covey would dominate the latter through sheer "weight of numbers." Unfortunately this critical experiment has not yet been performed. Two incidents, however, provide pertinent information. On November 15, 1936, an alien group of 14 birds wandered onto the range of a neighboring covey which contained 23 birds. Although these invaders did not constitute a majority of the combined covey, they represented a sizeable unit, which conceivably could have disputed for dominance in a majority-ruled order. No such dispute occurred; the aliens all assumed an attitude of subordinance and retired to themselves (Emlen, 1939). Experiment 9 (Table 1) of the present study was designed to test the "majority rule" theory by placing unequal numbers of birds from two covey sources together on an unoccupied covey range. In this synthetic covey the single male from source E, although refraining from intimate association with the 11 birds from source F, was seldom chased and did not exhibit the avoiding reaction characteristic of aliens on unfamiliar territory. The subsequent introduction of 3 more birds from source E in Experiment 10 made no appreciable change in this picture of loose association without definite group dominance.

These two observations do not eliminate majority dominance from the picture; they suggest, however, that territorial associations were more important than numerical inequalities in determining dominance rela-

tionships between natives and aliens in these mixed quail coveys.

2. *Territorial dominance.*—In species showing territorial behavior, aliens are attacked and driven out as a part of territory defense, the territory owner showing nearly complete local dominance over trespassers (Howard, 1920: 97; Tinbergen, 1939: 57; Lack, 1939: 177; Nice, 1941: 469, 470). Territory in the sense of a "defended area" (Noble, 1939: 267), however, does not help to explain the native-alien relationship in Valley Quail. With the exception of some unmated males during the nesting season, quail at Davis have never been observed to exhibit anything that resembles proprietory behavior toward a piece of land. Aliens are not molested on a covey range until they approach the covey itself. The chase which follows such an approach is typically short and directed merely away from the body of the covey, not across any territory boundary.

3. *Seniority of residence dominance.*—In observations at Davis the natives of a covey (the group in longest residence on the area) always acted as the dominant group. Where two or more successive introductions were made into an area, the order of dominance followed the order of introduction except as previous associations of the birds modified it. Where unequal groups from two independent sources were liberated together on an unoccupied range, inter-group dominance was essentially absent. This suggests that seniority of residence on a range may be a decisive factor in determining the dominance of natives over aliens.

The favorable psychological effect of "being locally established" has been demonstrated in various territorial species and in laboratory animals. Schjelderup-Ebbe (1935: 967) observed it and described it in detail for the domestic fowl. Whitman (1919) and Shoemaker (1939) detected it in doves and canaries, respectively. Noble, Wurm and Schmidt (1938: 23) showed that in non-breeding pigeons, a low-ranking bird after becoming established in a small cage by itself assumes a local dominance over superior pigeons subsequently introduced into the cage with it. Diebschlag (1941) found that when a flock of pigeons was moved about from cage to cage the dominant role shifted from one individual to another according to the cage occupied. Such locality-linked dominance has often been interpreted as a form of territorialism. Diebschlag, however, found that each male pigeon in a cage defended nothing beyond its resting place and that the area surrounding this small inviolate territory often served as a sort of buffer ground on which other birds were tolerated but dominated. Confidence gained through familiarity with the area seemed to be fundamental to the degree of dominance achieved.

In free-living Valley Quail, although the site of an encounter definitely influences the outcome, there is no evidence that territory, *per se,* provides the incentive for aggressive behavior. The dominating attitude

of established residents over aliens may better be attributed to confidence gained through familiarity with the topographical and vegetational features of the covey range. A bird suddenly released into unfamiliar surroundings is conceivably placed at a psychological disadvantage. In a peck-right society any such handicap would affect the social reactions and hence the position of a bird in the social order. Covey range may well be an adjunct to social aggressiveness without being an objective. This would seem to be the case in the quail population under study.

Summary

A series of experiments designed to test the social relationships between members of different coveys of Valley Quail at Davis, California confirm earlier observations that social barriers of non-recognition and active exclusion discourage inter-covey mixing. It was further noted in the experimental coveys that strangers were attacked only by birds of their own sex (observations between January and April), that active exclusion gradually subsided with continuous association, that unacquainted birds did not mingle freely even in the absence of active exclusion, and that partially established members of a covey dominated aliens of subsequent introductions. It is suggested that the dominance of aliens by established residents is in large degree related to a favorable psychological attitude gained through familiarity with the physical features of the covey range. Aliens acquire the "confidence" fundamental to social recognition only after a period of residence on the range.

Literature Cited

Alverdes, F.
1935 The behavior of mammalian herds and packs. Murchison, A handbook of social psychology, Chap. 6. Clark University Press, Worcester, Mass.

Carpenter, C. R.
1934 A field study of the behavior and social relations of howling monkeys. *Compt. Psychol. Monogr.*, 10: 1–168.

Diebschlag, E.
1941 Psychologische Beobachtungen über die Rangordnung bei der Haustaube. *Zeits. f. Tierpsychologie*, 4: 173–188. (Abstract by M. M. Nice in *Bird Banding*, 13: 43–44. Original not seen.)

Emlen, J. T., Jr.
1939 Seasonal movements of a low-density Valley Quail population. *Jour. Wildl. Man.*, 3: 118–130.

Howard, H. E.
1920 Territory in bird life. John Murray, London.

Lack, D.
1939 The behavior of the Robin. *Proc. Zool. Soc. Lond., ser. A.*, 109: 169–219.

Lorenz, K.
1931 Beiträge zur Ethologie sozialer Corviden. *Jour. f. Ornith.*, 79: 67–127.

Nice, M. M.
1939 The social kumpan and the Song Sparrow. *Auk*, 56: 255–262.
1941 The role of territory in bird life. *Amer. Midl. Nat.*, 26: 441–487.

NOBLE, G. K.
1939 The role of dominance in the social life of birds. *Auk,* 56: 263–273.
NOBLE, G. K., M. WURM, and A. SCHMIDT
1938 Social behavior of the Black-crowned Night Heron. *Auk,* 55: 7–40.
ODUM, E. P.
1941 Winter homing behavior of the Chickadee. *Bird Banding,* 12: 113–119.
ROOT, A. I. and E. R.
1940 The ABC and XYZ of bee culture. A. I. Root Co., Medina, Ohio.
SCHJELDERUP–EBBE, T.
1935 Social behavior of birds. Murchison, A handbook of social psychology, Chap. 20. Clark University Press, Worcester, Mass.
SHOEMAKER, H. H.
1939 Social hierarchy in flocks of the Canary. *Auk,* 56: 381–406.
TINBERGEN, N.
1939 The behavior of the Snow Bunting in spring. *Trans. Linn. Soc., N. Y.,* 5: 1–95.
TOMPKINS, G.
1933 Individuality and territoriality as displayed in winter by three passerine species. *Condor,* 35: 98–106.
WALLACE, G. J.
1941 Winter studies of color-banded Chickadees. *Bird Banding,* 12: 49–67.
WHEELER, W. M.
1910 Ants, their structure, development and behavior. Columbia Univ. Press, New York.
WHITMAN, C. O.
1919 The behavior of pigeons. Posthumous works of C. O. Whitman (ed. H. A. Carr). *Carnegie Inst. Washington,* 3: xii+161 pp.
WRIGHT, E. G.
1939 Marking birds by imping feathers. *Jour. Wildl. Man.,* 3: 238–239.

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