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VOCALIZATIONS OF SCALED QUAIL

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The Scaled Quail (*Callipepla squamata*) is typically a bird of the desert-grassland and Chihuahuan Desert associations. Its range extends from southeastern Arizona through much of New Mexico, southeastern Colorado, western Texas and Oklahoma, and across Mexico in a broad band to Hidalgo (Johnsgard 1973).

Several significant studies of Scaled Quail ecology have been conducted (Wallmo 1957, Schemnitz 1961, Hoffman 1965, Campbell et al. 1973), but little has been written on the vocal signals and social behavior of the species (Johnsgard 1973, Hatch 1975). Detailed analyses of vocalizations of closely related species in captivity have been performed by Williams (1969) for California Quail (*Lophortyx californicus*), by Ellis and Stokes (1966) for Gambel's Quail (*L. gambelii*), and by Stokes (1967) for Bobwhite (*Colinus virginianus*).

This study is based on observations and tape-recordings of free-living birds. I intend to describe the repertoire of vocal signals of Scaled Quail and discuss each signal in its selective context. This study may lay the framework for research to identify more completely the interacting forces shaping each behavior.

METHODS

I conducted field work from June 1972 through November 1973 and again on 14–16 May 1974, mainly in three contiguous square-miles of desert grassland just East of Cochise Stronghold (Dragoon Mountains) in Cochise County, southeastern Arizona. The 150 days of field work sampled all seasons but emphasized summer periods. Within the "Sunsites" development of the Horizon Corporation, the site was subdivided by dirt roads into a uniform grid of 96 blocks, each one-fourth by one-eighth mile. The study area lacked buildings, was free from grazing, and received little disturbance. The grid of roads aided both accessibility and observation of the birds and permitted me to pinpoint locations of sightings. Supplemental observations were made at a secondary site, a waterhole between Oracle and Oracle Junction, Pinal County, Arizona and on four wild quail that I kept as captives from January through August 1973.

I surveyed quail on systematic transects (10 mi per survey) on the Cochise County site. The vehicle served as a blind but I approached on foot if necessary to obtain a complete count by flushing a covey. I used a windmill as an observation tower and crawled through the grass to obtain behavioral data on undisturbed birds.

I determined sex and age of quail by plumage (Wallmo 1956). Sex could often be distinguished in the field during spring and summer by the color of the head and throat; fall and winter birds could be sexed with reasonable certainty only when in the hand.

With one- and two-entrance Stoddard quail traps baited with milo grain, I captured, banded, and back-tagged 72 Scaled Quail at the primary site. The color-coded vinyl backtags were attached by means of elastic loops that I could easily slip over the wings. These tags did not interfere with normal running or flight, and allowed recognition of individuals at a distance. No losses were caused by capturing and handling, and I saw some tagged birds as long as eight months after release.

I used a Sony TC-800B tape recorder and a Dan Gibson electronic parabolic microphone for all field recordings (tape speed 7½ ips). I also recorded two three-day-old chicks in the lab. I analyzed calls on a Kay Electric Company Sonograph, model 6061B, using the FL-1 circuit and the wide-band filter setting. The audiospectrograms reproduced here were judged typical by visual inspection.

RESULTS

Scaled Quail are monogamous, with sexes similar in size and plumage (Wallmo 1956). Both sexes are reproductively mature by the breeding season following their first winter. Primary sex ratio approximates 1:1, but differential female mortality results in a male-biased adult population (Campbell et al. 1973, Hickey 1955). During the early breeding period, of variable length and timing, the population disperses as pairs and single males; occasionally remnant groups persist when breeding conditions are unfavorable.

Both parents attend the young. Broods provide the nuclei for covey formation, consisting of brood mergers or the addition of unsuccessful pairs and unmated males. Essentially all Scaled Quail were found in coveys of three or more (up to 40) individuals from September through March (Anderson 1974).

This brief summary of the annual cycle suggests the types of interactions that may occur, which in turn influence the evolution of social signals. For the call descriptions and interpretations which follow, my data base for adult vocalizations is shown in Table 1. Each number shows the separate occasions on which a given call type was used. It does not count repetitions of a given call; thus the 312 *shriek* encounters actually represent thousands of the calls heard. In a very general way, the frequency distribution indicates the relative commonness of a call, but the sample is not

TABLE 1. Minimum sample sizes for behaviors described in this paper. (An encounter with a bird scored one observation for each behavior given by that bird, even if the behavior was repeated.)

Sex	Breeding status	*chekar*	*CHUPuh*	Contact notes	*tsing*	*TiCHUNK*	*squeal** a.	*squeal** b.	*squeal** c.	*shriek*	Tidbitting (*cut cut*)	Sentinel behavior
Male	Unmated	79			10		17	4	6	112		
Male	Mated, no brood	17	3	1	15		13	8	3		17	19
Female	Mated, no brood	20	6	4	13							
Unknown	Mated, no brood	9	4	3	6		2	1	7			
Male	Mated, with brood	8			16		4					11
Female	Mated, with brood	7	1		22		2				1	2
Unknown	Mated, with brood	12	3	1	12		2	3			1	4
Unknown	Non-breeding; in covey	114	27	12	117	2+	2	2	11		4	11
Unknown	Unknown	150+	10	1	21		9		18	200+		1
Minimum Totals		416	54	22	232	2		114		312	23	48

* *squeals* broken down by context:
a. another quail or pair of quail moving closer to caller
b. another animal (not Scaled Quail) approaching caller
c. context not determined.

unbiased. Loud or conspicuous calls (e.g. *chekar, shriek*) tended to be heard more easily than soft calls (e.g. *CHUPuh, cut cut*). My presence often disturbed the birds, probably increasing the use of *tsing*.

The table stratifies the calls by the sex and breeding status of the caller. Obviously, mated males without broods account for most of the tidbitting acts. Males and females showed no differences in the use of *chekar* or *tsing*. Where sex determination was not possible, some inferences are yet feasible. For example, when I watched mated pairs without broods, I identified males as the callers 24 times when the *squeal* vocalization was given, females never; for the 10 cases in which I heard *squeals* from one member of a mated pair but did not actually see the caller, it would be safe to assume the caller was the male.

In discussing probable functions of each call, I will omit reference to selection for species-distinctiveness. Four species of quail—Scaled, Gambel's, California, and Elegant (*Callipepla* [*Lophortyx*] *douglasii*)—are considered by some authorities to be congeneric (Johnsgard 1973, Hubbard 1974). It is not known to what extent selection for divergence or convergence has occurred. I will point out homologies and differences where these may be instructive.

THE *CHEKAR* (SEPARATION) CALL

A distinctive two-syllable *chekar* (Peterson 1961) was often given by individuals of either sex when separated from other quail (Table 1). Wallmo (1957) described it as *chin-tang* or *chuk-ching*, while Johnsgard (1973) interpreted it as *pay-cos'*. In all cases, the second syllable is somewhat longer than the first.

A calling quail tipped its head up slightly, opened its bill and pumped its tail on each syllable. Eyes remained open. Quail gave the call while standing or walking on the ground or from an elevated perch.

Figure 1 is a series of audiospectrograms representing portions of a continuous sequence of *chekars* that lasted nearly 15 min. The calls were made by a hen separated from her mate, who flushed when my vehicle stopped. Initially the hen gave two strong series of *chekars*, then reverted to low volume calls (part A), apparently inhibited by the appearance of the parabolic microphone. At low volume, these calls sounded more like

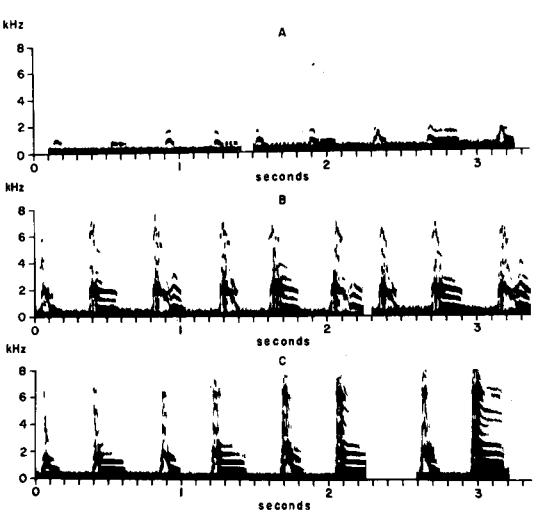

FIGURE 1. *Chekar* calls given by a female separated from her mate: A, low intensity calls; B and C, high intensity calls.

repetitions of *wip-woo* than like *chekar*. All sequences were initiated by a *wip* syllable, though either a *wip* or a *woo* syllable could have terminated the sequence (Fig. 1A).

After 11 sequences of from one to three *wip-woo* repetitions each, the quail graded into strong *chekar* series of three to seven repetitions each (Fig. 1B and C). Although spacing of notes was comparable at both volume extremes, the *chekars* sounded qualitatively different, because of the increase in overtones. At highest intensity, an uncommon variant appeared (the third, sixth, and ninth syllables in Fig. 1B), a sneezy *chip* that followed the normal *chekar*.

Shortly after a covey was flushed, one or more quail started the *chekar* call. The separated birds usually ran or flew toward the caller, even when this meant exposing their locations to a potential ground predator. A calling bird often moved toward other birds whom it could see or hear. A quail flying toward a caller frequently overshot or veered away from the actual position of the caller, and the birds converged on the ground. Calling generally ceased before or shortly after the covey was fully reassembled. Birds rarely called when a flushed covey landed together. Sumner (1935) found the tendency to answer so strong in California Quails that a mechanical imitation of their separation call in the winter often induced return calling by an undisturbed covey.

When different birds alternated calls during reassembly, there were no predictable patterns of exchange. Nor was there adequate precision in the responses of separated mates to suggest antiphonal calling of the form described for the Bobwhite (Stokes and Williams 1968).

Chekar calls reassemble covey members before dusk if they have scattered while feeding. Scaled Quail typically roost on or near the ground in a small compact group, often a part of the larger covey (Russell 1932). It is not known whether or not members of a roosting party are kin if the covey is comprised of several families. If separated at night, the quail remain where they land and do not assemble until daylight (Wallmo 1957).

An incubating female leaving the nest for either of her daily feeding periods gave the *chekar* call when she was some distance from the nest. The male flew or ran to join his mate, accompanying her as she ate, though seldom feeding with her. California Quail (Williams 1969), Gambel's Quail (Ellis and Stokes 1966), and Bobwhite (Stokes 1967) are known to be capable of recognizing their mate's call.

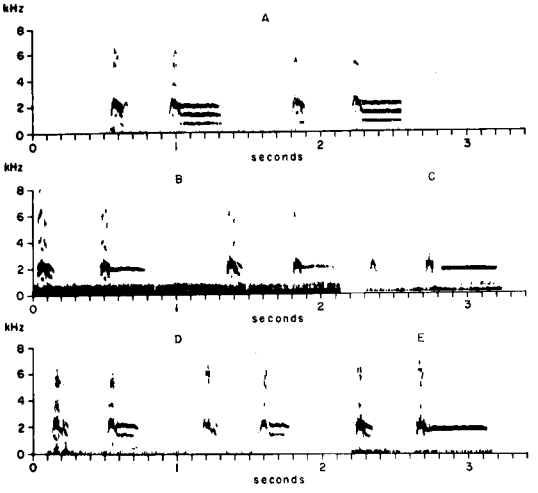

FIGURE 2. *Chekar* calls by five different unmated quail.

Unmated males gave series of *chekars* interspersed among *shrieks* (described later) advertising their single status. Five different unmated males gave the *chekars* shown in Fig. 2. These calls were usually given at full intensity. They varied from one to eleven *chekars* per series, averaging six to eight. Each series was separated from the next series or from a *shriek* by pauses of 2 to 15 s, and no predictable relationship between *shrieks* and *chekars* was evident.

CHUPuh

Figure 3 demonstrates a low-volume vocalization given by quail when seeking escape or when re-contacting associates after disturbance. It appears to coincide with the "group alarm cry" or *chink-chank'-a* described by Wallmo (1957) as being similar to the separation call but more rapid and with slightly different syllabication. It somewhat resembles the *wip-woo/chekar* type of call (Fig. 1), but differs from these by lacking the regular intervals of syllables and by the usual crowding of two syllables (*CHUPuh*) into the space of about 0.2 s. Figure 3C begins with a sequence which sounds like *CHUPuh CHUPuh CHUP?*, with a slightly rising inflection on the last note. Unlike *chekars*, in which both syllables are equally stressed (though the second syllable is longer), the *CHUPuh* calls distinctly emphasize the first syllable. Figure 3D shows unusual variants of the call.

Captive birds gave this call while frantically searching for an exit from the pen. If ap-

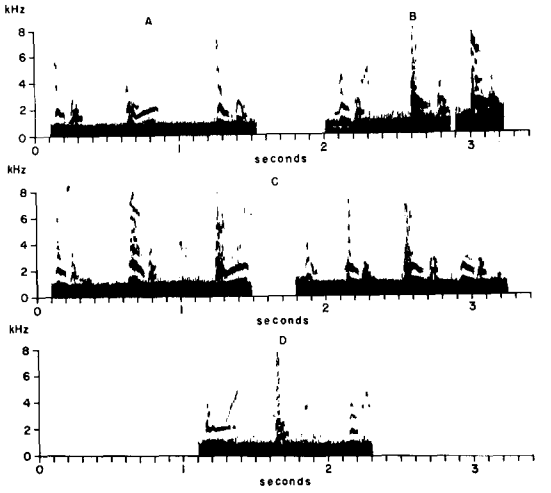

FIGURE 3. *CHUPuh* calls by captive quail seeking exit from pen.

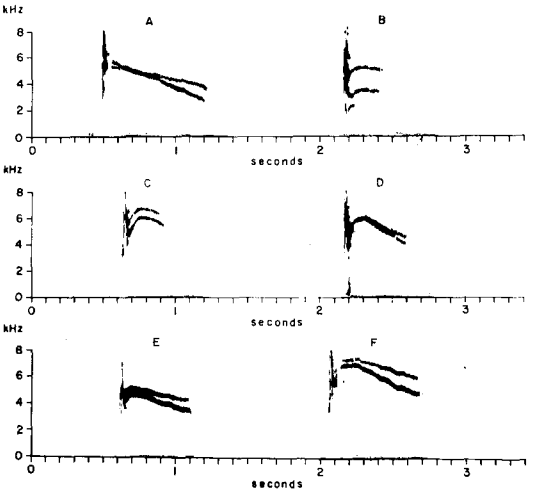

FIGURE 4. *Tsing* calls by six different adults in contexts of alarm.

proached too closely, a quail stood erect and uttered a *tsing* note. It then returned to a head-low, active search for escape, oriented away from the disturbance.

In the field I heard this low-volume call only 44 times, much less frequently than I heard the *chekar* or *tsing* (Table 1). It typically occurred when quail resumed contact after having been scattered by a disturbance or when a female approached her mate who was giving agonistic *squeal* calls (discussed later).

CONTACT NOTES

Wallmo (1957) reported "conversation notes," soft *clucks* and *chirps* within an undisturbed group or pair. I noted such calls on 22 occasions (Table 1), but since they were audible at just a few meters, the calls may have been more common. Gambel's Quail in my study area appeared to give similar notes much more frequently.

Because the calls were soft and given only by undisturbed birds, I was unable to record them. It is possible that they may coincide with *wip-woos* (low intensity form of *chekars*).

TSING

This call (spelled *tsinggg* by Wallmo 1957) was given by adults and larger juveniles of both sexes (Table 1). The calling bird jerked its head slightly with each utterance, with the eyes open. Most calls were given by birds standing or running, but flushed birds often gave them at the beginning of flight.

Figure 4 displays six audiospectrograms of *tsing* calls. Each is characterized by a quick, broad frequency pulse which becomes a high frequency descending slur, ending imprecisely. Several show a peculiar splitting of harmonic bands (Fig. 4A and 4D), suggesting dual control of sound production within the syrinx (Greenewalt 1968).

The usual stimulus eliciting the *tsing* call appeared to be the sight of potential danger approaching on the ground. Frequently avoidance followed, particularly if the quail was further approached. Cattle or deer approaching quail were as effective in eliciting the call as were coyotes and humans. If the potential danger did not approach, the calling quail might resume feeding or drinking, but seemed to keep the intruder in view and repeated the *tsing* call occasionally.

Trapped birds gave the call when approached closely and often when handled. At all times the calling bird kept its body erect, its crest raised, and its eyes oriented toward the alarming stimulus. Between calls the bird often flicked its erect crest, which is usually depressed when the bird is relaxed.

Other birds within hearing of the calling bird responded with alertness and avoided the stimulus if they could see it. The homologous call in California Quail, *pseu*, "will often throw a dozen covered cartons full of banded quail into a pandemonium of scuffling and scrambling" (Sumner 1935:205). He also found some quail responding to the call by approaching in a manner that he interpreted as a form of mobbing behavior which might distract the predator. Alternatively, the responding birds may have been

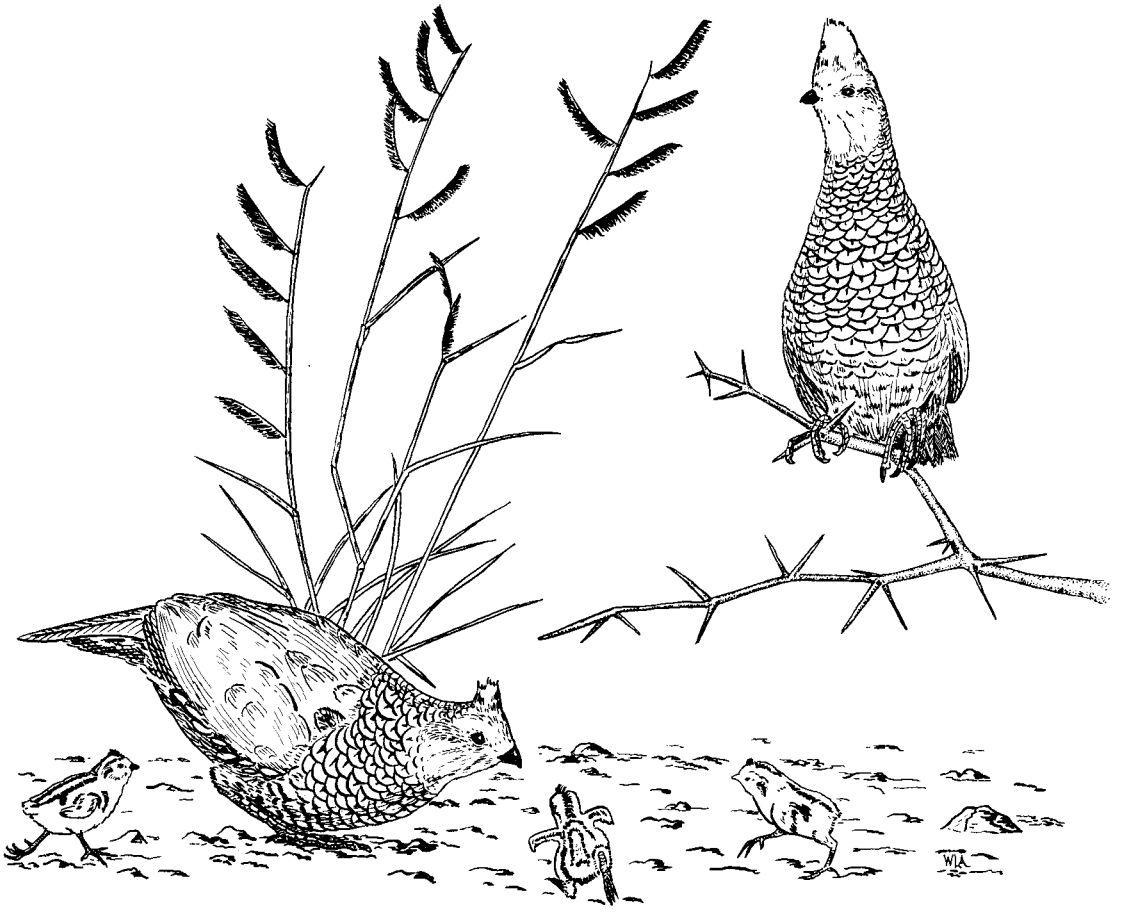

FIGURE 5. Male Scaled Quail (right) perched as sentinel while the hen and chicks feed below. The erect crests indicate that the quail have been alerted. If approached by a ground predator, the male may give the *tsing* call and jump to the ground to run or fly with the brood.

approaching to learn the predator's characteristics (Kruuk 1976).

Tsing calls occurred most predictably when adults with a young brood were disturbed. Often the adult male, perched above the ground as a sentinel, gave the *tsing* as he jumped down to flush with the family (Fig. 5). In about half the winter-coveys flushed, one or more birds gave the call. Even single males gave the note when alarmed at close range, generally concurrent with escape behavior. Agonistic encounters with other males sometimes were followed by *tsing* notes, perhaps accompanying an avoidance tendency.

TiCHUNK

Although the presence of an "aerial alarm response" has been noted for many galliforms (Johnsgard 1973), I found no recent references to its existence in Scaled Quail. Bendire (1892) offered a second-hand report of a gutteral *oom-oom-oom* given by a quail chased by a hawk. Ellis and Stokes (1966) were unable to elicit such a call in captive Gambel's Quail, but Williams (1969) found that California Quail frequently reacted to a sudden overhead stimulus.

Scaled Quail typically responded to an avian predator by freezing motionless or by ducking quickly into heavy cover. On 22 October 1973, a Cooper's Hawk (*Accipiter cooperii*) pursued several quail deep into the cover of low mesquite, causing the quail to burst out in many directions. Some uttered *tsing* notes, but two or more gave intense *TiCHUNK* calls. All flew but a short way, dropping into heavy cover. The hawk remained motionless a few seconds, then tried unsuccessfully to relocate the scattered quail.

SQUEAL (HEAD-THROW)

The *squeal* vocalization is a high intensity call, initiated as a broad-spectrum of noise that becomes an ascending complex of har-

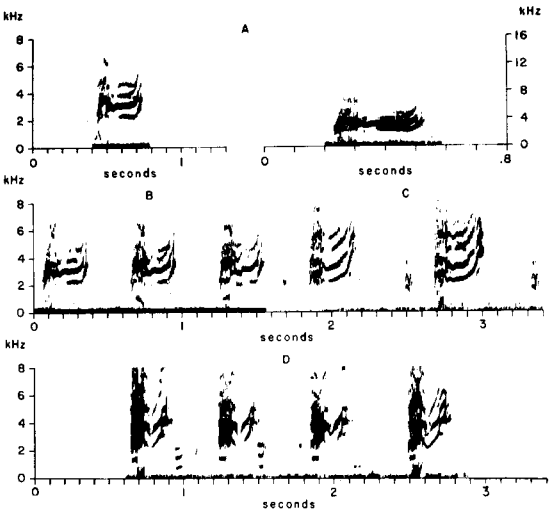

FIGURE 6. *Squeal* calls. A, the same call analyzed at both 8 kHz and 16 kHz scales; B and C, two sequences of calls by other males; and D, male *squeals* and the softer *CHUPuh* calls of the mate.

monics (Fig. 6). The quail tosses its head upward and backward vigorously, opening the bill and closing the eyes (Fig. 7). It repeats the call up to eight times, each repetition 0.4 to 0.8 s apart.

A male in breeding condition predictably gave the call when confronted with another male (or with his own image in a mirror, Johnsgard 1973). If avoidance did not occur immediately, other agonistic gestures (low aggressive rushes or actual fighting) followed, interrupted occasionally by bouts of *squealing*. Playback of recorded *squeals* induced more *squeals* from nearby single males, but mated males generally responded only if another male was in sight.

Williams (1969) noted but one instance in three years of a *squill* call by a female California Quail; Ellis and Stokes (1966) detected no *meah* calls by hen Gambel's Quail. I heard *squealing* by wild female Scaled Quail in only 2 of 57 instances in which the caller was seen (Table 1). On 28 June 1973, two pairs arrived at a waterhole simultaneously. One male *squealed*; the other male *squealed* back and moved away, only to encounter a female Scaled Quail with three small chicks. The male *squealed* and rushed at the female who *squealed* back. The male stopped and both birds bobbed their heads up and down rapidly, but no fighting occurred. On 29 June 1973, a pair was flushed from chicks still unable to fly. The parents circled, giving *tsing* and *chekar* calls. After considerable disturbance, the female gave two

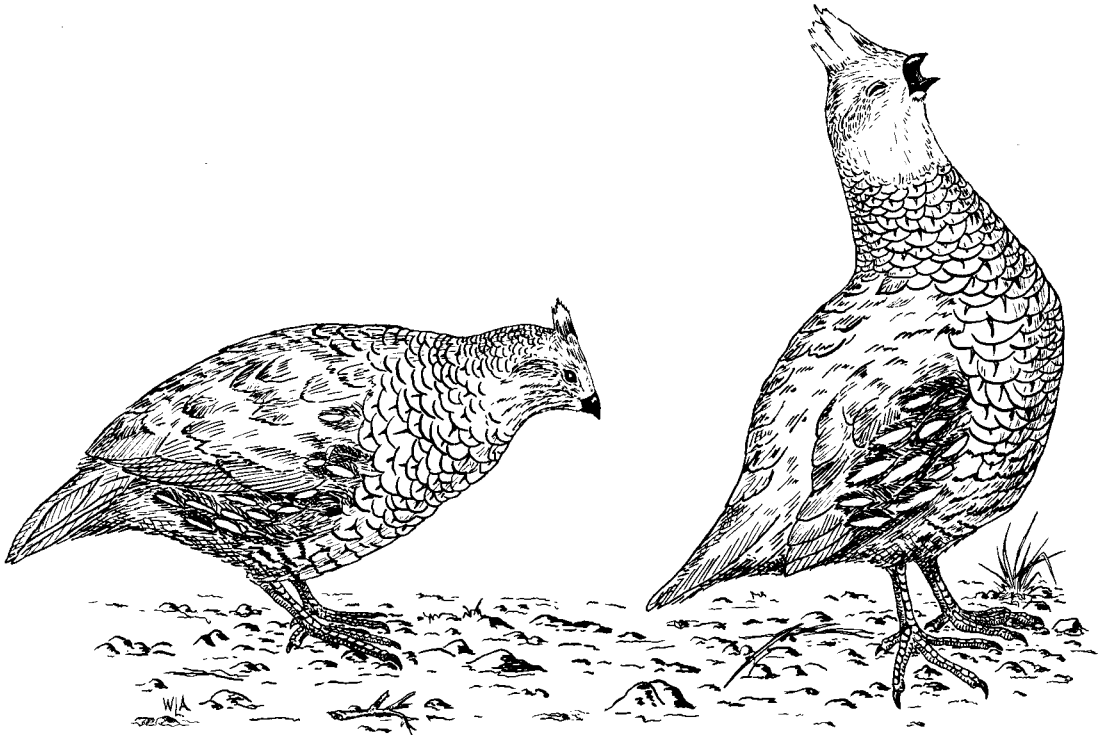

FIGURE 7. Postures of a mated pair of Scaled Quail when disturbed by another male or a mildly alarming stimulus. The male (right) gives *squeals* and the female may give *CHUPuh* calls.

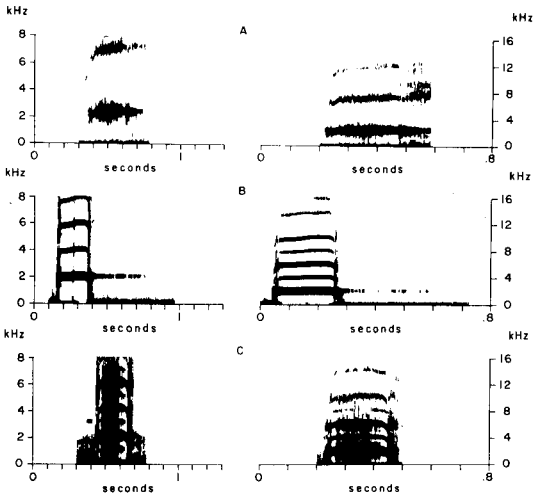

FIGURE 8. Comparison of male *shrieks* on both the 8 kHz and 16 kHz scales.

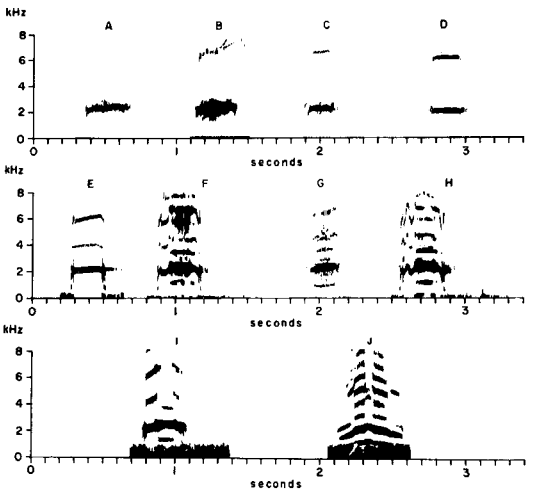

FIGURE 9. Advertisement calls of male quail: A–I, *shrieks* by male Scaled Quail; and J, *kaa* call by male Gambel's Quail.

squeals, then resumed the separation and alarm calls.

Figure 6C shows that a male quail may interject a short syllable between *squeals*, particularly in the later parts of a series. These interjections are given with the head at normal level between the violent head-throws. They appear to be a variant of the *CHUPuh* call.

Though primarily a male call, *squeals* also were given outside the breeding season (Table 1). Occasionally the apparent stimulus was not another Scaled Quail; I observed birds *squeal* when approached by humans, cattle, deer, Gambel's Quail, and even a Loggerhead Shrike (*Lanius ludovicianus*). Johnsgard (1973) reported *squeals* given by retreating quail, with some individuals also giving a *chip'* or *chip-eee'*, perhaps variants of the *tsing* or *CHUPuh* notes. In some cases the quail may be directing the call toward the intruder, demonstrating location and possibly aggressiveness so that a large non-predator (deer, cattle) may avoid approaching too closely. *Squeals* from individuals in a covey landing close together may be directed toward flockmates who have alighted too near for the comfort or safety of the caller.

Figure 6D presents further evidence of the alarm context in which the *squeal* may appear. As cattle approached, the male of a pair gave *squeals* while his mate uttered a series of *CHUPuhs* (Fig. 7). Unlike the uniform *CHUP* interjection occasionally given by males, the female's calls were not synchronized with the pattern of the male's *squeals*.

SHRIEK

I found the *shriek* to be the most variable of the major Scaled Quail calls. This variability may account for the variety of names applied to it: *cree* in New Mexico (Russell 1932), *squawk* or *kwock* in Texas (Wallmo 1957), and *whock* in Oklahoma (Schemnitz 1961).

Figures 8 and 9 illustrate some of the variation of the call. Figure 8 gives three examples as they appear when analyzed on both the 8 kHz and 16 kHz scales. Most whistles last 0.2 to 0.3 s but differ greatly in the number and arrangement of harmonics, as well as in purity of tone. Figure 9J shows the homologous call of a Gambel's Quail which called alternately in a long, unsynchronized series with a male Scaled Quail, whose call is shown in 9I.

Shrieks were given only by males, presumably by unmated ones (Table 1). Intervals between *shrieks* in a sample of 77 calls varied from 3 to 20 s, averaging 8.2 s. Periodically, a calling male interjected a series of *chekar* calls, then resumed the *shrieks*. If slightly inhibited, the male gave soft *pips* before resuming *shrieks*.

With each *shriek*, the quail tilted its head up, closed its eyes, and pumped its tail slightly. On *chekars*, the bill was tilted just above the horizontal and the eyes remained open.

Single quail typically called from a perch (Table 2). Only four of 107 observations involved calling from the ground, and one of those quail used a gravel dike to raise its effective height to 1.2 m. Choice of perch

TABLE 2. Average height of calling perches chosen by unmated male Scaled Quail.

Type of perch	No. of observations	Av. height (m)
Yucca stump	17	0.8
Yucca stalk	41	2.1
Mesquite	40	1.5
Sign or fence post	5	1.6
Ground	4	0.3
Total	107	1.5

usually reflected availability. Sites with good clearance on all sides were usually chosen, but the quail did not always select the highest available perch.

In 1973 calling began in April, coincident with the breakup of coveys. Both Wallmo (1957) and Schemnitz (1961) found similar initiation in their populations. Frequent calling in both morning and evening periods continued until broods appeared. Calling then declined noticeably, particularly in the afternoons. By early July, few *shrieks* were heard. On 18 July, however, I found a significant revival of calling, apparently in response to the heavy rains the preceding week. These rains may have flooded some nests, forcing females to re-nest, or may simply have improved the nutritional status of all birds. I heard no *shrieks* after 8 August 1973 and none at all in August 1972.

During the breeding season, playback of recorded *chekar* calls of female Scaled Quail stimulated increased calling (both *chekars* and *shrieks*) by unmated males but elicited no response from either sex of a mated pair (several dozen tests). When I flushed a pair with young, the female's *chekars* were also likely to induce calling by nearby males. My findings concur with those of Levy et al. (1966) that single males tend to approach *chekar* calls independent of any visual stimulus.

Williams (1969) found that administering testosterone proprionate daily to male California Quail produced aggressiveness and *cow* calling, behavior characteristic of unmated males in the breeding season. Male Scaled Quail giving *shrieks* are presumably in reproductive condition and capable of breeding. The presence of a mate may inhibit the *shriek* vocalization in males who may otherwise retain reproductive capabilities. Two examples illustrate this.

Marked male RWY was observed with his mate for long periods on seven days from 18 April through 18 May 1973. During this time I occasionally flushed the pair, who re-united quickly after giving *chekar* calls. At no time did RWY give the *shriek* call characteristic of unmated males. On 19 and 20 May, the female was gone and male RWY's behavior was totally different from that of the previous month. He gave repeated series of *shrieks* and *chekars*, challenged and fought several unmated males, and wandered extensively. Apparently this male (at least two years old, since I banded him as an adult the previous fall) succeeded in acquiring a new mate, for on 25 May and on five more occasions in the next month, I saw him with a female, and the *shriek* was no longer used.

A second case of a mated male assuming the behavior of an unmated bird was set up when I trapped a hen but not her mate. The male gave many *chekars*, but the female was inhibited from calling by her fear of the trap and me. After one-half hour of separation, the male gave a *shriek*, then more *chekars*, then several more *shrieks*. I released the female, who flew toward the male, and each gave soft *chekar* calls as they ran together.

TIDBITTING

During the breeding season I often observed a male Scaled Quail attract his mate to him when he found a choice food item, particularly an insect. Typically the male faced toward the food, pecked incompletely at it, and uttered a soft *cut cut* food call. This behavior in chickens was called "tidbitting" by Domm (1927). Stokes and Williams (1971, 1972) described and illustrated the display and call as found in galliforms.

The most common releaser for this behavior on my study area was a small moth. A male quail usually pecked it once or twice to subdue it, but would not consume it if his mate was near. Only once did I see a male present the food with his bill as is more commonly done by the Bobwhite (Williams et al. 1968).

A female generally responded immediately to the call by running to the male and consuming the food. The homologous food call in Red Jungle Fowl (*Gallus gallus*) is easy to locate, being brief, repetitive, and covering a broad frequency range (Stokes 1971). The sudden, accurate dashes made by a female quail out of sight from the male suggest that she is able to determine directionality from the sound. When a mated female's foraging brought her to a moth or other item suitable for the tidbitting display, she ate it immediately.

Either parent may tidbit to the young, but less commonly than for males to females dur-

ing courtship (Table 1; also Williams et al. 1968). Occasionally during the winter, a quail would discover a large or attractive food source and give the *cut cut* call. Nearby quail would immediately converge upon the calling bird and feed rapidly; often six to ten birds would be in contact at once.

OTHER POSSIBLE SEXUAL CALLS

Neither this study nor Johnsgard (1973) found any calling by Scaled Quail during copulation. Both male and female Gambel's Quail (Ellis and Stokes 1966) and California Quail (Williams 1969) and the female Bobwhite (Stokes 1967) occasionally call during copulation.

I had no opportunity to observe nest-building behavior in Scaled Quail. Williams (1969) described a call and associated behavior which accompanied nest-building in California Quail.

CHICK VOCALIZATIONS

Figure 10A illustrates the call of a captive three-day-old Scaled Quail chick; Wallmo (1957) referred to the call as *cherking*. It consists of short notes with ascending frequencies, usually terminated by a small descending leg. The homologous call in the domestic chick, "pleasure notes" (see audiospectrogram in Collias and Joos 1953) or *twitter* (Andrew 1964), is extremely similar in pattern. It also bears strong structural similarity to the *pipping* and *twitter* calls (possibly variants of the same call) of the young California Quail (Williams 1969). The *cherk* was given when a chick was in the presence of other quail, free from disturbance, and not hungry.

When separated from its companions, a young chick emitted lengthy series of *peeps*. Figure 10B shows the *peep peep* call of the same chick that gave the *cherks* in 10A. Young chicks gave four to five *peeps* per s, up to twelve *peeps* per series. Each series was separated by a pause of three to six s. The basic form spectrographically is that of a short inverted "U".

Figure 10C–E shows field recordings of chicks separated from their parents. The call is clearly analogous to that already discussed for separation calls (*chekars*) of the adults. As such it corresponds to the "lost call" of Bobwhite chicks (Stoddard 1931) and of California Quail chicks (Sumner 1935). Calling by both chicks and adults continued until reassembly occurred. Collias (1952) found a reciprocal relationship between calling of

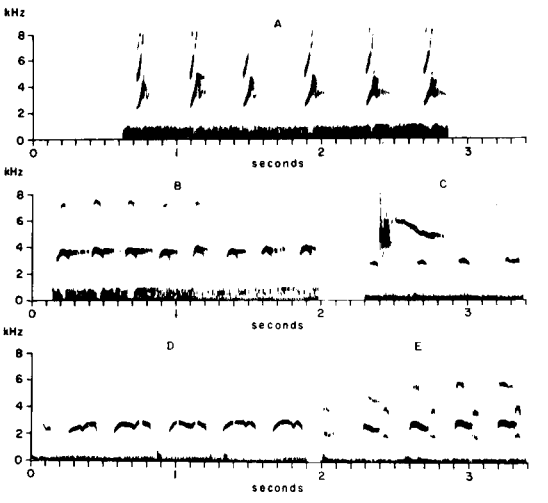

FIGURE 10. Calls by juvenile quail: A, *cherk* calls of three-day-old chick; B, *peep* calls of three-day-old chick; C, low intensity *peter* calls superimposed by *tsing* of adult; D and E, *peter* calls of older chicks.

domestic chicks and their hen. *Peep peep* calls stimulated clucking by the hen, which in turn inhibited peeping in the chick, particularly if they came into contact.

The *peep peep* call of very young chicks soon sounded more like *peter peter*. The number of notes per call series decreased from ten or twelve in the first week to series of six (Fig. 10D), then to five (Fig. 10E), and the fundamental frequency became lower. These trends continued until development of the adult *chekar* call with two syllables and many overtones (Figs. 1 and 3). Call configurations suggest that the *CHUPuh* call is derived from the same juvenile call.

Figure 10C shows four *peter* syllables over which an adult *tsing* is superimposed. Though simple in structure, the calls were made by the older chicks who also gave the calls in 10E. Just as occurs in adult *chekars*, inhibited chicks call at a lower volume in which harmonics drop out and overall structure is simplified.

I heard no *tsing* alarm calls in juvenile quail until they were at least half-grown. Wallmo (1957) first heard it in chicks seven weeks old. It was similar to the adult call but lacked the "metallic ring."

DISCUSSION

Visual signals are little used in Scaled Quail except for short-range purposes, such as between mates or rival males. The similarity of plumage of both sexes suggests selection for crypticity in Scaled Quail to reduce vulner-

TABLE 3. Synopsis of Scaled Quail vocalizations.

Name of call	Sex calling	Context	Probable function	Probable information content
chekar	Both	Visual isolation from one or more regular associates; *chekar* from another quail	Reassembly of separated birds—pair, brood, or covey. Proximity important for reproduction, parental investment, and self-protection respectively	Identifies caller, gives location of caller, and shows caller's motivation for reassembly. If call is subdued, may indicate a threat is still nearby
		Unmated bird early in breeding season	Long-range advertisement for mate	Gives caller's location and willingness to seek contact
CHUPuh	Both	Approach of another animal, potentially dangerous; reassembly after alarm	Communicating low intensity alarm and preventing associates from avoiding the caller	Identifies caller as non-threatening flockmate
	Female	*Squeal* of her mate	Preventing male from attacking or avoiding the female	Identifies caller as mate; non-threatening
contact notes	Both	Nearby presence of associates in nonsexual and non-threatening situation	Maintenance of contact with mate or group	Indicates caller is close by and undisturbed; perhaps encourages reciprocity by flockmates, without which the caller will cease calling and become disturbed
cherk	Both	Chick in presence of family, unthreatened, not hungry	Maintenance of contact with family	Same as adult contact notes
peep	Both	Chick separated from siblings or parents; chick cold, wet, or hungry	Reassembly of chick with usual companions; brings parental care when needed	Indicates chick is distressed; same information as adult *chekars*
tsing	Both	Approach of ground predator; capture	Alerting kin or flockmates of danger	Indicates caller is alarmed; posture and avoidance behavior of caller may indicate direction from which danger approaches
TiCHUNK	Both (?)	Extreme threat, such as hawk attack	Predator confusion; reduce likelihood of capture by increasing reaction time of predator	Perhaps deceives and startles the attacker by intense reaction
squeal	Mostly male	Male-male encounter during breeding season	Distance-increaser; reduction of actual fighting	Conveys degree to which caller is motivated aggressively; reflects dominance relationships
		Chekar calls of hen mated to the calling male	Inhibition of responsive calling by unmated males	Identifies caller as aggressive mate of the female giving *chekars*
		Disturbance by non-predator	Avoidance of further conflict	Alerts intruder to location and aggressive motivation of caller
shriek	Male	Lack of mate during breeding season	Advertisement of sex and single status to potential mates	Identifies caller as sexually-motivated, unmated male
		Responsive *chekar* calls from unknown bird	Determination of status of other bird	Same as above; challenges bird giving *chekars* to identify its own sex

TABLE 3. (Continued).

Name of call	Sex calling	Context	Probable function	Probable information content
cut cut	Male	Encounter with novel food item, female nearby	Attraction of female; enticement leading to copulation; strengthening of pair bond	Shows female a desired food item; signifies potential fitness of male
	Both	Novel or concentrated food, quail nearby	Parental investment as functional feeding of young; attraction of companions around caller as self-protection	Gives location of caller and a food source

ability to diurnal predators hunting by vision. Short-range signals such as the flicking of the crest, standing erect with slicked feathers, and escape movements themselves all readily convey fear motivation to other nearby quail without risking undue exposure to a predator. Certain calls are used instead to convey information about intensity of the alarm situation.

Compared to other forms of signals, sounds have several advantages: they (1) are relatively economical to produce, (2) decay rapidly, thus avoiding interference with further transmissions, (3) travel quickly to distant points, (4) are relatively independent of physical obstacles (compared to visual signals), and (5) provide a wide choice of available frequencies and intensities for signal use (Thorpe 1961:9). Final expressions are influenced by the physical and biological environment.

Otte (1974:406) described six basic types of information that may be conveyed in animal signals: (1) deictic, drawing attention to an individual or object, (2) identification, specifying age, sex, relationship, individual, species, and so on, (3) spatial, referring to a location, a direction, or a distance, (4) response level, reflecting the motivation of the signaler or the character of some exploitable resource, (5) temporal, indicating the timing of some event, and (6) event, informing on events taking place. Each signal may impart several types of information.

Table 3 presents a concise summary of the Scaled Quail calls, their usual contexts, their likely functions (as in Williams 1966, Alexander 1974), and their presumed information content (in the sense of Otte 1974, not as in information theory). My interpretations of the data correspond with evolutionary predictions, but the logical extension of this study would be an experimental, hypothesis-testing approach using captive birds of known age, sex, and relationship to other experimental birds. Though the table is nearly complete in itself, a few comments may be useful.

Both sexes share nearly all calls, consistent with the similar roles in parental care and the long period of flocking. The persistence with which separated birds give *chekars* until reassembled suggests strong advantages to flocking, despite the automatic disadvantages to group living (Alexander 1974). Two other calls, the *CHUPuh* and contact notes, may assure other conspecific quails of the nonthreatening motivation of the caller in situations of alarm and peacefulness respectively. *CHUPuh* notes by a hen when her mate is giving the agonistic *squeal* call may prevent him from mistakenly directing his aggression toward her.

The *squeal* appears homologous to the "caterwaul" of the Bobwhite (Stokes 1967, Hatch 1975), the *squill* of the California Quail (Sumner 1935), and the *meah* of the Gambel's Quail (Ellis and Stokes 1966). In Gambel's Quail, the *meah* may reduce the amount of actual fighting (Ellis and Stokes 1966). Williams (1969) placed two male California Quail in the presence of a female; the subordinate gave only four of the 18 *squill* series and those only before the birds had established a final dominance relation. This suggests that the *squeal* and its homologues may be used to indicate a male's willingness to fight. Fighting can be costly to either combatant, and a signal showing aggressive motivation may spare the caller significant expense. If both participants behave more agonistically ("calling the bluff"), actual fights may ensue.

In encounters between males, a visual signal may accompany the vocal one. In California and Gambel's quails, the head-throw call exposes the conspicuous black throat. The chestnut throat of the Mountain Quail (*Oreortyx pictus*) and the black and white throat of the Bobwhite are also conspicuous. The throat of the male Scaled Quail

is pale buffy to white, but it remains as one of the few distinctive features separating the sexes (Wallmo 1956). Critical tests on the possible functions of the throat patch have yet to be performed.

On one occasion I flushed the male of a pair without also forcing the female away. The male landed 75 m away near a single male. Both males *squealed.* The hen began a *chekar* series. The mated male flew toward her but overshot her by 40 m. She continued to *chekar* as the male ran toward her, but he stopped three times to give series of *squeals* which overpowered the volume of her calls. The context and the behavior which resulted suggested incipient antiphonal calling (Stokes and Williams 1968). In the two *Lophortyx* species they studied, the male superimposed the agonistic call over the separation call of the female, probably to "inhibit responsive calling by unmated males." The headthrow call, if my observation was not exceptional, may indicate the response level of the male (highly aggressive) and indirectly identify the female as already mated.

The *cut cut* food call is clearly in the male's reproductive interests if the tidbitting display increases his chances of mating, and provides the female with protein which may help her produce a full clutch of eggs. It is in both parents' interest as a functional feeding of their offspring. The use of the call after covey formation is less obvious. Kin selection (Hamilton 1964, Maynard Smith 1964) and protection from predation (Hamilton 1971, Pulliam 1973) are possible nonexclusive hypotheses that could be tested.

The *tsing* may have evolved to communicate alarm to kin or frequent associates while minimizing location cues that might attract predators. As a high, rather pure whistle which terminates imperceptibly, it is remarkably similar (probably by convergence) to alarm calls of many bird species (Marler 1957). Though given most frequently when flockmates (usually relatives) are near, it is occasionally given by single males or by birds in very large coveys. It is possible that the call, at least when given as the bird flushes immediately before a predator, may startle the latter and increase its reaction time (Humphries and Driver 1967). The *tsing* and its homologues in other quail have been labeled "distress calls," but intensive work is still necessary to determine how, in the several contexts within which such calls are given, the signaler itself is favored.

The Scaled Quail in this study did not hold and defend territories. A paired male defended his mate in relation to her position, without persistent topographic reference. Activity space overlap of different pairs was considerable.

Unmated males in the breeding season either wandered or remained near mated pairs, a tendency documented for several quail species (Emlen 1939, Genelly 1955, Ellis and Stokes 1966, Johnsgard 1973, Anderson 1974). Unlike passerine songs, which may both attract females and repel males, three different calls by Scaled Quail are employed: the *chekar,* the usual separation call which brings two birds together; the *shriek,* a "qualifier" which indicates that the caller is both male and unmated; and the *squeal,* the agonistic call directed toward other males.

My study supported the assertions by Wallmo (1957), Schemnitz (1961), and Johnsgard (1973) that the *shriek* call is characteristic of unmated males. A male losing his mate (even for several hours when she is trapped) may resume the call, presumably from a change in motivation (reverted to the status of an unmated male). This agrees with Williams (1969) on California Quail, Stokes (1967) on Bobwhite, and Ellis and Stokes (1966) on Gambel's Quail. D. E. Brown (pers. comm.) elicited *shrieks* from one paired male Scaled Quail by using a tape-recorded female call; he also observed another male call as his mate incubated nearby. These unusual observations may represent cases where the pair bond is weak or where a male is responding as if the recorded calls were those of his own mate.

Birds uttering *shrieks* or *chekars,* especially single males, frequently used elevated perches, a strategy which minimizes sound interference by vegetation and increases the effective range of the calls (Ficken and Ficken 1962, Morton 1975). *Chekars* are repetitive, with many harmonics and relatively low frequencies, attributes that favor long-distance transmission and ease of locatability (Marler 1957). The period during which single males use high and conspicuous perches coincides with the season of lowest pressure from aerial predators (Anderson 1974).

Apparent sentry behavior by quail is reported widely in the literature. Typically one individual flies up on a post, shrub, or tree and appears to watch alertly as other individuals feed below. My 48 observations of this behavior are subdivided by the sex and breeding status of the sentinel in Table 1.

Where sex was known, 30 of 32 sentinels were males. Nineteen observations involved males accompanying their mates, primarily as the incubating females left their nests for

short periods of feeding in mornings and evenings. Males tended to be nervous and easily triggered into giving the *squeal* call. Rarely did they eat as their mates fed, and rarely did the latter look up from eating. Again this is best interpreted as male reproductive effort, whether the watchfulness served to detect predators, rival males, or both.

Adult males exhibit similar alertness and attentiveness when with a brood. Sumner (1935) found that male California Quail fed mostly when the female and young rested in cover. A male usually perched within one-half meter of the ground as the family fed below (Fig. 5), changing his sentinel position to keep in close contact with the feeding brood. At the approach of a "threat," he typically jumped to the ground, with or without giving a *tsing* note, and ran or flushed with the brood.

Quail which perch as sentinels predictably use lower perches (nearly all below 0.5 m) than do calling bachelors (average 1.5 m, Table 2). Sentinels have no demand for long-range signals, and a higher perch would simply render them and their associates more visible to predators. When approached, bachelors tended to flush and fly away directly from the perch; sentinels usually dropped to the ground and flushed only if the brood flushed. The latter may reflect a male's commitment to defense of mate and young, though he himself may gain directly by using the others as cover.

Sentinel behavior was observed between 11 June and 28 October in 1973. When the social unit was more than two birds, only three of 28 sightings involved coveys that definitely consisted of more than one brood. The apparent decline of sentinel activity and the use of *tsing* calls after covey mergers (hence, decline in average relatedness of covey members) is consistent with the hypothesis that the behavior evolved because of advantages to the inclusive fitness of individuals. Marler (1956) similarly found that when family groups of the Chaffinch (*Fringilla coelebs*) dissolve in the winter so that most groups are composed of unrelated birds, the use of hawk alarm calls ceases.

Only the *chekar* vocalization and its equivalent in chicks were given at strikingly different intensities. The ability to control or grade a vocal display in relation to stimulus strength and nearness of conspecific individuals increases the potential information content of the call. The use of *wip-woos* when close to a brood or when danger still threatens not only economically performs the reassembly function of the loud *chekar* calls given when a covey is widely separated, but may also restrict the message to an appropriate recipient.

A study of vocalizations is a necessary preliminary to the application of any census technique which depends on song or call counts. Biologists extrapolate from spring call counts of pheasants, quail, and doves to predict fall populations, hence probable hunter harvests. Yet correlational studies may mislead on cause-effect interpretations. Most quail studies, including this one, describe the male announcement call as characteristic of *unmated* males. A prediction of fall populations would thus be based on counts of that population's unproductive members. Variations in survivorship may create large deviations in numbers of unmated males. When call counts and hunter harvests do correlate well, it may be because both factors fortuitously correlate with another factor related to productivity. For example, higher calling rates may reflect better nutritional conditions for all quail, which in turn account for higher productivity. This example merely emphasizes that we still need detailed life history studies, upon which we may make intelligent decisions in matters which may affect animal populations.

SUMMARY

Vocalizations of Scaled Quail were analyzed audiospectrographically and discussed in relation to contexts, functions, and information content. Four calls were associated with aggregation and contact, three calls with alarm or distress, three calls with sexual attraction, and a single call with threat/attack encounters. Very young chicks used two vocalizations and added others during maturation. Two calls were given primarily by males, but the remainder of the species' repertoire was shared by both sexes.

Social adaptations, including vocalizations, can be accounted for satisfactorily in terms of benefits to individuals and their kin. Behaviors change in frequency seasonally, coinciding with changes in reproductive effort, degree of relatedness of flockmates, and risk of predation.

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