

DISPLAYS AND VOCALIZATIONS OF THE SORA AND THE VIRGINIA RAIL

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Little is known about the ecology and the behavior of the Rallidae. Being shy birds which live in dense vegetation and rarely fly unless forced to do so, most species of rails are more often heard than seen. Most of the information available pertains to coots (*Fulica* spp.) and the gallinules (*Gallinula* spp., *Prophyryla* spp., *Porphyrio* spp.), species that regularly feed and move about in open areas (Howard 1940; Gullion 1952, 1953, 1954; Kornowski 1957; Askaner 1958; Navas 1960; Holyoak 1970; Wood 1974). The present study concerns the social behavior of the Sora (*Porzana carolina*) and the Virginia Rail (*Rallus limicola*), especially their methods of communicating in dense marsh vegetation.

METHODS

Field studies were conducted on Elk Creek Marsh, Worth Co., Iowa, 1963-1965, on the Ruthven Game Management Unit, Clay Co., Iowa, 1965-1966, and on Cedar Creek Natural History Area and adjoining private marshes of Anoka County, Minnesota, 1967-1968.

Most observations were made from blinds placed near nests. Twelve nests were observed during 149 h. Rails trapped in the vicinity of a blind were marked with paint or plastic nasal tabs so as to be individually identifiable. Sex was determined by size, males being slightly larger in both species (Horak 1964).

Captive rails were studied during the 1967-1969 breeding seasons in an outdoor flight pen on the Cedar Creek Natural History Area (Kaufmann 1977). Observation of these birds provided most of the information on social behavior, especially on the Sora. (During the three seasons five pairs of captive Soras formed pair bonds, and defended territories, and three nested. One pair of Soras defended a territory each season and nested twice. Five pairs of captive Virginia Rails formed pair bonds, three defended territories, and one nested. Seventy-eight Sora copulations and 37 Virginia Rail copulations were recorded during 645 h of observation.)

Activity was filmed with a 16-mm Arriflex and a Super-8 Anscomatic camera with zoom lenses. The 16-mm films were analyzed using a Bell and Howell time-and-motion study projector. Sketches were made from movies and 35-mm photos. Vocalizations were recorded on a Magnavox tape recorder at 3.75 inches (9.5 cm)/sec. Sonograms of selected tapes were prepared on a Kay Electric Company Sona-Graph. The descriptions of the colors of the rails are from Palmer (1962).

RESULTS

Descriptions of rail behavior were based on observations of captive birds which readily defended territories and bred in a simulated marsh. The terms characterizing rail displays have been taken from studies on gulls (*Laridae*) (Tinbergen 1959). Moorhen (*Gallinula chloropus*) (Howard 1940.

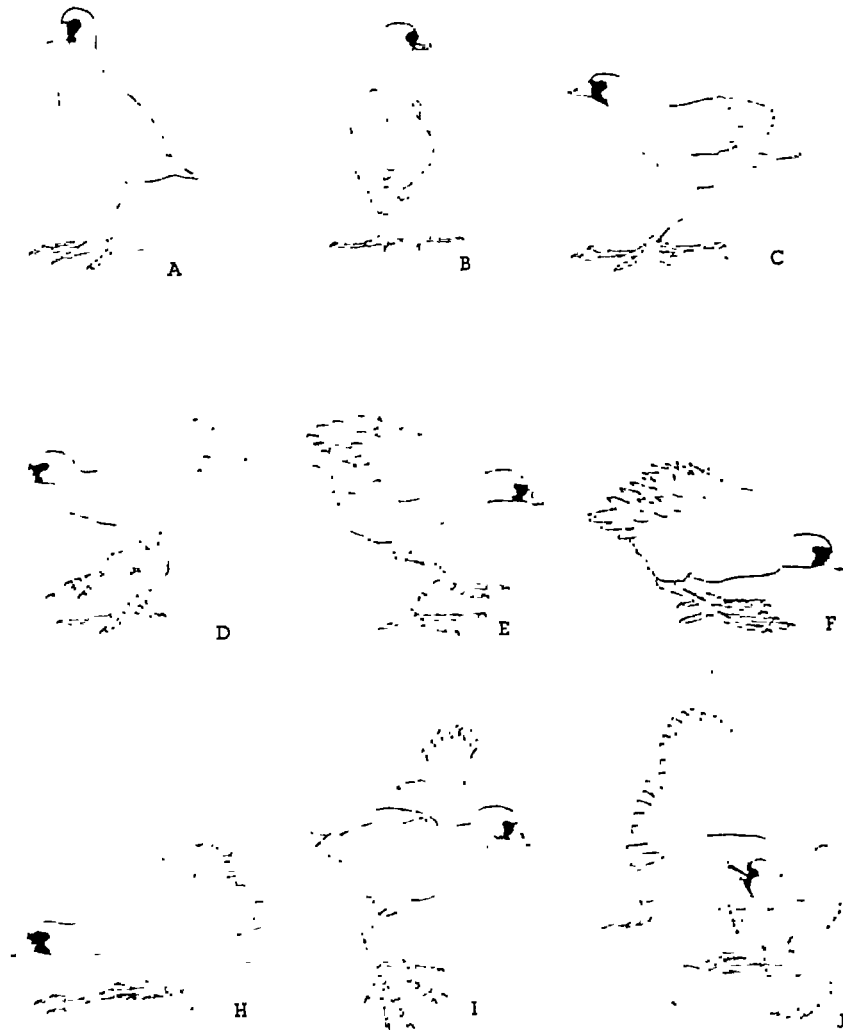


FIG. 1. Displays associated with hostile behavior in Soras: A. upright; B. open bill; C. forward with swanning—mild form; D. swanning—intense form; E. swanning while leaving opponent; F. swanning by raising back feathers; G. swanning by drooping wings; H. sparring; I. fighting.

Wood 1974), and American Coot (*Fulica americana*) (Gullion 1952). Descriptions apply to both species with the variations and exceptions noted.

Behavior associated with hostile encounters: Upright.—The bird assumes an extreme erect posture by stretching its neck upward and

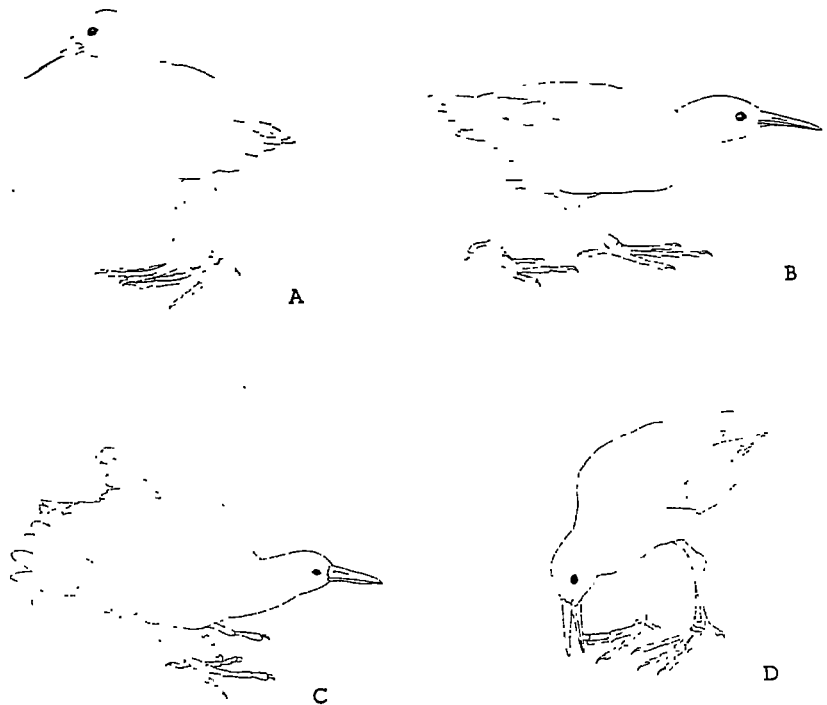


FIG. 2. Displays associated with hostile behavior in Virginia Rails: A. upright; B. forward; C. swanning at nest intrusion; D. substrate pecking.

straightening its legs. The opponent is faced and the bill is directed toward it. A white patch is occasionally exposed on the lesser coverts when the opponent is a dominant bird (Figs. 1A, 2A). In the Virginia Rail, the neck feathers are ruffled when the other bird responds with an "upright." This display appears to be derived from an intention movement of pecking and frequently precedes pecking.

Open-bill.—This display, in which the bill is opened and pointed toward a passing bird, was seen only in the Sora (Fig. 1B). It was most commonly seen during the nonbreeding season when two birds were close to one another and individual distance was seemingly violated.

Facing away.—The head is lowered and turned to one side, the bill pointing toward the substrate. "Facing away" was given as a response to a mild threat, such as the "forward" (see below) and frequently appeared to inhibit attack. It was also performed when a bird was being preened by its mate (Figs. 3B, 4B).

Forward.—The head is stretched forward, toward the opponent (Figs. 1C, 2B). Virginia Rails seem to extend the neck farther than Soras. Soras

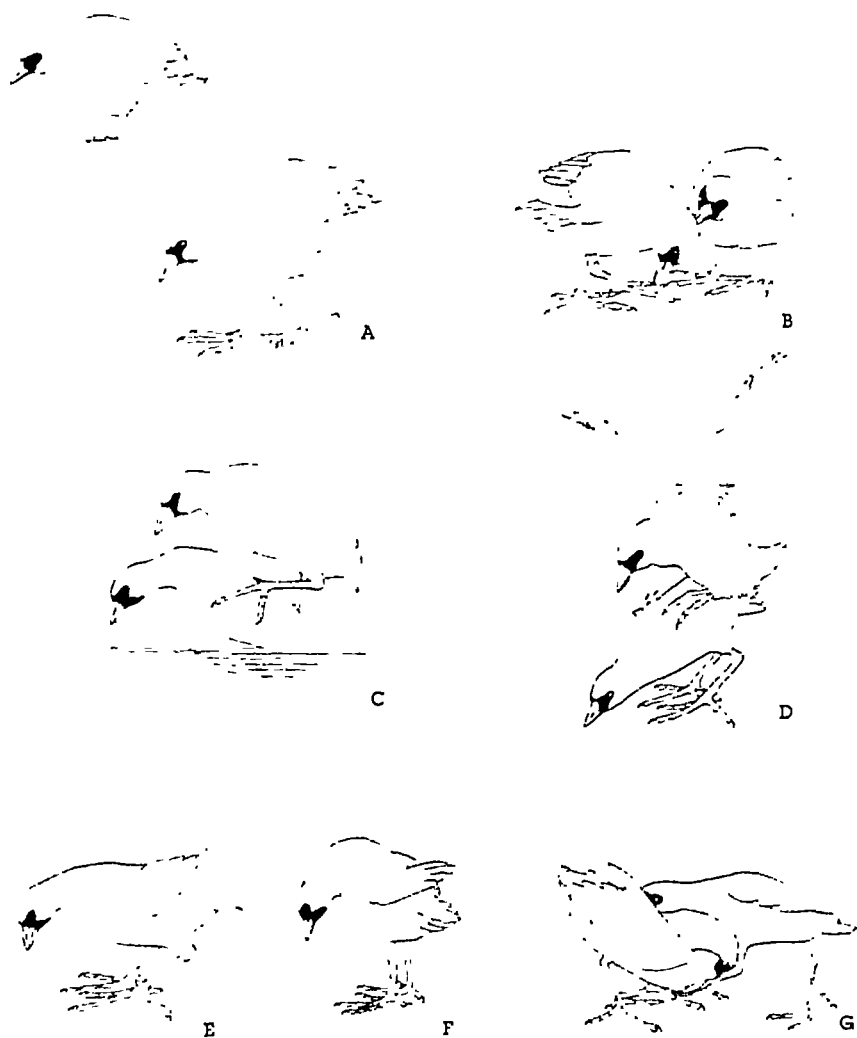


FIG. 3. Displays associated with sexual behavior in Soras: A. mates together; B. allopreening; C. male mounting female; D. copulation; E. post-copulatory bow after successful copulation; F. post-copulatory bow after unsuccessful copulation; G. meeting and passing.

usually included a variety of feather erection postures in a forward when two males were engaged in display at the boundaries of their territories. A forward appears to be derived from an incipient "chase" (see below), and a chase usually follows if the opponent does not flee.

Swanning.—This was a highly variable and dynamic display given when

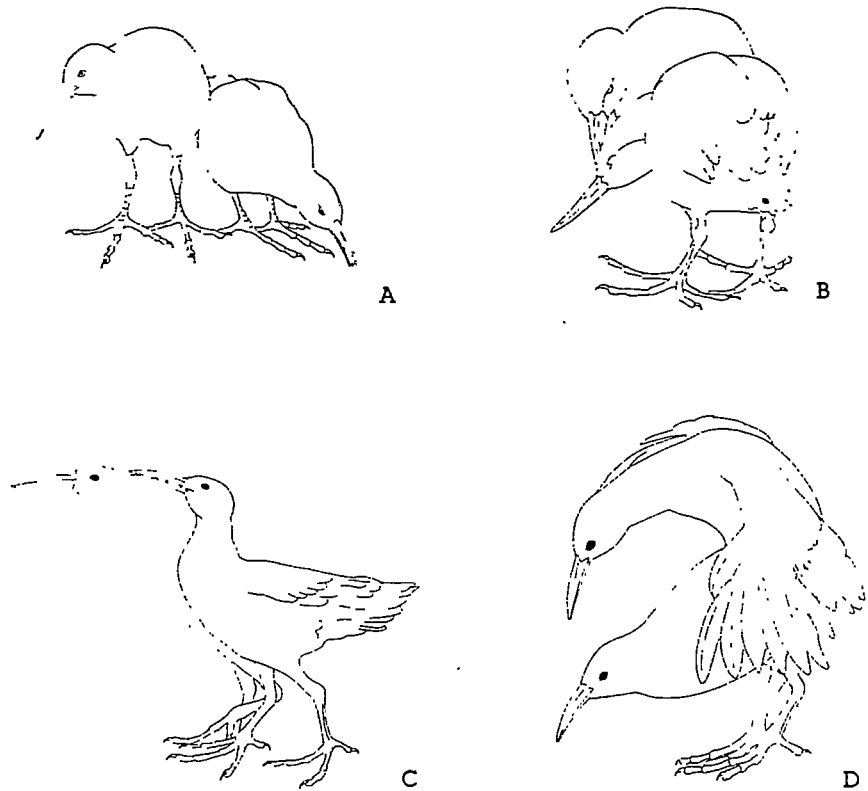


FIG. 4. Displays associated with sexual behavior in Virginia Rails: A. mates together; B. allopreening; C. male during pre-copulatory chase; D. copulation.

Soras of the same sex, usually males, met at territorial boundaries. Here the birds alternately faced and turned away from each other. When one bird approached the boundary, the other usually faced him in a forward; if one bird began to leave, the other also turned away. "Swanning" was interspersed with uprights, "substrate pecking" and fighting.

During intense swanning the contour feathers are fluffed, the scapulars and back feathers are raised above the back by lifting up the wings, and the undertail coverts are spread upward and laterally (Fig. 1D). Frequently the body was either tilted away from the opponent or the feathers were sleeked on the side facing the opponent and ruffled on the opposite side. Maximum spreading of the undertail coverts occurred when one bird turned away from its opponent, especially at the end of a territorial

dispute (Fig. 1E). On several occasions the back feathers were raised while the wings were held close to the body (Fig. 1F).

At times the primaries were exposed during swanning when the wings were drooped as both the tail and posterior part of the body were raised (Fig. 1H). This form of swanning occurred when I placed a dead Sora, frozen in an upright position, in another Sora's territory and when I disturbed a bird at its nest. A similar form of primary exposure occurred on several occasions during slow retreats of territory-holding birds after intrusion in another's territory. The wings were lifted from the back and the primaries were extended posteriorly above the tail (Fig. 1E). The retreating bird moved slowly, straightening its legs so that it appeared to be walking on stilts.

The black facial mask of the Sora, as probably viewed by an opponent provides a striking contrast with the yellow bill, which occasionally has an added touch of orange to scarlet-orange near the nares. Perhaps the face mask reinforces threat displays in which opponents face each other, since the facial coloration is heightened during the breeding season. During the nonbreeding season the reddish-brown irides turn brown and become more distinguishable from the mask and the bill shrinks slightly as it changes to a duller greenish-yellow.

At the end of an encounter, as the two birds simultaneously began to leave the territorial boundary, the feathers were slowly lowered to the normal position. The retreating birds were usually substrate pecking, and as they walked away the form of pecking more closely resembled that of normal feeding. Eventually real feeding movements occurred.

Although Virginia Rails fanned and dropped their wings during several hostile encounters, they did not demonstrate a boundary display comparable to that of Soras. It is possible that Virginia Rails would have exhibited as prolonged and elaborate swanning displays as the Soras, had two pairs of the former species bred synchronously. Virginia Rails perform swanning of short duration during chasing, pecking, and fighting. Swanning of longer duration occurs when chases end abruptly and when there is thwarting of an attack. Longer swanning occurred in three situations: (1) when a bird stopped chasing at its territorial boundary; (2) when a female ran to chase a male which was attacking her mate; and (3) when a rail ran toward me as I approached its nest (Fig. 2C). During longer swanning the wings are held laterally with the primaries and secondaries fanned and pointing upward and the chestnut upper wing coverts turned forward.

I suggest that swanning be used as a general descriptive term for all hostile behavior of Rallidae in which the wings are raised above the back.

appear to be raised by ruffling of rump feathers, or are spread laterally or downward. Observations of rails during boundary disputes and of investigators approaching nests indicated that swanning is a complex display of all possible intermediate wing postures instead of several discrete displays. Gullion (1952) first used the term "swanning" to describe the threat display American Coots directed towards other species. He described threat postures between male coots using wing arching as "paired display" because he believed it was courtship display. Wood (1974) substituted "mutual retreat" for "paired display" in his description of the Moorhen. My suggestion to standardize terminology by using swanning would include paired display of American Coots, mutual display of Moorhens, "distraction display" of Virginia Rails described by Weins (1966), and "wing-lifted walk" and "wing-spread" of Yellow Rails (*Coturnicops noveboracensis*) described by Stalheim (1973).

Substrate pecking.—Vigorous pecking movements are made at the ground, or into mud or water, several times in rapid succession. Soras usually keep the bill closed, but Virginia Rails often have the bill open (Fig. 2D). The undertail coverts are extended laterally beyond the tail. This display is variable and intermediate movements between "substrate pecking" and either actual pecking of another bird or movements identical to feeding are observed frequently. This display appears to be derived from aggressive pecking movements superimposed upon feeding movements and likely results from redirected aggression. If a territorial male approached another male while substrate pecking, the male being approached was pecked if it did not display or flee. If two males left their territorial boundary simultaneously the form of substrate pecking gradually changed to real feeding movements.

Virginia Rails were observed substrate pecking in four situations: (1) by a bird which was threatened by a dominant; (2) after threatening another bird which refused to flee; (3) when I disturbed a bird at hatching; and (4) by both sexes after copulation. Soras usually performed substrate pecking after turning away from another Sora following a bout of swanning, or after a meeting of the members of a pair.

Chasing, wing-snapping, and churning.—"Chasing," consisting of a rapid forward rush, was frequent in both species. Two behavior patterns were associated with chasing: (1) "wing-snapping," which was performed by both species and (2) "churning," which occurred only in Soras.

Wing-snapping consists of rapid flicking of the wings forward and tucking them in place. Virginia Rails performed wing-snapping during chases while Soras performed wing-snapping at the moment they stopped chasing.

Churning by Soras involved splashing water while treading rapidly with

unflexed feet. Churning was most frequently seen when a Sora approached its territorial boundary and stopped chasing. One male frequently performed churning when he was prevented from chasing another by the presence of a wire divider in the breeding pen. Males occasionally performed churning when I approached their nests. This display appears to be homologous with "churning" in the American Coot (Gullion 1952).

I am uncertain whether some Sora chases are homologous with the "spattering charge" of American Coots (Gullion 1952). During intense chases, the chasing Sora flaps its wings and splashes water with its feet, but these movements could be necessary simply to maintain balance when running over unstable substrates.

Fighting and sparring.—"Fighting" in both species consists of jumping upward as high as 30 cm and simultaneously pecking and clawing the breast of the opponent (Fig. 11, J). Soras also fight on the water or on a floating mat of vegetation in the same way as swimming coots, by clawing at each other's breasts while lying backward supporting themselves with their wings. Fighting was most frequent between males although it occurred occasionally between females. Fights were not observed between a male and a female; either the female retreated or her mate quickly came to her aid.

Fighting occurred most frequently between two pairs of Soras which had synchronized breeding cycles and adjacent territories. Often the males met at the boundary of their territories and jumped up and down while facing each other but did not fight. This I called "sparring." Fighting and sparring were observed infrequently in Virginia Rails, probably because only one pair nested successfully. The male of this pair often attacked his opponent's back, raking it with his claws, striking with the edges of his wings, and repeatedly pecking the head. The subordinate male was often forced under water in the process.

Behavior associated with pairing and copulation: Mates together.—In the first stage of pair formation, the male and female stand immobile, their long body axes usually parallel, within sight of each other but seemingly ignoring each other. For the first week or so they stand 10–30 cm apart for periods of only a few min, or 0.5 to several m apart for 15–30 min. After 2–4 weeks, they begin to bathe, feed, and preen in close proximity to each other, and bodily contact is occasionally observed in the Virginia Rail (Figs. 3A, 4A).

Social preening.—"Social preening" in both species includes allopreening, autopreening, facing away, bowing, and facing the mate. Virginia Rails also perform substrate pecking and "bill nibbling" during social preening.

In the Sora, social preening was observed only between mates, but in

the Virginia Rail dominant males preened subordinate birds during the nonbreeding season. Preening bouts between members of a pair lasted 1–5 min in the Sora but were usually more prolonged in the Virginia Rail, with some bouts lasting more than 20 min.

The bird being preened usually bowed its head or turned its head to one side, similar to the “bowing and nibbling” of the American Coot (Gullion 1952) and Moorhen (Wood 1974) (Figs. 3B, 4B). The rail often remained in this position for several seconds after its mate ceased allopreening. I believe that the facial pattern of Soras functions to reinforce threat displays and so heightens hostility between mates. When members of a pair of Soras looked directly at each other during a preening bout, they rapidly bowed, faced away, or allopreened. The movements of allopreening and autopreening appeared to be executed more stiffly by the Soras, suggesting a greater degree of ritualization than in the Virginia Rail.

Bill nibbling.—This activity, in which one bird gently pecks the bill of its mate, was observed frequently in the Virginia Rail during allopreening bouts or when both birds were feeding on the same food item. “Bill nibbling” was rare in Soras during preening bouts.

Courtship feeding.—This behavior was observed in the pair of captive Virginia Rails which bred successfully. The male gave “nasal peeps” when he found a live food item, e.g., invertebrates, and the female responded with similar calls. The male then carried the food in his bill giving nasal peeps as he approached and presented the food to the female. Several times he carried food over a distance of 9 m. The female always took the food and ate it.

Copulation.—Before copulation the members of the pair alternately call and come together while continuing to call. The Virginia Rail gives nasal “peeps” and the Sora gives “peeps.”

Soras usually perform a preening bout prior to copulation. In the “pre-copulatory chase” the male walks with a slightly stiff and erect posture, and gives soft *gwoo* calls. Occasionally he moves his head forward and back, but more often his head is held rigid in a slightly higher position than normal. His undertail coverts are spread laterally so that the tail appears to have white edges.

The male Virginia Rail approaches the female in a characteristic pre-copulatory chase without a preliminary preening bout. He struts toward the female, with his bill pointed up and slightly opened, and gives low, guttural growls. His steps are executed stiffly and his legs appear to be longer than in walking or other contexts. The head and neck move backward and forward in an exaggerated manner, the throat being puffed at each backward movement of the head (Fig. 4C). The undertail coverts are spread laterally as in the Sora.

The duration of the precopulatory chases of both species seems to depend on the receptiveness of the female. During the first week after pairing, the female rejects the copulatory attempts of the male by walking, running or flying from his precopulatory approaches, often travelling several meters within their territory. She spreads her white undertail coverts during these chases. As the time of egg-laying approaches, she is more likely to stand still, dip the end of her tail into the water, and stretch her head and neck forward. The male mounts from behind and the female lowers her head, touching the substrate with the tip of her bill or dipping it into the water (Fig. 3C).

If the female does not lower her head after the male has mounted, he pecks at her crown and either she runs out from beneath him or she responds to his pecks by lowering her head. If the female is receptive she then raises her tail and lowers her head until her body forms an angle of about 45° to the horizontal. The male makes treading movements with alternate steps on her back and then copulates. During copulation, the male Virginia Rail arches his wings but the male Sora flaps his wings, apparently to maintain balance (Figs. 3D, 4D). Copulation is brief, lasting a few seconds at most and then either the male dismounts or the female runs out from under the male.

The post-copulatory movements of the male Sora include some but not all of the components of swanning: the wings are uptilted, the undertail coverts are slightly ruffled and the scapulars are raised by a slight lifting of the wings. The head is lowered below the level of the body, giving the appearance of a bow (Fig. 3E). A more extreme form of bow was performed by males when mounting did not lead to copulation (Fig. 3F). After copulation, females perform a "body shake." The body shake consists of stretching the head forward, erecting the feathers, shaking the body feathers simultaneously and briefly sleeking them. The "wing shuffle" consists of raising the wings away from the body and shaking them.

The male Virginia Rail's post-copulatory movements consist of a head flick, followed by a body shake, and several substrate peckings. The female performs a wing-shuffle or a body shake, and occasionally substrate pecking.

Meeting and passing.—Prior to incubation, nearly every meeting of the member of a Sora pair begins with allopreening and ends with a copulation attempt. After egg-laying, however, meetings between the members of a pair are brief, usually at the time of changeover during incubation. The birds hurry toward one another, stop or nearly stop as they meet, and then continue on. As they come together they adopt a variety of postures. In one posture, the head and tail point downward and the back is arched, as in a bow. In the other form, the head and tail are tilted upward, giving

the bird a U shape (Fig. 3G). While both sexes were observed in both postures, the relative frequency each sex was observed in these postures was not noted because this behavior went unnoticed until near the end of the study. These postures appear to correspond to those occurring in the "meeting and passing ceremony" described for the Moorhen by Howard (1940).

Appeasement behavior of chicks: Begging.—Day-old Sora chicks begged toward their parents with loud, plaintive peeping calls and gaping. Gaping first consisted of raising the head and neck upward with the mouth open. By the second day after hatching, the chicks pecked at the tip of the parents' bill. The frequency of pecking appeared to increase as the interval between feedings increased. Pecking appeared to stimulate the brooding parent to call *tug*. *Tug* calls may have acted to entice the other parent to bring food to the nest.

"Begging" young crouched on their metatarsi, waved their wings asynchronously, and alternately gaped and bowed so that their bald forehead and scarlet cere faced the adult (Fig. 5). The down on the head was depressed, but there were no striking color changes of the bared skin of the head. Several weeks after they were able to stand on their toes young Soras continued to crouch on their metatarsi while begging. Waving of the wings made the chick conspicuous.

Begging was first observed in Sora chicks after 3 days of age, when they were able to run to the parent bringing food to the nest. Begging movements were observed after the end of the first day in hand-reared Soras. Begging could have occurred earlier in chicks raised by Soras, but these movements could not be seen because the chicks were usually underneath the adult on the nest. This suggests that begging is elicited by the approach of an adult, and may not be necessary to stimulate an adult to bring food. The main function of begging appears to be appeasement, i.e., the inhibiting of attack by the parents because: (1) begging was elicited by the approach of an adult rather than directed toward the adult brooding the young; (2) the Sora chicks performed the begging display at the highest intensity when they were attacked by the parents; (3) the parent Sora attacked its young with increasing frequency when the young began to lose the bright coloration displayed during begging; (4) the harshest attack made by a male was directed toward a juvenile which failed to beg; (5) juveniles continued to beg after they were able to feed themselves; (6) similarity of the body postures of the begging display and of the "hiding crouch" during a nest disturbance suggests that the begging display reflects tendencies both to flee and to stay.

Virginia Rail chicks did not perform a crouch when begging as did Soras. Virginia Rail chicks peeped when adults approached them and pecked at



FIG. 5. Begging by a 3-day-old Sora.

food in the bill of the adult. After the first day the chicks ran to the approaching adult, occasionally waving their wings, but stood on their toes.

Vocalizations: Vocalizations associated with hostility and alarm.—Both species have a loud “descending call” which appears to function in territorial defense and as contact call between members of a pair.

The Soras descending call was usually 2–3 sec long and consisted of 10–30 notes. The call progressively decreased in pitch, especially the harmonics of the higher frequencies, and it was reminiscent of the “whinny” of a horse (Fig. 6A). The bird’s body contracted and the tail flicked up and down during each note. The white undertail coverts were spread laterally, making the tail flicking conspicuous. The bill pointed downward, except during a territorial dispute when the bird faced its opponent.

Soras gave the descending call frequently during spring migration and throughout the breeding season in response to the calls of the Virginia Rails and other Soras, to a variety of loud noises, and to the sound of splashing water. The descending call of paired males elicited a similar call from the female, usually before the male completed his call (Fig. 6B). The female’s call was shorter, more variable, and higher in frequency than that of the male. Sometimes the notes are discontinuous and of alternately high and low frequencies which I called “twittering” (Fig. 6C). A female “twittered” whenever a male other than her mate approached, whereupon

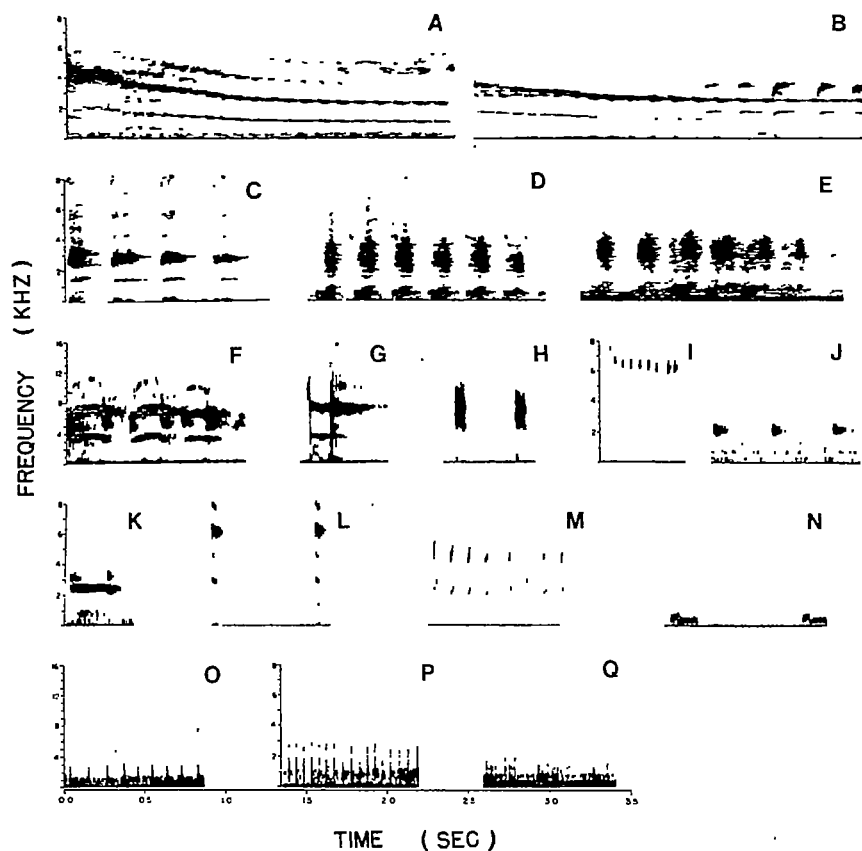


FIG. 6. Vocalizations of Soras and Virginia Rails: A. descending call of a male Sora; B. descending call of a male Sora joined by his mate; C. "twittering" of a female Sora; D. descending call of a male Virginia Rail; E. female Virginia Rail duetting with mate after his first note; F. *kiu* of a Sora; G. *keep* of a Sora; H. *kick-it* of a Virginia Rail; I. *kadic-kadic* of a Virginia Rail; J. *tick* of a Virginia Rail; K. "squawk" of a Virginia Rail; L. "peeps" of a Sora; M. nasal "peeps" of a Virginia Rail; N. *gwooo* of a male Sora; O. slow "gargle" of a Sora; P. fast "gargle" of a Sora; Q. "purr" of a Virginia Rail.

her mate chased the intruder. A female Sora gave a softer version when she was unreceptive during a precopulatory chase.

A one- or two-note cry, described as *kee*, *weep*, *kee-you*, and *per-weep*, often preceded a Sora descending call. These cries were also given separately. The *per-weep* was most common during spring migration and has been reported during nocturnal flight (R. Oehlenschläger, pers. comm.). The *per-weep* was not given in the breeding pen, but an aggressive, un-

mated male gave this call frequently after he was isolated in a separate pen.

The descending call of Virginia Rails was usually 1.5–2 sec in length and consisted of 9–12 notes (Fig. 6D). The notes decreased slightly in amplitude and frequency, particularly at the end of the call. The descending call of the female was higher in frequency than that of the male. The call was reminiscent of the *raebh* of a drake Mallard (*Anas platyrhynchos*) or the grunt of a pig. The head was held erect during the call, the tail was flicked up and down with each note, and the undertail coverts were spread laterally.

The descending call of Virginia Rails was given in response to other rail calls, loud noises, and the sound of splashing water. The female gave the descending call in response to her mate, beginning to call before the male finished (Fig. 6E). During a bout of duetting the notes tend to become progressively more precisely synchronized. Incubating females often gave single *kuk* calls, resembling a single note of the descending call. The male immediately responded with the descending call, and the female joined in (after his first or second note) with the descending call.

Territorial males occasionally gave two distinct variants of the typical descending call: one call has a raspy quality, the other has a hollow quality, and its amplitude is greater at lower frequencies. A few observations indicated that the raspy-sounding descending call elicited a descending call from a mate but not from rival males, whereas the rival males gave a descending call in response to a hollow-sounding descending call but the mate did not respond.

A sharp *kiu* was given when I entered the pen and alarmed the rails. This is a short, high frequency call, with some harmonics reaching 16 kHz (Fig. 6F). The *kiu* of the Sora and of the Virginia Rail were indistinguishable to my ear. Both species reacted to *kiu* of either species by sleeking their feathers and flicking their tails up and down.

A short, high frequency call similar to the *kiu* was given by adults of both species whenever I approached a nest with eggs close to hatching. The members of a pair gave the call alternately, one higher-pitched than the other. Although they called only 1 or 2 m from me, identification of the sexes was difficult because they remained in the densest vegetation and stopped calling if I approached too closely. Glimpses of wild color-marked birds running for cover indicated it was the female which gave the higher pitched call. The alternation of calling is probably responsible for the ventriloquial effect attributed to rails. The calls of the two species were easily distinguishable from each other and from the *kiu*. The Sora's call is phonetically rendered as a *keep* (Fig. 6G) and that of the Virginia Rail's as a *skew*.

A variety of "squawks" and "squeals" were given by both species when they were attacked. A sharp *kuc* was occasionally uttered by a Virginia Rail immediately before being chased. A rapid, two-note *cheek-it* was given by young Soras whenever I handled them. This latter call was first heard at 2 days of age and was given for 2 months.

Calls associated with pair formation, copulation, and nesting.—The Sora's "spring peeper call" (resembling the call of the spring peeper [*Hyla crucifer*]) has been described as a "mate-attraction" or "readiness-to-pair" call (Brewster 1902, Pospichal and Marshall 1954). I only heard such a call once from a wild bird and once from a captive bird.

The *kadic-kadic* of Virginia Rails is a high frequency call with short double notes (Fig. 6I). I did not hear this call by captive birds, but I often heard it in the wild shortly after this species arrived in my study areas in spring. Brewster (1902) believed this call functioned to attract a mate.

A short, often repeated *tick* was given by adult Virginia Rails in the early stages of pair formation (Fig. 6J). A louder *kick-it* was frequently heard in the wild during the breeding season but not from captive birds (Fig. 6H). The males of two captive pairs of Virginia Rails gave a large number of squawks immediately prior to nesting (Fig. 6K).

Both species gave soft, "peep"-like calls which appeared to function in maintaining contact between the members of a pair. Both "peeps" are short (0.05 sec) but the "peep" of the Sora is higher in pitch than the nasal "peep" of the Virginia Rail (Fig. 6L, M). Most Sora's "peeps" led to meetings, while Virginia Rail's nasal "peeps" appeared to serve as contact notes.

Virginia Rails also uttered several other soft calls for pair contact. A *tipit*, consisting of rapid, soft sounds resembling water dripping, was given in the same situations as nasal "peeps." Occasionally, a bird gave a complete range of intermediate calls, starting with soft *tipits* which became louder nasal "peeps," then loud plaintive "peeps" and eventually became loud "squawks" and "squeals." A soft purring call was frequently given by either sex when they were close together (Fig. 6Q). This "purr" was often associated with bill nibbling.

Calls given by males during a precopulatory chase are soft and low in amplitude and pitch. The Sora's *gwoo* resembles a soft "cooing" (Fig. 6N). It was also occasionally given during swanning displays between males. The Virginia Rail's "growl" resembles the low guttural sounds made by a person's empty stomach. Virginia Rails occasionally gave a "growl" immediately before being attacked.

Both adults of two pairs of captive Soras gave a gargle-like call at the time of nest relief. The incubating bird gave the "gargle" with increasing loudness, pitch and frequency of notes per second until the mate came

and a changeover of birds incubating occurred. The frequency of "gargles" per second increased from 10–22 notes/sec (Fig. 6O, P). A third pair of Soras was not heard to call prior to nest relief, nor was the pair of Virginia Rails.

While on the nest, single, short *tugs* were given by an adult Sora whenever food was brought to it by the mate. The *tug* sounds like the "gargle" but at a slower rate.

The first calls of rail chicks are soft wheezy "peeps." These calls are given more frequently and are louder and longer when the chicks are cold or hungry. I could not distinguish the wheezy "peeps" of Soras from those of Virginia Rails.

Miscellaneous calls.—A nasal coot-like call was given infrequently by either sex of Soras while feeding. On several occasions a frog-like *roock* was given by a Virginia Rail. The function of these calls is unknown.

DISCUSSION

The ancestral rallid stock appears to have been a generalized forest-dwelling species which gave rise to *Rallus* and *Porzana* (Olson 1973). Both species which I studied have many displays in common. It is not possible to be certain if these displays are similar because of a common ancestry or because of convergent evolution in the marsh habitat.

In contrasting the two species, Soras had a larger repertoire of displays than Virginia Rails. The Soras also performed several displays in a more elaborate and/or ritualized fashion than the homologous (or analogous) displays of Virginia Rails. Swanning was frequently performed by male Soras whereas swanning was rarely performed by male and female Virginia Rails. Social preening seemed stiffer and more ritualized in Soras than in Virginia Rails and in Soras was given before early attempts to copulate. Post-copulatory displays of Soras had a stereotyped form. Members of Sora pairs gave a meeting and passing display upon meeting. Young Soras have more elaborate begging postures reinforced by conspicuous plumage patterns than do Virginia Rails. Members of Sora pairs tended to do more duetting whereas members of Virginia Rails called in both duets and antiphonally.

Many of the differences in these displays are associated with the stronger territorial behavior of Soras. Defense of a well-defined territory plays a greater role in the breeding biology of Soras than Virginia Rails. Soras have evolved more elaborate swanning displays with which to defend their territories. The facial pattern of Soras appears to reinforce frontal threat postures. There may be stronger tendencies of attack and fleeing between members of a pair of Soras as a result of this behavior and coloration. Social preening may be more important in thwarting the aggressiveness

of the male in Soras than in Virginia Rails. Soras appear to avoid facing each other during social preening and quickly turn their heads if they directly face each other. As pair formation ensues and incubation begins, encounters by members of Sora pairs lead to the meet and pass display instead of social preening. Perhaps "meeting and passing" is performed when the tendency to attack the mate is lowered.

SUMMARY

The displays and vocalizations of the Sora (*Porzana carolina*) and the Virginia Rail (*Rallus limicola*) were studied at three different sites over a period of 4 years. Many displays and vocalizations are common to both species, but some homologous displays were more elaborate and/or ritualized in the Sora than in the Virginia Rail. In addition, Soras had a larger repertoire of displays. Most notable of these differences were "swanning" displays by male Soras at territorial boundaries, more ritualized preening by Sora mates, performance of the "meeting and passing" display as well as a standard form of the post-copulatory display, and more elaborate begging postures assumed by Sora young. Differences between species may be attributable to the more aggressive, territorial nature of the Sora.

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