GENERAL NOTES

Courtship feeding calls in gallinaceous birds.—Most male gallinaceous birds perform courtship feeding to attract a female. During the courtship, the male dabbles or holds some unusual food or quasi food while giving a special call. This almost invariably causes any nearby female to approach and take the food. The combination of call and display movement is commonly referred to as tidbitting (Domm and Davis, 1948). The call alone we designate the "food call" because both male and female may give it any time of year.

The calls were recorded at the San Diego Zoo and at the private collection of Alfred D. Hinkle in Alpine, California. We are grateful to Mr. Hinkle and K. C. Lint, Curator of Birds at the San Diego Zoo, for their invaluable assistance. We have described tidbitting and the situations in which it occurs elsewhere (Stokes and Williams, 1971). The present paper describes the form of the courtship feeding calls in galliforms and discusses the possible derivation of the call.

To release tidbitting we merely tossed some unusual food, such as mealworms or berries, to the birds. During the breeding season the male almost invariably reacted and started to call the instant he touched the food. Conditions for release of the call, besides food, included having a female in view, being uninhibited by a nearby dominant male, and suitable motivation associated with breeding condition. In monogamous species the male calls throughout the duration of the pair bond. We reported on this in greater detail for Bobwhite Quail (Williams et al., 1968). Polygynous species, in contrast, generally call only during the courtship stage. Dominant males, at least in Red Jungle Fowl, tend to inhibit subordinate males from calling (Stokes, 1971).

Form of the calls.—Tidbitting calls of 21 representative species of the 50 galliforms whose calls we studied are shown in Figures 1 and 2. All calls were recorded on a Uher 4000-Report L tape recorder at $7\frac{1}{2}$ ips using Uher Model 696 semidirectional microphone. Sound spectrographs were made on a Kay Sound Spectrograph Model 6061A using Fl-1 and wideband settings.

Food calls of all galliforms are soft and have signal function over less than 100 feet. In all species the call is a single frequently repeated note, with little variation in pitch or length between notes. An exception is the slight pitch undulation in the Gray Peacock Pheasant (Figure 1I). Mean duration of the individual call notes range from 0.23 ms in the Brown Eared and Palawan Peacock Pheasants to only 0.02 ms in the Bobwhite and Coturnix Quail (Figure 2C, 2F). In general, the longer the note the slower the rate of calling. The shortest notes also have formants.

The following generalizations seem to apply:

Type 1 call.—Long notes: low rate of calling, no formants, large birds, bird merely dabbles with food, beak held close to ground, polygynous (Figure 1).

Type 2 call.—Short notes: high rate of calling, frequent formants, small species that hold food in beak while calling, beak usually several inches above ground, monogamous (Figure 2).

In most respects, the four species of jungle fowl resemble Type 1 on the basis of size and behavior, but the form of the call closely resembles that of Type 2.

Diversity between species in the food call.—We had predicted that the food call would prove to be a conservative behavioral character. The call is soft and short-ranged; therefore the need for species-specificity would seem minimal, even though

the call is sexual in function. Among the true pheasants (Phasianinae) it shows considerable similarity between species. Differences between the four species of *Lophura* seem to be more in calling rate than form of the individual notes. Figures 1A, 1B, and 1C depict calls of three *Lophura* species. The calls of the two closely related species of *Phasianus*, the Ring-necked and Green pheasants, are likewise similar to each other (Figure 1D, 1E). Unfortunately we failed to use playback of recorded food calls to see if pheasants would respond to calls of other species. Young Bobwhite and California Quail chicks rapidly learned to respond to the food calls of a domestic hen that was caring for them.

The food calls of the partridge and quail show considerably more diversity. This is especially clear in the New World Quail, Odontophorinae (Figure 2A, 2B, 2C). Several of these quail have some degree of sympatry, which perhaps has contributed sufficient selective pressure for evolution of distinct species differences.

Systematic relationships in the food calls.—It seems more probable that the differences in calls have arisen from selective pressures imposed by the bird's size and the specific environment in which it lives. The food call must be easily pinpointed to be effective in attracting the female. Birds use any of three different



Figure 1. Sound spectrographs of courtship feeding calls in 11 Phasianinae. A, Silver Pheasant, Lophura nychthemera; B, Swinhoe Pheasant, Lophura swinhoei; C, Siamese Fireback, Lophura diardi; D, Green Pheasant, Phasianus versicolor; E, Ring-necked Pheasant, Phasianus colchicus; F, Lady Amherst Pheasant, Chrysolophus amherstiae; G, Hume's Pheasant, Syrmaticus humiae; H, Palawan Peacock Pheasant, Polyplectron emphanum; I, Burmese Gray Peacock Pheasant, Polyplectron bicalcaratum; J, Red Jungle Fowl, Gallus gallus; K, Brown Eared Pheasant, Crossoptilon mantchuricum.

devices for locating sounds: phase differences, intensity differences, and differences in arrival time of the sound between one ear and the other. Sounds located by phase difference must have low frequency and be relatively sustained. Intensity differences are used especially by small birds using high frequency sounds. Differences in arrival time of sound are most easily detected by birds with large heads and where the sound has abrupt discontinuities. Virtually all feeding calls in galliforms have such a pattern. Highest frequencies, either in the fundamental or higher formants, occur largely in small galliforms (quail and partridge), suggesting that these small species may rely upon intensity differences in addition to arrival time for sound location. In contrast the larger species, with their low-pitched, more sustained calls, may rely upon phase differences.

Derivation of the feeding calls.—Andrew (1964, 1969) has postulated that calls of the domestic chick, and perhaps of birds in general, are given in response to what he calls "stimulus contrast." Anything in the environment, regardless of sensory modality, that has a strong contrast with its surroundings, or with the expected, tends to be aversive. In the domestic chick this releases the peep call. Objects that have intermediate contrast tend to elicit attention and exploration.



Figure 2. Sound spectrographs of courtship feeding calls in 10 quail and partridge. A, Scaled Quail, Callipepla squamata; B, Mearns' Quail, Cyrtonyx montezumae; C, Bobwhite Quail, Colinus virginianus; D, Black-breasted Quail, Coturnix coromandelica; E, Chinese Painted Quail, Excalfactoria chinensis; F, Coturnix Quail, Coturnix coturnix; G, Chukar Partridge, Alectoris graeca; H, Gray Francolin, Francolinus pondicereanus; I, Erckel's Francolin, Francolinus erckelii; J, Roulroul Partridge, Rollulus roulroul.

In chicks this leads to the twitter call. Andrew has demonstrated that the chick's twitter develops into several adult calls, one of which is the food call.

When chicks are injected with testosterone the shift from simple twitter to food call occurs quickly. The effect of testosterone on all calls is to make them more prolonged and to occur in bouts. Andrew's theory on the ontogeny of food calls seems to fit galliforms in general. The call is released most readily when there is stimulus contrast, i.e. strange food is much more likely to elicit calling than the normal food supply. Secondly, at least in Bobwhite Quail, the food call is essentially identical in juveniles, in adults outside of the breeding season, and in breeding males. The chief difference is that calling bouts are more sustained and released more readily in breeding males than among females or juveniles.

Andrew (idem) found a continuum in the form of chick calls going from the twitter through peep. In general we found little variation in the feeding call in adult male galliforms. This suggests that there has been some degree of ritualization and development of typical intensity (Morris, 1957) which could serve to make the call more functional as a lure for the female.

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Further examples of dual singing by southwest Pacific birds.—A previous paper (Diamond and Terborgh, Auk, 85: 62, 1968) analyzed synchronized duetting between a mated male and female for six species of New Guinea birds. The present paper, based on subsequent field work, briefly describes nine additional cases from New Guinea, New Britain, Fiji, and Samoa. All nine examples involve monomorphic species, and in no instance was I able to collect the singers and prove that they were a male and a female. However the degree of vocal coordination makes it likely that these cases represent male-female duetting rather than male-male countersinging. Cases 1 through 8 are so-called antiphonal duets, while cases 6 and 9 are so-called unison duets (see Diamond and Terborgh, ibid., p. 62 for terminology). Species 1, 2, 4, 5, and 7 are confined to forest, while species 3, 6, 8, and 9 live both in forest and in open second-growth.