VOCALIZATIONS AND BEHAVIOR IN CAPTIVE GAMBEL QUAIL

C. R. ELLIS, JR., and A. W. STOKES

The life history and ecology of the Gambel Quail (*Lophortyx gambelii*) are fairly well known. Gorsuch (1934) has written the best life history of the bird in Arizona, and Edminster (1954) has summarized information on the species for its entire range. But except for Gullion's work (1962), relatively little has been done on the calls and social behavior of the bird. This paper catalogs and describes the calls and associated behavior of Gambel Quail. A detailed comparison of calls in this group will appear later.

Most of the birds used in the study were trapped in the wild in southern Utah, but some were raised in captivity. The latter were more tame in their reactions to humans.

The birds were held and observed in two pens made from poultry mesh. One pen was $40 \times 60 \times 7$ feet; the other was $40 \times 12 \times 7$ feet. Both were subdivided into smaller subpens by poultry mesh partitions. The birds were clipped on one wing to prevent flight over the three-foot-high partitions. Food and water were freely available in standard containers; a roofed shelter and brush provided cover and loafing spots. To minimize disturbance from passersby, canvas screens enclosed the area.

Observation and recording of calls were done from a blind. Calls and verbal notes were recorded on a Webcor Model EP 2612-1 tape recorder in the blind. Most recordings were made at a tape speed of 3.75 inches per second; the microphone was an Electro-Voice Model 664, hung in the center of the pen. When possible, behavioral situations were manipulated to have the calling bird in the subpen containing the microphone. Birds were separated by placing them in nearby brooder houses; depending on which of several houses were used, auditory as well as visual isolation was obtained. Spatial isolation only was achieved by putting the wing-clipped bird in an adjacent subpen.

Samples of calls were analyzed on a Kay Electric Co. Sound Spectrograph. Included in this paper are typical sonograms of all but one of the calls observed. These were judged typical on the basis of visual inspection, or by measurement of physical characteristics.

The tape recordings and the majority of observations were made in the summer of 1962. Preliminary observations began in spring, 1961. The senior author was a participant in the National Science Foundation Undergraduate Research Participation Program. Additional support was provided by NSF Grant No. G-21348, and by the Division of Research, Utah State University.

Bird calls may be placed in the following categories, which are based largely on the scheme suggested by Collias (1960): (1) Feeding relationships; (2) Responses to enemies; (3) Reproductive behavior—(a) Sexual phase: Courtship and agonistic behavior, and (b) Parent-young phase; (4) Group activity. We will first discuss group activity and then proceed to more complex patterns. The calls, the circumstances in which they have been observed, and their possible functions are summarized in table 1.

GROUP ACTIVITY

Gambel Quail are gregarious through much of the year (Gullion, 1962); consequently much of their behavior is group activity, with associated calls serving func-

TABLE 1

Name of call	Sex of caller	Season of year	Stimulus or cause of call	Possible function of call
Contact	Both	SFWS	Other birds.	Social integration.
Ut-growl	Both	SFWS	Satisfaction after deprivation of food & water.	—
Chipping call	Both	SFWS	Strange objects; terrestrial predators.	Ground predator alarm.
Squawk-chip	Both	SFWS	Escape from stressful situation.	Higher intensity alarm.
Holding squeal	Both	SFWS	Restraining bird by holding in hand.	
Kaa-call	♂ Only	Spring	Breeding condition + lack of ♀.	Advertisement (Song?).
Wit-wut call	Both	SFWS	♀: Agonistic situations.* ♂: Agonistic & courting situations.	♀: Agonistic display. ♂: Agonistic & courting display.
Location call	Both	SFWS	Breeding season: separation from mate. Other times: dispersion of covey (?)	Bringing together separated pairs. Covey reassembly.
Copulation call	♀ = yes ♀ = ?	Spring Summer	Copulation and/or ejaculation.	
Meah-call	♂ Only	Spring & Summer	Intense and protracted agonistic situations.	Reduction of physical combat.

* Intense fighting rare in ♀♀.

tions of the covey rather than the pair situation. These contact calls are seldom if ever given by an isolated bird.

The basic contact note. This call sounds like a rising *took*! (fig. 1A). It carried only a short distance and occurred at any time of day. Most often it was associated with feeding, where it formed a continuous low "chatter." It was heard when birds were preening, roosting, or loafing, but inactive birds were usually silent. There was no apparent sex difference in the call.

The ut-growl. This conversational call consists of the basic contact note plus a rising trill (fig. 1B); the emphasis is on the trill. The call was given when birds found food or water, especially after deprivation of them. Both sexes gave the call. The *ut-growl* was given occasionally in fragmentary form; sometimes only the isolated trill was given. However, the version shown in figure 1B was typical. The stimulus for the call is obscure and further observation is needed.

The location call. This call will be treated fully under "reproductive behavior," but its probable function in group activity demands recognition here.

FEEDING RELATIONSHIPS

In the adult birds observed, we noted no specific food call. In the closely related California Quail (*L. californicus*), Rumsey (personal communication), the parents used a specific call that brought chicks on the run. The male Bobwhite (*Colinus virginianus*) gives a food call that attracts the female (Stokes and Williams, unpublished observations).

RESPONSES TO ENEMIES

Aerial predators. Although a specific alarm call was anticipated in both natural and experimental situations, none was heard. Quail new to our pens seemed unfamiliar

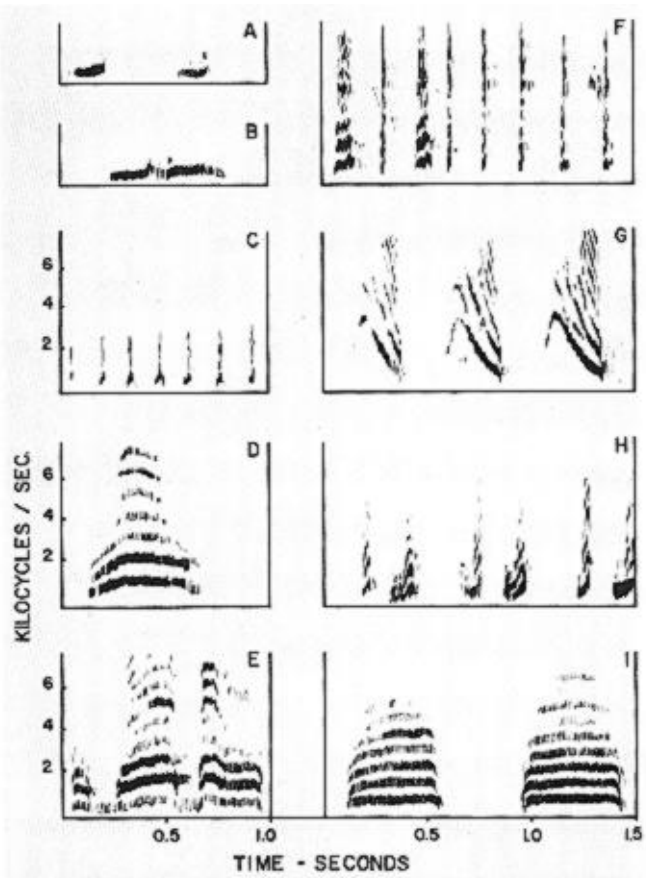

Figure 1. Vocalizations of the Gambel Quail: A. Took call; B. *Ut*-Growl; C. Chipping call; D. *Kaa* call; E. Location call; F. *Squawk-Chip* call; G. Hand-held distress call; H. *Wit-Wut* call; I. *Meah* call.

with and chary of the screams of low-flying California Gulls (*Larus californicus*). When hearing such screams, the quail hurriedly took cover, but no calls were ever heard from them. At other times passing hawks alarmed wild passerines in the study area. The latter in turn alerted the quail, but even a direct overflight of the hawk caused no calling as the quail ran for cover. Attempts to imitate the soaring flight of raptors by sailing paper plates gave inconclusive results. If a specific call for aerial predators is present, it must require a stronger or more specific stimulus to elicit it.

The chipping call. An alarm call (fig. 1C) given at a very low threshold of stimulation is the sharp, staccato *chip-chip-chip* heard when something suspicious is discovered in the environment. Usually it was evoked by a close-range stimulus (fig. 2B); however, barriers and screens surrounding the study area afforded the birds little opportunity to react to more distant stimuli. In an adjacent pen of California Quail a similar call was given on the discovery of a cat more than 50 yards away.

Numerous garter snakes (*Thamnophis* sp.) inhabited the area, and the discovery of one by the quail evoked much *chipping*; however, the response did not last long if

the still-visible snake stopped moving. In one typical situation, *chipping* by the first bird to see the snake quickly brought all birds to the scene. They walked back and forth with short, mincing steps, the plumage tightly compressed, and keeping about two feet away. With necks craned they examined the suspicious object, and seemed to waver between curiosity and fear. Each series of *chips* started off at a fast rate and then slowed (fig. 1C). As interest waned, the calling stopped, and the birds wandered away. The range of stimuli that evoked the response was wide and included large insects, mice, new or different water dishes, pieces of rope, and many other inanimate objects. Discovery of a human in the blind usually evoked *chipping*, followed by withdrawal. There were times when the birds *chipped* without discernible cause, as during a storm when wind-caused noise was general. Williams (personal communication) said that a homologous call in the California Quail can reflect ". . . a general state of nervousness and alarm . . ." rather than a specific reaction to a specific stimulus.

The squawk-chip call. A second alarm call is composed of a raucous *squawk* followed by a variable number of *chip* notes (fig. 1F). There may be more than one *squawk*, and they may be repeated or alternated with *chips*. The call always occurred when a bird, male or female, escaped human pursuit. Another situation often seen was the pecking of a bird (usually a male) by another male. If taken unaware, the victim often jumped up and ran, giving the call as he fled. A bird released from the hand usually *squawk-chipped* upon taking flight. *Squawk-chipping* sometimes persisted for several minutes after short but intense disturbances. Mated males often *squawk-chipped* for several minutes after the removal of their partners, before changing to the *location call.* Thus it appears that *squawk-chipping* is an alarm given in more intense situations than those evoking ordinary *chipping*. It seems likely that the *squawk* part of the call is an aggressive component, especially in the surprise attack situation mentioned above.

The hand-held distress call. (See fig. 1G.) A quail held in the hand sometimes gave a call that sounded like *kee-OW*!; usually there were several repetitions. Not all birds could be induced to give it, and the proximate stimulus for it was obscure. It bore no relation to the known social order of the flock. The spectrogram of the call resembles that of analogous calls of domestic fowl (Collias and Joos, 1960), the Chukar Partridge (*Alectoris graeca*), and California and Bobwhite Quails. In all of these species the downward component is present, although the upward part may be missing.

REPRODUCTIVE BEHAVIOR

Sexual Phase

In Arizona, Gorsuch (1934) observed pairing early in the spring; some birds came into physiological breeding condition as early as mid-February. When regular observations in the present study began (late May 1962) mating activity was already in progress. Several pairs thought likely to nest were separated from the flock and disturbed as little as possible. The remainder of the flock was used for experimentation.

The kaa-call. (See fig. 1D.) This is undoubtedly the call described by Gorsuch (1934) as "whistling." Although at close range it sounds like a clear, inflected *ka-AA-aa*, the call could easily be termed a whistle if heard from a distance. It was given only by males beginning early in the season; but by July only an escaped male, who stayed (mateless) in the vicinity of the pens, was giving it. No male ever gave it who was or had been paired. *Kaa*-calling was usually done from an elevated perch such as

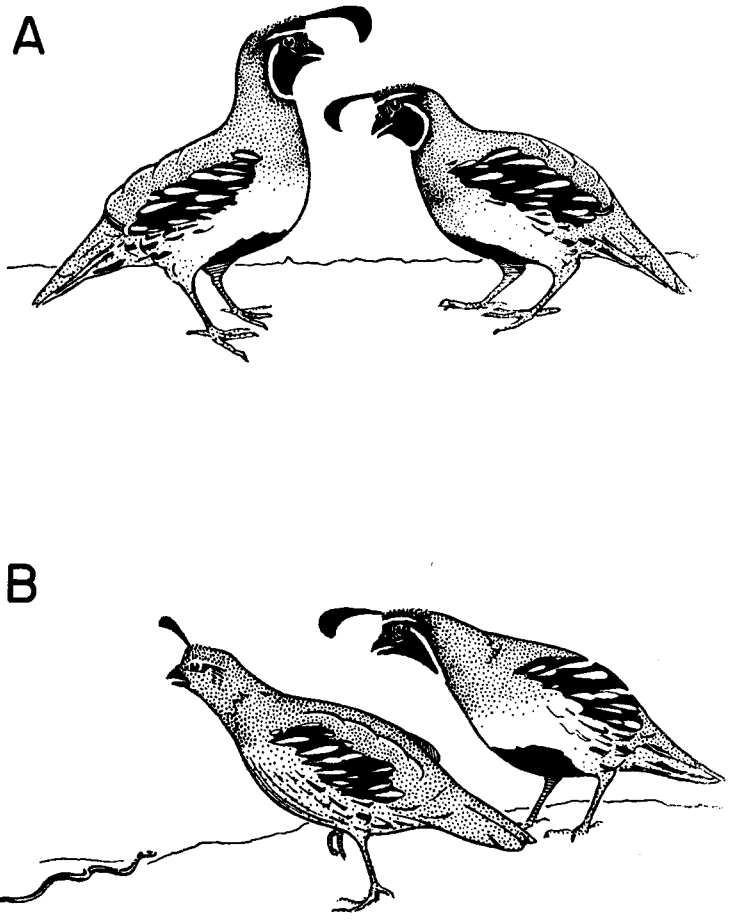

Figure 2. A. Mutual agonistic display of males, either *Wit-wut* or *Meah* calls could be heard here; B. Reaction to a strange stimulus (snake); birds *Chipping* excitedly.

the top of a bush (fig. 3A); a few birds called occasionally from loafing positions on the ground. A *kaa*-calling male was often alert and looked about "expectantly" between calls. There was no definite direction or orientation to these "searching looks." The escaped male referred to seldom gave any call except this one, even in July. Gorsuch (1934) offers evidence suggesting that the *kaa*-call functions to advertise available males during the early part of the breeding season, making it analogous to the advertising song of many passerine species (Armstrong, 1963).

The wit-wut call. As with many species, there is an aggressive element in the courtship of the male Gambel Quail (Baerends and van der Cingel, 1962; Hinde, 1953; Stokes, 1961). One of the most common displays of the cock to the hen also occurred in agonistic situations between two males. Figure 1H shows a representative version of the *wit-wut* call. Although the sample was small, there was no difference in the appearance of the call between agonistic and courtship situations.

In courtship the male faced the female directly with legs extended but not on

tiptoe. The tail was depressed, the back approximately level, and the head and neck upright. The display consisted of a bowing or bobbing motion, mainly in the head and neck. The black plume was held mainly vertical although it was vibrated incidentally by the bobbing. Accompanying the display was a two-noted call that sounded like a strident *wit-WUT*! The call and the display always occurred together. The display continued for as many as 10 repetitions, or as long as the hen remained nearby. Usually the hen responded by feeding, wandering away, or preening, in that order of frequency. The male usually followed the female; only if he was unable to do so was the display given at distances over two feet.

The lateness of the first observations in the breeding season very possibly precluded witnessing early sexual displays. Specifically, two incidents occurred that were never repeated and that hint at the existence of other displays.

In the spring of 1961 a female was observed to lower and flutter her wings at the approach of the male, who ignored her. The birds were together in the same pen, but both had just previously been removed from an adjacent pen. The male was preoccupied with attempts to rejoin his former pen-mates and never responded to the female's display. She did not display to other males presented experimentally. This is, however, a common display in female Bobwhite during early stages of pair formation and reflects both sexual and escape tendencies (Stokes, unpublished observations).

The other incident occurred on 12 June 1962; it involved a pair with a strong pair bond (*i.e.*, the birds spent much time together and had copulated). The male picked up a piece of grass and carried it several feet toward the female, but dropped it before reaching her. This suggests incipient nest-building behavior, which in some galliforms has become ritualized between members of a pair (Stokes, 1961). Ambient noise made it impossible to determine whether a call accompanied the behavior.

The location call. (See figs. 3B and 1E.) When a pair of mated birds is separated, the most common response of one or both is to give a very distinctive call. It is variable in shape (unlike some others) but is always recognizable. The typical version sounds like a high-pitched *ka-KAA-ka-ka*, and thus far no sex differences have been found in it. The call occurred in several situations; the one mentioned above is the best understood. Paired birds that had been together only a few hours gave the call upon separation. In other cases birds that had been together several days failed to call upon separation. But mated birds (criterion: copulation) never failed to call upon the removal of one partner. This was usually true for both sexes; but in two cases separation produced calling in only one partner, a female in one case and a male in the other. Visual isolation seems to be the primary stimulus eliciting the call. Birds separated only a few inches by an opaque barrier called to each other, whereas birds separated by poultry mesh did not. In one experiment the female of a closely mated pair was removed. Then her location call and those of three other females were played to the cock through a partly concealed loudspeaker. In one of four trials the male oriented toward the source of the calls, and it seemed that his behavior was definitely in response to the call of his own mate. Biases in the experiment could have been the presence of artifacts ("blips") on the tape or the inappropriate placement of the speaker. Thus, although the results were inconclusive, further experimentation is clearly warranted.

Other situations in which the location call was given are less clear. Some males were never with a female; some of these "bachelor" males location-called when no stimulus was discernible. Sometimes an unmated male gave it upon hearing other males call. Males whose mates were with them occasionally location-called. In this

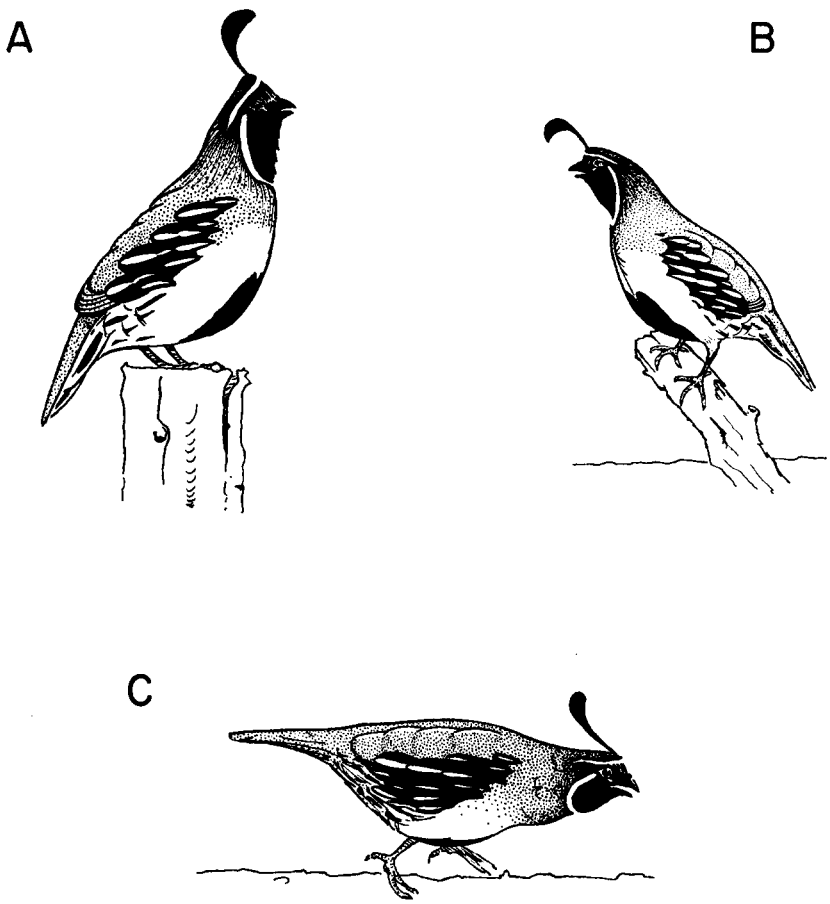

Figure 3. A. Male *kaa*-calling from perch; B. male giving location call; C. male charging an adversary, plume position characteristic.

situation the male had been perched on a lookout for several minutes. A mated female was never heard to give the call when in the same pen with her partner.

It is likely that the location call has both a sexual and a nonsexual "rally" function as does the rally call of the Chukar Partridge (Stokes, 1961), thus serving to reunite scattered individuals of a winter covey. This rally function can be invoked to explain location-calling in other than the separated-pair situations discussed above. Since the entire flock of birds had been together in one large pen before the study began, separation into several smaller groups may have broken up social relationships among the covey, leading to location-calling as a rallying call.

In the case of separated paired birds, it might be argued that the resulting calling was nothing more than rallying. But if a substitute male was introduced into a pen with a separated female, she continued to call until the original male was returned. Furthermore, in one case a pair of birds called to each other for many weeks, during

which time they never saw each other; a call by the male always evoked an answering call by the female. The reciprocal response in that male, however, disappeared quickly; he soon stopped answering the female's calls, even though as late as the end of summer the female showed signs of "remembering" her early partner.

The copulation call. The female, and probably the male, gave calls during copulation, but attempts to record them were unsuccessful. It sounded like a series of short squeals and did not begin until after the male began treading. Williams (personal communication) demonstrated that male as well as female California Quail calls during copulation.

Agonistic Aspect

Much of the agonistic behavior observed was associated with sexuality in males. A successful method of eliciting fights was to introduce a female into a pen of sexually deprived males. If this female was one who had previously shown signs of pairing with one of the (now) deprived males, fighting was limited to that male and one or two others. But if the female was new to all males, fighting was general and prolonged. It was directed initially at the female, who was vigorously pursued around the pen. After a few minutes one particular male could be seen to take her side, becoming her "champion." This male began to repel others and stopped his own attacks on the female. During lulls in the fighting he displayed to her with the *wit-wut* call. His displays usually brought fresh attacks on himself, and it was during this time that the severest fights between males took place. In an intense situation both males displayed standing face-to-face, pecking at the other between calls. Prolonged individual fights were rare. But in the few observed the combatants flew up vertically, each trying to gain the advantage of height over the other (these occasions were in 1961 before the birds' wings had been clipped). The denouement of a fight was often the sudden escape of one of the birds; often the victor pursued the vanquished, sometimes for several turns around the pen (fig. 3C). In no known case and regardless of his social rank did a female's first "champion" subsequently lose her. Dominant males might prevent full courtship by attacking, and copulation attempts were seldom successful, but the female remained with that male.

The meah call. (See figs. 2A and 1I.) On many occasions when two males fought to an impasse, one suddenly gave a call remarkably like the *meow* of a cat. Sometimes the opponent responded antiphonally. In all observations of this frequent behavior, no relation was detected between the caller and the ultimate "winner" of the encounter. The call is probably the result of conflict between escape and aggressive tendencies, and functions to reduce the amount of actual fighting. Invariably an encounter with much *meah*-calling finished with fewer blows being struck. No female was ever observed to *meah*-call; fighting in the females was limited to simple dominance skirmishes.

Meah-calling also occurred as in response to location-calling by a female whose mate had been removed. The *meah* was superimposed on the latter part of the female's call, and was given by a male who had previously been paired with the female. Birds that were totally sexually deprived often *meah*-called in response to the location call of females. On two occasions deprived males responded to taped playbacks of a female location call even though her own partner made no response.

Interpretation of the significance of the call in this last situation is difficult and needs further experimentation. But thwarting of the sexual drive of the male, who is not a "bachelor" by choice, must be a component of the stimulus.

SUMMARY

Gambel Quail were studied under conditions of seminatural captivity in order to describe and catalog the vocal repertory and associated behavior. Observation was done from a blind. Calls were recorded on magnetic tape and later analyzed on a sound spectrograph. Sonograms of representative versions of all but one of the observed calls are included, and the social context and possible functions of the calls are discussed.

LITERATURE CITED

ARMSTRONG, E. A. 1963. A study of bird song. Oxford University Press, London.

BAERENDS, G. P., and N. A. VAN DER CINGEL. 1962. On the phylogenetic origin of the snap display in the common heron (*Ardea cinerea* L.). Symp. Zool. Soc. Lond., 8:7–24.

COLLIAS, N. E. 1960. The analysis of animal sounds. *In* Animal sounds and communication. (Publication No. 7, American Institute of Biological Sciences, Washington.)

COLLIAS, N. E., and M. JOOS. 1953. The spectrographic analysis of sound signals of the domestic fowl. Behaviour, 5:175–188.

EDMINSTER, F. C. 1954. American game birds of field and forest. Chas. Scribner's Sons, New York.

GORSUCH, D. M. 1934. Life history of the Gambel Quail in Arizona. University of Arizona Biol Sci. Bull. No. 2.

GULLION, G. W. 1962. Organization and movements of coveys of a Gambel Quail population. Condor, 64:402–415.

HINDE, R. A. 1953. The conflict between drives in the courtship and copulation of the Chaffinch (*Fringilla coelebs*). Behaviour, 5:1–31.

STOKES, A. W. 1961. Voice and social behavior of the Chukar partridge. Condor, 63:111–127.

Department of Wildlife Management, Utah State University, Logan, Utah, 20 March 1965.