ANTIPHONAL CALLING IN QUAIL

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THIS paper reports the occurrence, causation, and adaptiveness of antiphonal calling in three species of North American quail (Odontophorinae): The Bobwhite (*Colinus virginianus*), the California Quail (*Lophortyx californicus*), and the Gambel's Quail (*L. gambelii*).

Armstrong (1963: 180) has reviewed antiphonal singing in birds. It can be defined as the alternation of calling between members of a pair or potential mates. Timing is often so accurate that the mutual calling sounds as though it comes from one individual. Antiphonal calling is characteristic of tropical species that live in dense foliage and form an extended pair bond. It is much less common, although widespread, outside of the tropics. It presumably functions to maintain the pair bond and in some species develops through learning. Diamond and Terborgh (1968) discuss several possible functions of duetting in New Guinea birds. Precise duetting or antiphonal calling has been reported from at least two Central American species of Odontophorinae. Griscom (1932: 108), in quoting A. W. Anthony, described perfect duetting between two *Dactylortyx thoracicus* kept on opposite sides of a house in Quatamala. The natives stated "there would be no song if the two birds could see each other." Skutch (1947: 221) indicated that *Odontophorus gujanensis* probably duets in a manner similar to that reported by Chapman (1929: 275) for *O. marmoratus*. Chapman observed two birds standing one to two feet apart and singing a duet in perfect unison. The only other galliform for which antiphonal calling has been reported is *Francolinus ahantensis* (Holman, 1947: 630). All these species inhabit dense vegetation that prevents visual contact at a distance.

Recently Thorpe (1963), Thorpe and North (1965), and Grimes (1965) have made quantitative studies of the time relationships between the alternate calls of male and female birds.

The antiphonal calling we have heard in quail has been entirely from birds confined in pens as large as 20 × 40 feet in which they often went through their complete annual cycle. Details of these arrangements and the vocal repertoires of these species have been presented elsewhere (Ellis and Stokes, 1966; Stokes, 1967; H. W. Williams, "The voice of the California Quail, *Lophortyx californicus* with particular reference to ontogeny," Ph.D. dissertation, Utah State University, 1966).

These three species of quail spend the winter in coveys of mixed sexes and ages. Cover in quail habitat is often dense. When an individual becomes separated from the group it gives a repeated "separation" call.

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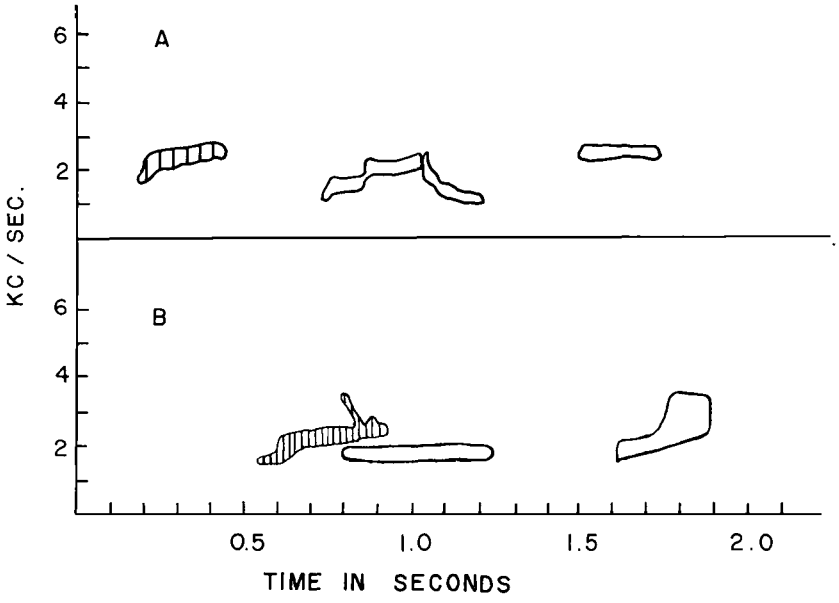

Figure 1. Antiphonal calling in Bobwhite. A. Female's *hoy* (vertical lines) followed by male's *hoy-poo*. B. Female's *hoy* (vertical lines) overlapped by male's *bob-white*.

Members of the group respond, but not antiphonally, thus allowing the separated member to locate and rejoin the covey. Most birds pair while in the covey. At this stage unmated males give a special sexual call to announce their unmated status. In the Bobwhite this is the *bob-white*; in California and Gambel's quail it is the *cow* call. Once paired, males rarely if ever give this call unless the mate dies or becomes separated for an extended period. A member of a pair temporarily separated from the mate will give the "separation" call. The mate upon hearing this call will respond antiphonally with a similar separation call. Separation calling by the female may release antiphonal sexual calling from an unmated male as well as from her own mate. We could readily elicit such calling by separating a pair visually and having unmated males in the vicinity.

Characteristics of Antiphonal Calling in Quail

Bobwhite.—The first type of antiphonal calling frequently occurred when a mated male and female were placed out of sight of each other. Within 1 to 10 minutes the hen would give a 1- or 2-syllable separation call, variously described as *hoy*, *hoy-poo*, or *koi-lee*. This elicited an almost immediate response by her mate, who responded antiphonally with a very similar separation call (Figure 1 A). Data for two series are shown

TABLE 1
TIME RELATIONSHIPS TO ANTIPHONAL CALLING IN BOBWHITE

No. calls in series	*Reaction Time (ms)*[1]		*Type of antiphony*
	Mean	*Range*	
5	700	570–1,030	Female–male mate
7	580	420– 730	"
14	340	240– 550	Female-unmated male
7	370	210– 470	"
8	350	300– 460	"
12	360	270– 520	"
6	320	270– 390	"
18	360	210– 670	"
9	310	270– 370	"
9	350	300– 420	"
11	320	260– 400	"

[1] Time between onset of female's call to onset of first syllable of male's call. Measured in milliseconds (ms).

at the top of Table 1. This was actually a more common form of antiphonal calling than the data suggest.

A more common form of antiphonal calling in Bobwhite was that between an unmated male and a hen who had become separated from her mate. As in the previous situation above, the hen gave a separation call. Thereupon an unmated male within hearing responded antiphonally with the *bob-white* sexual call. Normally, the unmated male responded only after the female had given several calls. The male might start his response with a sudden series of loud *ah-bob-white* calls; more often his first indication of antiphonal response was a very soft *ah*, then *ah-bob*, and finally the full *ah-bob-white* or *bob-white* following each successive female call (Figure 1 B). Records of those complete series that were composed of at least six antiphonal exchanges are summarized in Table 1. Although at least three different unmated males were involved here, their mean reaction times varied only slightly between series (310–370 ms). The minimum reaction time for each series ranged from 210 to 300 ms. Only 5 of 94 exchanges exceeded 500 ms. No consistent change in the reaction time occurred throughout a series of antiphonal calling, nor did the reaction time depend upon the completeness of the male's *bob-white* response.

At times the separation call of an isolated mated female elicited both a separation call *hoy-poo* from her mate and a sexual call *ah-bob-white* from an unmated male, both in antiphonal manner.

California Quail.—Outside of the breeding season males and females of this species give a separation call whenever out of contact with the flock. This is a *cu ca cow* repeated in a series from one to nine times. With the onset of breeding, males give a sexual *cow* call until mated. Breeding males

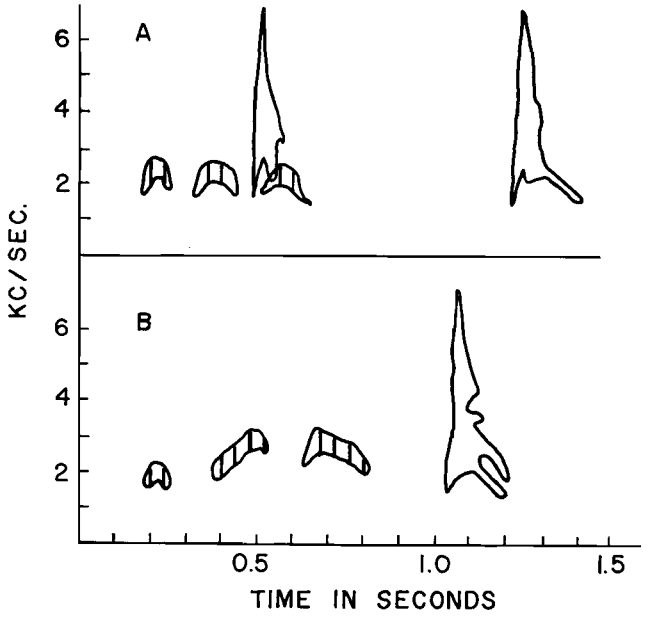

Figure 2. Antiphonal calling in the California Quail. A. The male's "sneeze" calls, the first overlapping the female's *cu ca cow* call (vertical lines). B. The same, but without overlap.

also give an aggressive "sneeze" call, which tends to space out males. We observed withdrawal of subordinate males on hearing the "sneeze" call of caged dominant males even though they were in no danger of attack from the caged male (H. W. Williams, *op. cit.*). Unmated females in the breeding season also give the *cu ca cow* call, which functions to indicate their unmated status. Mated females give the *cu ca cow* call only when separated from their mate.

Whenever a mated pair was separated, one of the birds, it might be the male or the female, gave the separation call. The mate might then respond with the same call. Alternate calling between the pair followed. True antiphonal calling did not normally occur in this situation although the reaction time between male and female *cu ca cow* calling was on one occasion only 190 ms. Unmated males might also give the separation call in response to the female, but much more irregularly, probably because of dominance by the mated male.

True antiphonal calling was considerably less common in California Quail than in Bobwhite. It did occur under the following circumstances. When a mated female was separated from her mate she would give the

separation call. Her mate might then respond antiphonally with the "sneeze" call, often with extreme precision in overlapping the female's separation call (Figure 2 A). At other times the "sneeze" call followed but did not overlap the female's separation call (Figure 2 B). The release of this antiphonal "snneze" call seemed related to calling by unmated males in response to the calling of the separated female.

Mean reaction time in calling sequences involving five mated pairs was 410 ms (range, 110–760 ms). In a typical calling bout the male gave 4 separation calls and 3 sneeze calls in response to 15 separation calls from the female, a much lower incidence than in Bobwhite.

Gambel's Quail.—The vocal repertoire of this species is very similar to that of the closely-related California Quail. We have no quantitative data on the occurrence of antiphonal calling in Gambel's Quail. However when members of a pair are separated, the female gives the separation call upon which the male superimposes a *meah* call (Ellis and Stokes, 1966: 79).

DISCUSSION

Reaction time.—A characteristic of antiphonal calling is the brief time between calling of one bird and the response of the second. In tropical shrikes (Laniidae) (Grimes, 1965; Thorpe, 1963) mean reaction time has been about 120 ms and as brief as 68 ms. This is about one-third the time found in quail.

If the respondent reacts to the very onset of a call, one might expect him on occasion to respond antiphonally to an inappropriate sound or call of another species. In quail this was prevented by the male's not responding to the female until she had given several separation calls. The delay apparently attuned the male to the rhythm of the female's calling. Even then, he usually delayed full response by responding at first with soft calls.

Function and evolution of antiphonal calling.—The response of a male to the repeated calling of a female could conceivably take any of three forms: He might call asynchronously and at irregular intervals; his calls might synchronize with but not overlap the female's calls; and finally his calls might be both antiphonal and overlapping those of the female. The shorter the reaction time (greater overlapping), the greater the masking of the first bird's call, and the more difficult it would be for the responder to be certain of the identity of the caller and vice versa. Hence, one might expect natural selection to favor that type of antiphonal calling in which the calls of the two sexes did not overlap. However, in quail and other birds unmated males that can also respond to the separation call of the female are often in the vicinity. Selection might then favor those mated males that shorten their reaction time or respond antiphonally with an aggressive call, thus serving to inhibit responsive calling by unmated males.

Similarly natural selection would favor those unmated males with short reaction time.

Some indirect evidence for the function of the shortened reaction time seen during the breeding season lies in the calling behavior of quail separated from the winter covey. In winter the separated bird typically gives several calls in succession, then stops. Only then do members of the covey answer. This type of irregular back-and-forth calling continues until the covey is reestablished. The calling birds impart maximum information as to identity and location, thus assuring that the lost birds rejoin the proper covey. There seems to be no selective advantage for antiphonal responses in this situation, and certainly not for overlapping signals.

Another explanation of the evolution of overlapping antiphony relates to the signal value of bird songs. Characteristically, antiphonal calling by two individuals is so closely timed that it sounds like the call of a single bird. If the releasing mechanism in an unmated male were so precise that he responded only to the song of the female, any masking of her song by that of her mate could reduce its releasing value to an unmated male. The masking effect would be greatest where overlap was greatest.

Antiphonal calling in Bobwhite is not entirely homologous with that in both the California and Gambel's quail. The male Bobwhite responds antiphonally to his separated mate with the separation call. This is a call that under all circumstances functions to bring individuals together. The male California Quail may respond to his separated mate in the same way, but certainly with less precision and overlapping. In contrast both the California and Gambel's quail males respond to the separation call of their mates with an aggressive call. This aggressive call, while synchronous with that of the female, is really being directed toward potential rival males in the vicinity and has a repellant function. Power (1966) has also ascribed an aggressive motivation to duetting in the Orange-chinned Parakeet (*Brotogeris jugularis*).

Finally, only in the Bobwhite have we observed an unmated male respond antiphonally to a female; the motivation of the unmated male seems to be sexual, leading to possible pair formation. Hence it is clear, even within the Odontophorinae, that antiphony may have several functions, being involved in pair formation, spacing of males, and reuniting of separated mates.

SUMMARY

Antiphonal calling is described for three species of quail. In Bobwhite an unmated male will respond antiphonally with a *bob-white* call to any female giving a separation call. Either male or female will call antiphonally to its mate when separated. Antiphonal calling in California and Gam-

bel's quail is mostly limited to the aggressive "sneeze" or "meah" call given by a male when separated from its mate. Several functions of antiphonal calling and the selective pressures bringing it about are postulated.

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